AVIAN POPULATION DENSITIES, HABITAT USE, AND FORAGING ECOLOGY IN THINNED AND UNTHINNED HARDWOOD FORESTS IN SOUTHWESTERN VIRGINIA

by

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(ABSTRACT)

I examined impacts of thinning on bird population densities and habitat use in Appalachian mixed-hardwood forests during 1984 and 1985 at three thinned and three unthinned stands in the Jefferson National Forest, southwestern Virginia. Densities of shrubs, saplings, trees, and snags, canopy and ground cover, and foliage volume were the structural variables most influenced by thinning. Populations of shrub/understory birds were higher in thinned stands than unthinned stands. Canopy-dwelling species showed variable population responses to thinning.

Habitat use similarities were used to group 13 bird species into three categories: (1) shrub/conifer species included the tufted titmouse, blue-gray gnatcatcher, wood thrush, ovenbird, and hooded warbler, (2) generalist species included the eastern wood-pewee, red-eyed vireo, black-and-white warbler, and scarlet tanager, and (3) mature/deciduous species included the white-breasted nuthatch, solitary vireo, blackburnian warbler, and worm-eating warbler. Shrub, snag, and conifer density and ground cover were the four habitat variables most important in separating used from unused sites.

Foraging behavior and resource use of seven bird species were examined in two thinned and two unthinned stands. No differences in foraging methods or niche breadth were found between the stands for all species. Differences in foraging and tree heights were due to tree height differences between the stands.

For most species, foraging resource use was equal to availability. Short, small diameter trees were rarely used. Oaks were used most often, and red maple and conifers were rarely used for foraging. The opportunistic nature of avian foraging behavior and the vegetative differences between thinned and unthinned stands led to the foraging differences noted.

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INTRODUCTION

Thinning is a common intermediate silvicultural treatment in Appalachian hardwood forests. Studies on the effects of intermediate treatments on wildlife habitat have concentrated on describing changes in forage production following treatment. However, intermediate treatments have the additional impact of altering the physical structure of the stand. It is the structure of the forest stand that has greatest influence on the organization of the associated avian community.

Despite its prevalence in forest management, little data is available on the impacts of thinning practices on forest avifauna. Because of this lack of information, this study was implemented to assess the impact of thinning practices on avian populations and habitat use in Appalachian hardwood forests. The results are written in four sections. Section I is a thorough literature review of the previous work done on the topic. Section II examines the impacts of thinning on avian population densities and habitat use. Section III reports the foraging ecology of selected bird species in thinned and unthinned stands. Section IV is a general conclusions section which summarizes the results of the three sections.

SECTION I

LITERATURE REVIEW

There have been numerous studies on impacts of silvicultural practices on bird populations and habitat use. Many studies have involved sampling stands representing a vegetation gradient from clearcuts to undisturbed, mature sites (Conner and Adkisson 1975, Conner et al. 1979, Titterington et al. 1979, Crawford et al. 1981, Freedman et al. 1981). These studies have all noted changes in bird populations and/or communities due to logging practices.

Hagar (1960) assessed bird population responses following clearcutting in the Douglas-fir (*Pseudotsuga menziesii*) forest of northwestern California. Webb et al. (1977) studied effects of forestry activities on songbird populations of 5 stands representing different logging intensities. Franzreb and Ohmart (1978) and Szaro and Balda (1979) studied impacts of silvicultural practices on birds in mixed-conifer forests of Arizona. These studies have all noted variable population responses, and they have concluded that species' habitat preferences are important determinants of population responses to logging practices.

McArthur (1980) assessed impacts of silvicultural practices in hardwood forests of West Virginia by studying a selectively cut plot and a control plot. Population densities were 60% lower for red-eyed vireos, white-breasted nuthatches, wood thrushes, ovenbirds, scarlet tanagers, and eastern wood-pewees in a selectively logged stand compared to a control stand. Solitary vireos had a population density 60% greater, and great crested flycatchers, black-and-white warblers, hooded warblers, and rufous-sided towhees showed no population differences. Dingledine (1983) noted no specific population declines in an oak stand 1 year after a firewood cut where snags were mostly removed, but he did not a higher total density for 3 cut stands compared to 3 control stands.

Little research has been done on the effects of intermediate silvicultural treatments on forest avifauna. Zeedyk and Evans (1975:119) stated that impacts of intermediate cuts on bird populations are variable and not well defined. Thinning is an intermediate operation conducted in a stand any time prior to harvest (Daniel et al. 1979:419). The objective of thinning is primarily to redistribute growth potential and improve quality of the residual stand. Intermediate treatments can also be used to improve wildlife habitat. Thinning combined with control of stump sprouting improved habitat by increasing production of desireable wildlife plants (Crawford 1971).

Mannan and Meslow (1984) reported avian population differences between managed stands which had been thinned and old-growth Douglas-fir stands in Oregon. They found that birds more abundant in managed stands were attracted to the open vegetative structure, and birds more abundant in old-growth stands were dependent on the presence of understory vegetation and large (>31 cm dbh) snags. Johnston (1970) noted a bird population density of approximately 800 pairs/40.5 ha in a deciduous forest in southwestern Virginia which, because of extensive vegetation modification, resembled a heavily thinned stand.

Based on habitat use similarities, Crawford et al. (1981) predicted avian population responses to thinning practices conducted in Appalachian hardwood forests. They classified the ovenbird, white-breasted nuthatch, and wood thrush as species dependent on closed-canopy situations, and predicted that intermediate treatments, such as low thinning, which leave a closed overstory canopy would favor these species. The black-and-white warbler, hooded warbler, red-eyed vireo, scarlet tanager, tufted titmouse, and blue-gray gnatcatcher were classified as species favoring a closed canopy. They predicted that crown thinning of overmature trees would increase populations of hooded warblers, while low thinning would favor the other species. Eastern wood-pewees would benefit from selection thinning that removes overmature and suppressed trees <7 cm dbh, while intensive crown thinning would favor open-canopy species such as rufous-sided towhees and indigo buntings (Crawford et al. 1981).

Kilgore (1971) reported population increases of 57% and 42% for western wood-pewees (Contopus sordidulus) from pre-treatment levels the breeding season immediately following and one year after, respectively, a spring slash removal and prescribed burn in a giant sequoia (Sequoiadendron giganteum) forest. He reported eradication of the rufous-sided towhee, hermit thrush (Catharus guttatus), and Nashville warbler (Vermivora ruficapilla) both breeding seasons following the treatment. Hermit warblers (Dendroica occidentalis) were not reported to decline; however, using his data, I calculated a 58% and 31% population decline from pre-treatment densities during the respective breeding seasons following the treatment. There were no population changes for dark-eyed juncos, western tanagers (Piranga ludoviciana), solitary vireos, and mountain chickadees (Parus gambeli)

Bock and Lynch (1970) noted increases in populations of open-ground, brush dependent species such as the Brewer's sparrow (Spizella breweri) and chipping sparrow (S. passerina), and in flycatchers such as western wood-pewees and olive-sided flycatchers (Nuttallornis borealis) in a 5-year-old burned mixed-conifer stand compared to an unburned control stand in California.

Stand vegetation structure is modified by logging practices. Dingledine (1983) reported lower tree densities and foliage diverstiy in 3 stands of northern oaks (Quercus spp.) subjected to an intensive firewood removal compared to 3 untreated stands. He found greater basal area in the treated stands. Percent canopy cover was lower in the 1-7 m stratum, and there was no difference in the >7 m and <1 m strata. He noted a 35% decline in snag densities after cutting at the treated plots, and snag densities were lower than the controls.

McArthur (1980) noted similar results with lower ground cover, canopy cover, and densities of trees <7.6 cm dbh, 30.5-38.1 cm dbh, and >38.1 cm dbh in a selectively logged stand compared to a control stand. He also reported a 20% reduction in basal area at the logged stand, and a decrease of 80% in shrub density at the treated stand.

Mannan and Meslow (1984) found that density of trees 2.5-10 cm dbh and ≥51 cm dbh, tree height diversity, and density of snags were the variables most important in discriminanting managed Douglas-fir stands from unmanaged, old-growth stands. Managed stands were subjected to frequent thinning, and tree densities were 300 stems/ha less than unmanaged stands.

They reported that total foliage volume was twice as great in the unmanaged stands compared to the thinned stands due primarily to the presence of understory trees.

SECTION II

AVIAN POPULATIONS AND HABITAT USE IN THINNED AND UNTHINNED HARDWOOD FORESTS

There have been numerous studies on impacts of silvicultural practices on bird populations and habitat use. Many studies have involved sampling stands representing a vegetation gradient from clearcuts to undisturbed, mature sites (Conner and Adkisson 1975, Conner et al. 1979, Titterington et al. 1979, Crawford et al. 1981, Freedman et al. 1981).

Zeedyk and Evans (1975:119) stated that impacts of intermediate cuts on bird populations are variable and not well defined. Thinning is an intermediate operation conducted in a stand any time prior to harvest (Daniel et al. 1979:419). The objective of thinning is primarily to redistribute growth potential and improve quality of the residual stand, and intermediate treatments can be used to improve wildlife habitat. Thinning combined with control of stump sprouting improved habitat by increasing production of desireable wildlife plants (Crawford 1971).

Little research has been done on the effects of intermediate silvicultural treatments on forest avifauna. Mannan and Meslow (1984) reported avian population differences between managed stands which had been thinned and old-growth Douglas-fir stands in Oregon. They found that some species were more abundant in managed stands, while others, particularly cavity-nesting birds, were more abundant in old-growth stands. Johnston (1970) noted a bird population density of approximately

800 pairs/40.5 ha in a deciduous forest in southwestern Virginia which, because of extensive vegetation modification, resembled a heavily thinned stand.

The purpose of this study was to assess the impact of thinning practices on avifauna in Appalachian mixed-hardwood forests. The general hypothesis tested was that differences in vegetation structure and composition between thinned and unthinned stands did not result in avian population differences due to alterations in suitable habitat. My objectives were to: (1) identify vegetation components that distinguish thinned from unthinned stands, (2) compare avian populations between thinned and unthinned stands and identify species population responses to thinning activities, (3) identify and quantify habitat components that are important determinants of avian habitat use and population density and are modified by thinning activities, and (4) develop general thinning prescriptions to improve avian habitat in Appalachian mixed-hardwood forests.

STUDY AREA

The study was conducted on the Blacksburg Ranger District, Jefferson National Forest, Montgomery and Giles Counties, southwestern Virginia. Most of the study stands were in the oak (Quercus spp.)-hickory (Carya spp.) cover type (Burns 1983). The Appalachian mixed-hardwood and oak-pine (Pinus spp.) cover types were interspersed with the dominant cover type (Burns 1983). The canopy was dominated by white oak (Q. alba) chestnut oak (Q. prinus), scarlet oak (Q. coccinea), black oak (Q.

veluntina), and northern red oak (*Q. rubra*). Other important canopy species were pignut hickory (*C. glabra*), bitternut hickory (*C. cordiformis*), red maple (*Acer rubrum*), pitch pine (*P. rigida*), and eastern white pine (*P. strobus*). Moist sites were characterized by the presence of yellow poplar (*Liriodendron tulipifera*), black birch (*Betula lenta*), and eastern hemlock (*Tsuga canadensis*). Important intermediate and codominant trees included blackgum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), and black locust (*Robinia pseudoacacia*). Dominant understory trees and shrubs were flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum*), downy serviceberry (*Amelanchier arborea*), mountain laurel (*Kalmia latifolia*), witch-hazel (*Hamamelis virginia*), Allegheny chinkapin (*Castanea pumila*), and American chestnut (*C. dentata*).

Three mature stands (6.6-7.9 ha) subjected to different thinning operations were selected. An unthinned control stand (8.0 ha) as similar as possible to each thinned stand was selected to represent pre-thinning conditions. The unthinned stand was as similar as possible to the thinned stand with regard to slope, aspect, slope position, major topographic features, and cover type. The 6 stands were considered representative of the oak-hickory cover type in the central Appalachians (S. M. Zedaker, pers. commun.). Four stands were at 550-730 m elevation, and 2 stands were at 1065-1100 m.

METHODS

Avian Populations and Vegetation Sampling

Transects were established for censusing avian populations and gathering habitat use data. Transect length varied from 100 to 400 m, depending on the site and the irregularities of the cut boundaries and were positioned to incorporate as much of a contiguous stand as possible. All transects were ≥25 m from abrupt forest edges and were spaced 50 m apart and parallel to each other without regard to topography and habitat features. Vegetation sampling stations were located at 25-m intervals along the transects which also provided a grid to assist in estimating bird locations and distances.

The variable strip transect method (Emlen 1977, Conner and Dickson 1980) was used to estimate population densities. Only observations ≤30 m from a transect were used to estimate density. Although this allows for a 10-m belt of overlap between the transects, I feel that the chance of duplicate observations is minimal because of mobility of birds and the effort made to avoid duplicate counts. A map of the stand with the transect layout was used during each census to plot bird locations.

Each stand was censused 9 times from 8 May to 8 July, 1984 and 1985. Censuses of each stand were conducted at 5-10 day intervals with the starting point and observers changed with successive censuses. Stand pairs were censused simultaneously by separate observers. Avian population densities were calculated for those species with ≥5 observations from the 18 censuses. Diversity (H') was calculated as

$-\Sigma(p_i \times \ln p_i)$ (MacArthur and MacArthur 1961), where p_i is the species' proportion of the total population density, and equitability (J') was calculated as H'/H'_{max} where $H'_{max} = \ln(S)$ and S = species richness (Hair 1980).

Vegetation Sampling

Vegetation was sampled at 384 stations using the methods of James and Shugart (1970) and Noon (1981) at 0.04-ha circular plots. For each tree ≥8 cm dbh closest to the station center in each compass quadrant, species, height (m), crown height (m), and dbh (cm) were measured, and crown radius (m) at the longest branch was estimated. These data were used to estimate foliage volume (m^3/ha) for the canopy layers using the approach of Mawson et al. (1976). Foliage height diversity (FHD) was calculated using FHD $= -\Sigma(p_i \times \ln p_i)$ (MacArthur and MacArthur 1961), where p_i is the proportion of the total foliage volume accounted for by foliage layer *i*. Trees were any woody stems ≥8 cm dbh, saplings were woody stems 3-8 cm dbh, and shrubs were woody stems <3 cm dbh.

Statistical Analyses

Avian population densities in paired stands were compared using a *t*-test. Differences in vegetation variables between the thinned and unthinned stands were tested with a Wilcoxon 2-Sample Test. An original set of 122 variables was reduced to 55 by deleting 1 of each variable pair with $r \geq 0.70$ (Noon 1981). The second set was reduced to 22 variables by using a Principal Components Analysis (PCA) and deleting 1 of 2 variables with approximately equal factor loadings. Variables were kept because of known importance in avian habitat use, their importance in reflecting habitat changes due to thinning, and bringing out patterns in vegetation structure. PCA was done on these 22 habitat variables to ordinate the 384 sampling stations in the 6 stands. The first 3 principal components were retained. Johnson (1981) discusses the use of PCA in wildlife habitat studies.

Observations of stationary birds ≤25 m from a vegetation sampling station were associated with the sampling station. I assumed birds used some aspect of the habitat reflected in the vegetation sampled at the station. Thirteen species were chosen for intensive study because they were present on ≥10% (N = 38) of the 384 stations and were generally evenly distributed across the 6 stands. Differences in habitat use by these species was tested with a t-test comparing the mean scores of stations where the species was present and absent on the 3 components. Habitat relationships of the 13 species were qualitatively assessed by plotting the mean component scores for the species' presence along the 3-dimensional axis defined by the first 3 components.

I used 2-group discriminant function analysis (DFA) with stepwise inclusion of habitat variables to determine vegetative variables important in habitat use. In the DFA, I compared stations where each species was present and absent. Habitat variables were retained if the F-statistic from a 1-way analysis of covariance had a significance level of $P \leq 0.10$. Means (SE) were then calculated for each habitat variable selected by the DFA for stations where each species was present and absent. Williams (1981, 1983) discusses the theory and application of DFA to ecological studies.

I conducted multiple linear regression (MLR) for 10 species to find vegetation variables important in influencing species' abundances. The habitat variables used in the regressions were the means of the habitat variables measured at four 0.04-ha plots in a 0.5-ha plot. I formed rectangular (50 x 100 m) 0.5-ha plots from the grid created by the transects and vegetation sampling stations which were the observational units used in the regressions. The dependent variable was the total number of observations of a particular species in the four 0.04-ha plots. This pooling of the 0.04-ha circular plots was done to reduce the skew in the count data and to approximate a normal distribution. MLR was done initially on the thinned and unthinned plots separately. I tested the significant (P < 0.05) regressions for the thinned and unthinned stands for coincidence using a F-test (Ott 1984). The separate regression equations were found to be coincident so I pooled the stands. Stands were not included in the analysis if the species was observed on <50% of the plots. MLR was done using the best 4-variable model selected by the max-R stepwise procedure. Appropriate transformations (log, square-root, or arc-sine) were applied to non-normal variables (Sokal and Rohlf 1981). SAS (1985) computer programs were used.

RESULTS AND DISCUSSION

Vegetation in Thinned and Unthinned Hardwood Forests

Each thinned stand was given a free thinning. Based on the results of the vegetation analysis, I classified the stands differently with regard to the type of thinning. Thin 1 was given a heavy low thinning in 1981, where primarily intermediate and codominant trees were cut. Thin 2 was given a light crown thinning in 1982 with dominant, codominant, and intermediate trees being removed. Thin 3 was given a heavy selection thin in 1983 where large diameter (>38 cm dbh) and overtopped trees were removed. Thin 3 was burned in Spring 1984 to control maple stump sprouting.

Snag density was lower in the 3 thinned stands than in the respective controls (Table 1). Shrub densities were higher than the controls at Thin 1 and Thin 2, but lower than the control at Thin 3. The controlled burning at Thin 3 reduced shrub densities. Oak sapling density was lower at Thin 1 and Thin 2 than their respective controls. Oak sapling density was higher and maple sapling density was lower in Thin 3 than Control 3 due to the increased light reaching the ground favoring the intolerant oaks which suppressed the shade tolerant maples (Daniel et al. 1979). Total sapling density was lower at Thin 1 and Thin 3 than the respective controls (Table 1).

Canopy cover was lower and ground cover was higher in the 3 thinned stands than at their respective controls (Table 1). Density of trees 8-15 cm dbh was lower in the 3 thinned stands, while density of trees 15-38 cm dbh was lower in Thin 1 and Thin 3. Thin 1 had a higher density of trees 38-69 cm dbh, while Thin 3 had a lower density than the control. Basal area (m^2/ha) was higher at Thin 1 than Control 1, and lower at Thin 3 than Control 3. Tree height was greater at Thin 1 and Thin 2 than their respective controls (Table 1).

Total foliage volume was lower at Thin 3 than Control 3, and understory foliage volume (0-6 m) was lower in Thin 1 and Thin 2 than their respective controls (Table 1). Mid-canopy foliage volume (6-18 m) was lower in Thin 1 and Thin 3 than their respective controls, and upper canopy foliage volume (>18 m) was lower at all thinned stands than their respective controls. FHD was higher in Thin 1 and lower in Thin 3 than their respective controls (Table 1).

Dingledine (1983) reported lower tree and snag densities, understory canopy cover and FHD in oak stands subjected to an intensive firewood removal compared to untreated stands. I found snag densities an average of 55% lower at thinned stands than unthinned stands (Table 1). McArthur (1980) noted similar results with lower ground and canopy cover, basal area and tree densities in a selectively logged stand compared to a control stand. In contrast to my findings, McArthur (1980) noted a decrease of 80% in shrub density at the treated stand. Mannan and Meslow (1984) studied managed stands subjected to frequent thinning, and tree densities were 300 stems/ha less than in unmanaged stands. They reported greater total foliage volume in the unmanaged stands compared to the thinned stands due to the presence of understory trees.

Avian Population and Community Differences between Thinned and Unthinned Stands

Few species showed differences in population density between thinned and unthinned stands (Table 2). The most consistent population responses to thinning were with the species using the shrub/sapling layer. Rufous-sided towhee, wood thrush, indigo bunting, dark-eyed junco, and hooded warbler densities were higher in the thinned stands than in the respective controls. Towhees and indigo buntings were absent from Thin 3 in 1984 after the burn, but were present in 1985 after the shrub layer became established by growth of the stump sprouts. Crawford et al. (1981) characterized towhees and buntings as species that favor stands with open canopies and dense understories. They stated that intensive thinning, as at Thin 3, would create favorable conditions for these species. Hooded warblers have been classified as species favoring mature stands with closed canopies with dense understories (Crawford et al. 1981). In my study, hooded warblers had higher densities in stands with dense understories and relatively open canopies. Thinning that provides a canopy closure of >80% resulted in suitable habitat for hooded warblers.

Eleven of 22 species had significantly higher densities at Thin 1 than Control 1 (Table 2). These population increases probably are due to the greater diversity of habitat components at Thin 1 resulting from thinning and the overall higher site quality which resulted in taller trees with more foliage. Population densities generally were not different between Thin 2 and Control 2. These similarities are due to the relative uniformity of the 2 stands; the light crown thinning conducted at Thin 2 resulted in few vegetation differences between the two stands (Table 1). Shurb/understory species such as towhees, hooded warblers, and wood thrush had higher densities at Thin 2. Thin 3 and Control 3 were considerably different in vegetation structure but had relatively few differences in avian population densities (Table 1). However, what differences existed were of considerable magnitude.

Blackburnian warblers had a much lower population densities at Thin 3 than Control 3 (Table 2). Red-eyed vireos had inconsistent population differences between the respective thinned and unthinned stands. They were at a higher density at Thin 1 than Control 1 and a lower density at Thin 2 and Thin 3 than the respective controls (Table 2). Crawford et al. (1981) reported that red-eyed vireos favored stands with closed canopies. Webb et al. (1977) reported that red-eyed vireo populations were not affected by logging, while blackburnian warbler populations declined at all logging intensities. Apfelbaum and Haney (1981) noted population declines of >50% in red-eyed vireos and blackburnian warblers 1 year following a fire in a coniferous forest in Michigan, and populations of solitary vireos and ovenbirds were eradicated. Dark-eyed juncos were present the year following the fire after being previously absent.

McArthur (1980) found population densities 60% lower for 6 species of understory and canopy-dwelling birds in a selectively logged stand compared to a control stand. He found a population density 60% greater for solitary vireos in the logged stand, and no population differences for 4 species. Dingledine (1983) noted higher total density in stands subjected to a firewood cut compared to control stands.

My results both support and refute the predictions of Crawford et al. (1981). Thin 1 was given a heavy low thinning. Higher population densities were found for the eastern wood-pewee, blue-gray gnatcatcher, tufted titmouse, scarlet tanager, red-eyed vireo, white-breasted nuthatch, and wood thrush as Crawford et al. (1981) predicted. Contrary to their predictions, however, no population differences were noted for ovenbirds and hooded and black-and-white warblers, and a higher population density was noted for rufous-sided towhees (Table 2).

Thin 2 was given a light crown thinning, and wood thrush, hooded warbler, and rufous-sided towhee population densities were higher at Thin 2 than Control 2. The wood thrush was predicted to decrease with crown thinning (Crawford et al. 1981). Red-eyed vireo density was lower in Thin 2. Eastern wood-pewees were virtually absent at Control 2, while black-and-white warblers were absent from Thin 2. Crawford et al. (1981) predicted that closed-canopy species would benefit from light crown thinnings. However, shrub/understory dependent species benefitted from the crown thinning while some canopy-dwelling species did not.

Thin 3 was given a heavy selection thin, and most species did not show population differences between Thin 3 and Control 3. Eastern wood-pewee populations were not higher as Crawford et al. (1981) predicted. I found lower population densities for red-eyed vireos which Crawford et al. (1981) predicted would increase. Rufous-sided towhee and indigo bunting populations were higher in Thin 3, as Crawford et al. (1981) predicted. These two species were absent from Control 3.

Understory removal by burning results in population declines in understory-dependent species, but their population densities increase once the shrub and understory becomes re-established. Bock and Lynch (1970) reported higher densities of open-ground, brush dependent species such as the Brewer's sparrow (Spizella breweri) and chipping sparrow (S. passerina) in a 5-year-old burned mixed-conifer stand compared to a unburned control stand. Kilgore (1971) reported eradication of rufous-sided towhees, hermit thrushes (Catharus guttatus), and Nashville warblers (Vermivora ruficapilla) both breeding seasons following a slash removal and controlled burn in a conifer forest. Both studies reported higher densities of flycatchers in the burned stands.

Populations of canopy-dwelling birds appear to vary inconsistently with different silvicultural practices. Therefore, it is not prudent to make generalized predictions for the group concerning their population responses to silvicultural practices. Predictions should be made either on a finer scale dictated by habitat use similarities or on the species level. Mannan et al. (1984) stated that population responses by guilds cannot be inferred from the response of a single species because of response inconsistencies among guild members. This problem can be severe when man-induced habitat changes are subtle (Mannan et al. 1984), as in my study.

Community parameters were similar between the respective thinned and unthinned stands. Total population density was higher at Thin 1 than Control 1, and it was not different between the other stand pairs (Table

2). BSD and J' were higher at Thin 1 and Thin 3 than their respective controls, and BSD and J' were lower in Thin 2 than Control 2. Community similarity indices (Krebs 1978:395) were 1.00, 0.93, and 0.95, respectively, for thinned/unthinned stand pairs 1, 2, and 3.

Habitat Use by Selected Species in Thinned and Unthinned Hardwood Stands

Thirteen bird species had adequate sample sizes ($n \geq 38$, see Morrison 1984) for DFA and PCA. DFA has been used to determine habitat variables important in separating sites where birds are present and absent in particular habitats (Noon et al. 1980, Smith et al. 1981). PCA and DFA has been employed mostly to distinguish species' differences in habitat use along a vegetation gradient defined by the principal component or discriminant function (James 1971, Titterington et al. 1979, Crawford et al. 1981, Noon 1981).

A bird was considered present at a station if 1 or more observations occurred there, otherwise it was considered absent. Each station was used once in the DFA and PCA. There were 3 general habitat use categories into which I classified the 13 species. These categories were based on similarities in vegetation use from the DFA and PCA analyses and population differences between thinned and unthinned stands.

Principal Components Analysis.—PCA yielded 3 components useful in ordinating the sampling stations (Table 3). Component I explained 18% of the variance, and it represented a gradient from stands with high basal areas, high densities of maple trees, and high upper-canopy foliage volume (>18 m) on the positive end to stands with high densities of oak saplings and shrubs and low basal areas and maple densities at the negative end. I interpreted the component to be a thinned-unthinned gradient. Control 3 was the only stand with a mean positive score and was different from the other 5 stands (Table 4). Thin 3 and Thin 2 had the highest negative scores. Thin 3 and Control 3 were the only treatment pair to differ in their mean scores.

Component II explained an additional 14% of the variance (Table 3). It represented a gradient of stands with high densities of trees 8-15 cm dbh and 3-8 cm dbh with high canopy cover and high understory (0-6 m) foliage volume with short trees at the positive end to stands with tall trees, dense upper canopies, and open understories on the negative end. I interpreted the component as a thinned-unthinned gradient useful in separating the individual pairs of stands. Each thinned/unthinned pair was significantly different from each other on the component (Table 4).

Component III accounted for an additional 11% of the variance (Table 3). It ordinated the sampling stations with high hickory densities, densities of saplings (3-8 cm dbh), and FHD at the positive end to sites with high densities of snags, medium-sized trees (18-35 cm dbh), and oak trees with low hickory densities on the negative end. This component ordinated the stands along an elevational gradient which was expressed by hickory densities being higher at the low elevation stands. Control 3 and Thin 3 had the lowest hickory densities and were the only stands with negative mean scores on Component III (Tables 1,4).

Species Using Shrub/Conifer Sites.—These species included the tufted titmouse, blue-gray gnatcatcher, wood thrush, ovenbird, and hooded warbler (Fig. 1). They were present at stations with dense understories, low basal areas, and short trees with high hickory densities. Conifer densities were generally high and snag densities and ground cover were generally low (Table 5). However, the hooded warbler was present at stations with more ground cover than the other shrub/conifer species. Conifer densities at present stations were generally 100 stems/ha and shrub densities were ≥ 7,000 stems/ha for this bird species group. Blue-gray gnatcatchers, wood thrushes, and hooded warblers were found at stations with similar snag densities (Table 5). Snag density was not selected to discriminate tufted titmouse presence or absence. Conifer density was not selected to discriminate wood thrush, hooded warbler, and blue-gray gnatcatcher habitat use (Table 5).

Wood thrushes were present at stations with closed canopies, high shrub densities, and low snag densities (Table 5). There was no difference between stations where wood thrushes were present and absent on Component I and II (Figs. 2, 3). On Component III, wood thrushes were found at stations with high densities of hickory shrubs and saplings (Fig. 4). There were proportionately more wood thrush observations in thinned stands (Table 7).

Crawford et al. (1981) reported that the wood thrush was a closed-canopy dependent species favoring rather open conditions with mature trees and high basal areas. Bertin (1977) and McArthur (1980) found that wood thrushes favored areas with large trees, extensive canopy, and a patchy distribution of shrubs and saplings. Bertin (1977) found that habitat occupancy was positively related with moisture regime, tree diameter, herb cover, and shrub cover. Moisture regime was the most important variable, accounting for 76% of the variability. Kahl et al.

(1985) found wood thrush territories in Missouri had closed canopies (>80%) with moderate densities of shrubs (1200-1500 stems/ha). These densities were much lower than shrub densities reported from my study. Kahl et al. (1985) concluded that wood thrushes require relatively dense subcanopies indicative of high shrub/sapling densities.

James (1971) and James et al. (1984) characterized the wood thrush as having considerable geographic variation in the type of habitat selected, yet favoring closed canopy situations with high densities of medium-sized trees. Healy (1979) reported that wood thrush favored cove hardwoods with low densities short (5-8 m) trees and understory basal area. Tassone (1981) found the wood thrushes associated with hardwood leave strips with well-developed overstories and mid-stories.

High shrub and sapling densities are important variables in distinguishing hooded warbler presence (Table 5). Stations where hooded warblers were present differed from those where they were absent on Component I and III, indicating use of sites with high shrub and sapling densities (Figs. 2, 4). There was no difference on Component II (Fig. 3) indicating the use of areas with tall, dense canopies and dense understories. Hooded warbler population density was negatively related with oak tree density, and positively related with density of maple saplings (Table 6). There were proportionately more observations of hooded warblers in thinned stands (Table 7).

Research has shown the hooded warbler to be fairly consistent in its habitat selection. Crawford et al. (1981) classified it as a species preferring mature stands with closed canopies and high shrub densities. Smith (1977) classified the hooded warbler as a moist forest species favoring sites with large trees and avoiding intermediate-sized trees. James (1971) reported that hooded warblers favor sites with large trees, and Anderson and Shugart (1974) reported that hooded warblers were found in areas with dense shrub and understory cover. McArthur (1980) found hooded warblers favoring habitats with high shrub densities, and they were not restricted to areas of larger trees.

Blue-gray gnatcatchers were present at stations with high shrub densities, diverse foliage layering, and low ground cover (Table 5). There was no difference between gnatcatcher presence and absence on Components I and II (Figs. 2, 3). However, gnatcatchers were found at stations with high hickory densities on Component III (Fig. 4). Gnatcatcher density was positively related with density of hickory saplings and negatively related with ground and canopy cover (Table 6). Observations of habitat use were evenly distributed across thinned and unthinned stands (Table 7).

The gnatcatcher has been characterized as a species with wide habitat preferences (James 1971, Crawford et al. 1981) selecting areas with open understories and large trees (Anderson and Shugart 1974). Smith (1977) found gnatcatchers favoring sites with tall trees and a closed canopy with low shrub and sapling densities. Crawford et al. (1981) also found the gnatcatcher using mature stands.

The tufted titmouse was found at stations with relatively high shrub and conifer densities and low ground cover (Table 5), a pattern similar to that of the blue-gray gnatcatcher. Hickory tree densities were higher at stations where the titmouse was present (Table 5), and population density was positively related with the density of shrubs and hickory trees (Table 6). The titmouse was present at stations with high hickory densities on Component III (Fig. 4). There was no difference on Component I and II between sites with and without titmice (Figs. 2, 3), although present stations were skewed towards dense understories on Component II. Titmouse habitat use observations were equally distributed across thinned and unthinned stands (Table 7).

The titmouse shows wide latitude in its habitat use. Crawford et al. (1981) reported a wide habitat use pattern, and Anderson and Shugart (1974), Smith (1977), and Tassone (1981) reported that the titmouse selects areas with open understories and closed canopies with well-developed subcanopies.

Ovenbird habitat use was characterized by high densities of shrubs, conifers, and oak trees with low ground cover (Table 5). Ovenbirds were present at stations with high densities of shrubs, saplings, and small trees (8-15 cm dbh) on Components I and II (Figs. 2, 3). On Component III, ovenbirds were present at stations with high densities of hickories (Fig. 4). Ovenbird population density was positively related with the same variables important in discriminanting between presence and absence (Table 6). There were proportionately more ovenbird observations in unthinned stands (Table 7).

The ovenbird is considered a closed-canopy, moist forest dependent species (James 1971, Shugart and James 1973, Smith 1977, Crawford et al. 1981). Noon et al. (1980) reported geographic differences in habitat use by ovenbirds, ranging from favoring deciduous forest stands in Maryland, Ohio, Maine, and Vermont to favoring coniferous stands in Michigan. Despite this shift, ovenbirds consistently established territories in sites with high, closed canopies (Noon et al. 1980). Sherry and Holmes (1985) found a slight preference for deciduous vegetation within a broad habitat use pattern by ovenbirds in New Hampshire. Healy (1979) reported a significant preference for oak-pine forests in southwestern Virginia. She speculated that the broad habitat tolerance of the ovenbird may be a local phenomenon, possibly due to competitive interaction with the ground-nesting worm-eating warbler and black-and-white warbler. Collins et al. (1982) found that ovenbirds in Minnesota occur in mature, mixed coniferous-deciduous forests in which their association with conifers may be a secondary one. Their habitat was characterized by having moderate ground and shrub cover and closed canopies.

Species General in Habitat Use.—The eastern wood-pewee, red-eyed vireo, black-and-white warbler, and scarlet tanager were classified as generalists in their habitat use. These species were found at stations with generally high basal areas, high densities of deciduous trees, tall trees, and open understories (Fig. 1).

Black-and-white warblers were present at stations with low conifer densities, moderate snag and shrub densities, and high ground cover (Table 5). There was no separation of presence and absence stations on Component I (Fig. 2), but there was separation on Component II; stations with tall trees and high upper-canopy foliage volumes were preferred (Fig. 3). On Component III, black-and-white warblers were present at stations with high snag densities and medium-sized trees (15-38 cm dbh) and low hickory densities (Fig. 4). Observations of habitat use were equally distributed across thinned and unthinned stands.

The black-and-white warbler has been classified as a species that favors closed-canopy habitats (Crawford et al. 1981). Crawford et al. (1981) reported black-and-white warblers favored pole stands, with their population density negatively related to shrub density. Shugart and James (1973) found black-and-white warblers at low densities in a xeric forest and at high densities in a mesic forest in northwestern Arkansas. James' (1971) ordination placed the black-and-white warbler in stands with high densities of medium-sized trees, tall closed canopies, with low shrub densities. Healy (1979) reported that understory density was not as important in habitat selection as a uniform distribution of understory trees.

Noon et al. (1980) reported that black-and-white warblers in the central and southern parts of their range selected forest stands with many large trees, well-developed canopies, and low shrub densities. Black-and-white warblers in Maine and Michigan occupied open forests with high shrub densities. In Minnesota, Collins et al. (1982) found black-and-white warblers using second-growth stands with high levels of shrub cover, moderate conifer densities, and open canopies. Black-and-white warblers in my study appeared to use habitat more similar to that used by birds in the northern part of its range.

Eastern wood-pewees were present at relatively high densities in stands with low conifer densities (Tables 1, 2). I found eastern wood-pewees using stations with low densities of small trees (8-15 cm dbh) and oak saplings (Table 5). Foliage volume at 0-6 m and 6-18 m was much lower at present stations (Table 5). On Component I, pewees were present at stations with high basal area and open understories (Fig. 2). On

Component II, pewees were present at stations with tall trees and dense upper canopies (Fig. 3), and they were present at stations on Component III with moderately high densities of trees 15-38 cm dbh and snags (Fig. 4). Pewee population density was negatively related to densities of conifers and small trees, and positively related with densities of maple saplings and oak trees (Table 6). There were proportionately more pewee observations of habitat use in thinned stands (Table 7).

Noon et al. (1980) reported that pewees showed consistent selection of deciduous forest habitats with high, closed canopies, large trees, and open understories. Karr (1968), Hespenheide (1971), Shugart and James (1973), and Healy (1979) found pewees selecting habitats with low understory densities. However, Hespenheide (1971) also reported that pewees occurred in forests with a dense understory up to 6-7 m if there is a broken canopy layer above the understory. In Missouri, pewees select pole to mature forests with a well-developed shrub-understory layer (Kahl et al. 1985). Optimum pewee habitat had densities of 150-200 stems 10-30 cm dbh/ha and 2100-2800 stems <2.5 cm dbh/ha. Canopy height of 16-20 m was considered the most important habitat component to pewees; they avoided habitat with canopies <12 m (Kahl et al. 1985). Conner and Adkisson (1975) reported that pewees were found in mature oak stands with trees 23-25 m, but not in pole stands with trees 8-11 m.

My results support the contentions of Hespenheide (1971) regarding habitat suitability for pewees. In my study, pewee densities were highest at Thin 1 and Control 1, stands with tall canopies and dense understories (Tables 1, 2). Pewee densities were next highest at Thin 3 and Control 3, stands with open understories and short canopies. Pewee densities were lowest at Thin 2 and Control 2, stands with high densities of conifers, dense understories, and short canopies. These combined habitat features resulted in relatively unsuitable pewee habitat.

The red-eyed vireo was present at stations with high basal areas, tall trees, high upper-canopy foliage volume, and low densities of conifers and small trees (8-15 cm dbh) (Table 5, Figs. 2, 3). Ground cover was lower at sites where vireos where present than at stations where none were seen (Table 5). Population density was positively related to densities of medium-sized trees (15-38 cm dbh) and hickory trees and negatively related to conifer densities and foliage volume in the subcanopy (6-18 m) (Table 6). Observations of habitat use were equally distributed across thinned and unthinned stands (Table 7).

Crawford et al. (1981) classified the red-eyed vireo as a species utilizing closed-canopy habitats. Throughout its extensive range, the red-eyed vireo is consistent in its habitat selection of a variety of deciduous forest habitats (McArthur 1980, Crawford et al. 1981, Kahl et al. 1985, Sherry and Holmes 1985). Robbins (1978) reported a negative relationship between red-eyed vireo and conifer densities, and Healy (1979) reported a negative association with understory conifer density. Key habitat features are relatively tall, closed canopies with high foliage volumes (James 1971, Anderson and Shugart 1974, James 1976, Smith 1977, Evans 1978, Robbins 1978, Kahl et al. 1985).

Stations used by scarlet tanager were characterized by low conifer and maple sapling densities, low mid-canopy (6-18 m) foliage volume and high snag densities (Table 5). Stations where scarlet tanagers were present and absent did not differ on Component I and III (Figs. 2, 4), but they did show an orientation toward stations with tall trees, dense upper canopies, and open understories (Fig. 3). Tanager densities were positively related to canopy cover and shrub density and negatively related to densities of saplings 3-8 cm dbh and trees 8-15 cm dbh (Table 6). Scarlet tanager observations of habitat use were equally distributed across thinned and unthinned stands (Table 7).

Crawford et al. (1981) described the scarlet tanager as a species using a wide variety of closed-canopy habitats. Scarlet tanager density was positively related to basal area of medium-sized trees (22-36 cm dbh) (Crawford et al. 1981). Consistent habitat features include relatively high densities of shrubs and saplings and tall, closed canopies in deciduous stands (James 1971, Anderson and Shugart 1974, Evans 1978, Robbins 1978, Healy 1979, Kahl et al. 1985).

Species Using Mature/Deciduous Sites.—The white-breasted nuthatch, solitary vireo, worm-eating warbler, and blackburnian warbler were classified as species favoring mature, deciduous areas. These species used stations with tall trees, high basal areas, high densities of maples, open understories, and dense upper canopies (Fig. 1). The worm-eating warbler was uniquely located on Component III, indicating use of stations with high hickory densities. Shrub and conifer densities at stations where these species were present were generally low (Table 5).

White-breasted nuthatches used stations with high basal areas, dense upper canopies, diverse foliage layering, and low densities of small trees (8-15 cm dbh) and conifers (Table 5). Basal area and ground cover were positively related and densities of medium-sized trees (15-38 cm dbh) and conifers were negatively related to nuthatch density (Table 6).

Nuthatches were present at stations with high basal areas and maple tree densities on Component I (Fig. 2) and dense upper canopies and tall trees on Component II (Fig. 3). There was no selection evident on Component III (Fig. 4). There were equal observations of nuthatch habitat use in thinned and unthinned stands (Table 7).

Crawford et al. (1981) classified the nuthatch as a closed-canopy dependent species favoring mature sites with relatively open shrub and understory layers. James (1971), Anderson and Shugart (1974), Evans (1978), and Noon et al. (1980) reported the same general habitat preferences. In my study, shrub densities varied considerably among the three stands with the highest nuthatch densities. Kahl et al. (1985) reported shrub densities of 2800-3500 stems/ha as the optimum range for nuthatch habitat in Missouri. Smith (1977) noted a positive relationship between nuthatch use and total stem density. It appears that if habitat conditions are met with regard to tall trees, closed canopies, low densities of understory trees and conifers, and open ground cover, shrub densities can vary without affecting nuthatch habitat use and population density.

Solitary vireos used stations with high densities of maple trees, low densities of small trees (8-15 cm dbh) and oak saplings, and high ground cover (Table 5). Solitary vireo densities were negatively related to FHD, and positively related to densities of maple saplings and conifers and ground cover (Table 6). Solitary vireos were present at stations with high basal areas and maple tree densities on Component I (Fig. 2), and they were present at stations with tall trees and high upper-canopy foliage volume on Component II (Fig. 3). On Component III, solitary vireos were found at stations with high densities of snags and trees 15-38 cm dbh and low hickory densities (Fig. 4). Observations of habitat use were equally distributed across thinned and unthinned stands (Table 7).

Solitary vireos were common at elevations above 750 m, which is reflected by their high densities at Thin 3 and Control 3 (Table 4). Maple tree density was highest at Control 3, and conifer density was lowest at Thin 3 and Control 3 (Table 1). Solitary vireos were present at Thin 1. However, I feel that the population density at Thin 1 reflects pre- and post-breeding dispersal from the higher elevation breeding sites. Most of my observations were before and after the peak of breeding activity in early May and early July.

There is little published data on solitary vireo habitat use in eastern deciduous forests. Healy (1979) reported broad habitat selection patterns for the solitary vireo in southwestern Virginia. She found that vireo density was related positively to basal area of conifers and foliage volume of understory conifers and negatively correlated with basal area of understory conifers. Density of trees 11-15 m tall was higher at transects where vireos were present. In northern West Virginia, Clack (1983) found solitary vireos confined to cove hardwood stands with tall, dense canopies, few shrubs, and high ground cover. He found densities of 208 trees 8-15 cm dbh/ha and 70 trees ≥38 cm dbh/ha on 15 singing male 0.04-ha plots. These values are similar to the densities of 217 trees 8-15 cm dbh/ha and 47 trees 38-69 cm dbh/ha from my data (Table 5). James (1979) reported solitary vireos occupying submature deciduous forests with moderate shrub densities, and tree density was 873 stems/ha with basal area 34.5 m^2/ha at 3 nests in western Pennsylvania. These values are similar to the tree density of 576 stems/ha and basal area of 28.1 m^2/ha obtained by different methods on my study.

Worm-eating warblers used sites with high densities of large trees (38-69 cm dbh) and moderate densities of maple and oak saplings, tall trees, low snag densities, and low ground cover (Table 5). Worm-eating warblers were present at stations with high basal areas on Component I (Fig. 2), and at stations with high densities of hickory trees and saplings on Component III (Fig. 4). There was no separation on Component II (Fig. 3). Worm-eating warblers had the highest mean score on Component III, indicating a unique association with hickories. Worm-eating warbler densities were equally distributed at the 4 low elevation stands, indicating their distribution below 750 m (Table 2). There was a tendency to use stations located in unthinned stands (Table 7).

Worm-eating warblers were almost exclusively associated with cove hardwood areas. The 4 low elevation stands all had coves. Healy (1979) found that worm-eating warblers preferred cove habitats. She characterized cove hardwood habitat as consisting of high basal areas (>25 m^2/ha) with hickories accounting for 7% of the basal area. Hickories were important codominant trees, and oaks and maples were dominant overstory trees, and the understory was sparse (Healy 1979). Tall trees, low to moderate sapling and high large tree densities in moist habitats with low ground cover have been reported as important habitat attributes of worm-eating warbler habitat in West Virginia (Clack 1983), Illinois (Graber et al. 1983), and Arkansas (Shugart and James 1973). Robbins (1978) reported a positive correlation for canopy height and a negative correlation for ground cover and worm-eating warbler breeding densities in the eastern United States. In Missouri, Kahl et al. (1985) characterized the worm-eating warbler as using pole and sawtimber stands with dense understories. Optimum habitat for worm-eating warblers had densities of trees ≥30 cm dbh of 25-50 stems/ha and saplings of 750-1150 stems/ha with canopy heights ranging from 12-16 m (Kahl et al. 1985).

Blackburnian warblers used stations with high maple tree and snag densities, open understories, high ground cover, and moderately dense upper canopies (Table 5). Population density was negatively related to oak sapling density, and positively related to density of hickory trees and conifers and ground cover (Table 6). Blackburnian warblers were present at stations with high basal areas and maple tree density on Component I (Fig. 2), at stations with low hickory densities and high densities of snags and medium-sized trees (15-38 cm dbh) on Component III (Fig. 4). There was no separation on Component II, indicating a balance between stations with tall trees with moderate upper-canopy foliage volumes and dense understories (Fig. 3). There were proportionately more observations of habitat use in unthinned stands (Table 7). Blackburnian warblers, like solitary vireos, were more common at elevations above 750 m.

Webb et al. (1977) reported population declines in blackburnian warblers at various logging intensities. Blackburnian warblers occupy coniferous forests in the northern part of their range (Morse 1976, 1985, Greenberg 1979, Collins et al. 1982) and mixed-deciduous forests in the Appalachians (Brooks 1947, Greenberg 1979). Morse (1985) reported that habitat use is dependent on tall conifers.

Holmes and Robinson (1981) and Sherry and Holmes (1985) noted that blackburnian warblers were at low densities in a northern hardwood forest and seemed to center their foraging activities and territories in areas with groups of conifers. Collins et al. (1982) reported that important aspects of blackburnian warbler habitat use in Minnesota were moderate ground cover and shrub cover, >75% canopy cover, and large conifers. The importance of conifers to blackburnian warblers in deciduous stands is evidenced by its significant positive relationship to population density (Table 6). Blackburnian warblers foraged on conifers 10% of the time at Thin 3 and Control 3 (see Section III).

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The predictions of Crawford et al. (1981) were mostly supported by my study. However, my results suggest some species, particularly the wood thrush and ovenbird could be considered as species favoring shrub/conifer stands with closed canopies. The black-and-white warbler should be considered a generalist rather than a closed-canopy species.

The results from my study and others (Hagar 1960, Kilgore 1971, Conner et al. 1977, Webb et al. 1977, Franzreb and Ohmart 1978, Titterington et al. 1979, McArthur 1980, Mannan and Meslow 1984) support the contention that silvicultural practices cannot be categorically described as beneficial or detrimental to bird populations (Crawford et al. 1981:691). The habitat preference of a species dictates whether a particular silvicultural practice in a given habitat type will result in a population change.

Selection thinning practices which open the canopy to 70-80% and increase FHD by increasing the shrub and understory layers through stump sprouting will lead to population increases in understory species such as the wood thrush, hooded warbler, rufous-sided towhee, and indigo bunting. Thinning from below which alters the foliage distribution so that a higher proportion is in the upper canopy should favor the generalist species such as red-eyed vireos and scarlet tanagers. Eastern wood-pewee populations will be maintained in deciduous stands if the intermediate and codominant layers are relatively open and there is a tall canopy.

Heavy thinning from above, particularly in cove hardwood habitats, will reduce populations of worm-eating warblers. Light-intensity low thins would likely not impact this species. The species preferring shrub/conifer sites should not suffer thinning-induced population declines so long as shrub, tree, and conifer densities are maintained at high levels and the canopy closure is >80%.

Species favoring mature, deciduous closed-canopy situations appear the most vulnerable to thinning induced-population declines. Of these species, the blackburnian warbler appears particularly sensitive to habitat changes. High basal area, ground cover, and maple tree densities with moderate shrub and conifer densities and low sapling densities should maintain populations of this species. White-breasted nuthatch populations will be maintained in mature, deciduous stands if basal areas are kept $\geq$ 28 m^2/ha and densities of large, tall trees are high. A selection thin of trees $\leq$38 cm dbh can be conducted while maintaining high upper-canopy foliage volume without impacting this species. Generalists such as the black-and-white warbler will not suffer population declines in deciduous stands, so long as shrub densities are not reduced below 5000 stems/ha and conifer densities are low (≤30 stems/ha).

The 4 habitat variables that were most consistently significant in separating bird presence and absence were conifer density, shrub density, snag density, and ground cover (Table 5). The shrub/conifer species were present at stations with high (≥75 stems/ha) conifer densities, while most of the generalist and mature/deciduous species were present at stations with low (≤50 stems/ha) conifer densities. This has ramifications, considering the planned conversion of 5,691 ha (14,063 ac) or 2% of the forest to conifers with a minimum stocking of 618 stems/ha on the Jefferson National Forest (U.S. Forest Service 1985). The generalist and mature/deciduous species will likely avoid these stands as evidenced by their low population densities at Thin 2 and Control 2, stands with high conifer densities. However, the shrub/conifer species might utilize these stands, particularly if thinning of the deciduous component is conducted and sprouting is allowed to occur, and deciduous trees still constitute a substantial portion (40-50%) of the stand.

The biological significance of snag densities to avian habitat use is unknown. However, most of the snags I sampled were small diameter (8-15 cm dbh) American chestnut, which are too small use by cavity-nesting birds for nesting and foraging. Perhaps the importance of snags lies in their relationship to other habitat parameters.

The current objective of wildlife management in forest ecosystems is to maintain natural diversity and viable populations of all native vertebrates (Mannan and Meslow 1984, Peterson 1984). Thinning and other silvicultural practices provide forest managers with considerable choice in vegetation manipulation methods available to improve habitat for forest avifauna.

By creating a diversity of mature forest cover types, the populations and diversity of Appalachian forest avifauna will be maintained. Shrub/conifer species can be featured in oak-pine stands, generalist species can be featured in mature, oak-hickory stands, and mature/deciduous species can be featured in mature, mixed-hardwood stands. Thinning activities can be coordinated in the different cover types to improve avian habitat. However, this habitat improvement is temporary and relatively expensive because thinning is done prior to regeneration harvests which revert the stand to a seedling stage.

Table 1. Mean (SE) of 22 habitat variables at three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85.

Variable	Thin 1 (N=58)	Control 1 (N=68)	Thin 2 (N=56)	Control 2 (N=68)	Thin 3 (N=67)	Control 3 (N=72)
Tree basal area (m^2/ha)	28.3(1.3)	24.7(0.8)*[1]	25.8(0.9)	27.3(1.0)	22.3(0.9)	33.7(0.7)***
Trees 3-8 cm dbh/ha	466(24)	689(35)***	824(47)	823(48)	301(16)	506(23)***
Trees 8-15 cm dbh/ha	119(10)	323(13)***	261(17)	308(14)*	136(10)	299(11)***
Trees 15-38 cm dbh/ha	264(16)	363(14)***	290(14)	285(14)	242(10)	365(14)***
Trees 38-69 cm dbh/ha	62(6)	23(4)***	41(4)	49(4)	37(4)	66(5)***
Snags ≥8 cm dbh/ha	31(4)	103(9)***	46(5)	68(6)**	65(6)	177(9)***
Shrubs/ha	10,918(580)	8,013(474)***	8,429(628)	6,428(576)**	2,756(293)	3,344(288)*
Total foliage volume (m^3/ha x10^5)	7.84(0.75)	9.58(0.99)	7.57(0.93)	10.19(1.79)	6.24(0.94)	8.49(0.66)***
Foliage volume 0-6 m (m^3/ha x10^4)	1.07(0.22)	5.23(1.09)***	3.31(0.51)	7.20(1.22)*	1.96(0.24)	2.45(0.58)
Foliage volume 6-18 m (m^3/ha x10^5)	3.82(0.32)	6.46(0.70)***	5.10(0.76)	7.11(1.01)	5.15(0.69)	5.93(0.43)*
Foliage volume >18 m (m^3/ha x10^5)	3.92(0.68)	2.63(0.53)***	2.17(0.39)	2.36(0.96)***	0.96(0.31)	2.46(0.37)***
Foliage height diversity (H')	0.56(0.03)	0.48(0.03)*	0.59(0.02)	0.51(0.03)	0.37(0.03)	0.53(0.03)***
Maple saplings/ha	125(14)	173(20)	151(15)	189(199)	39(6)	239(19)***
Maple trees/ha	35(7)	56(8)	41(6)	54(6)	42(7)	293(14)***
Oak saplings/ha	45(8)	141(17)***	80(18)	171(17)***	82(12)	5(2)***
Oak trees/ha	278(17)	518(23)***	276(16)	328(18)*	302(13)	352(14)*
Hickory saplings/ha	55(7)	53(8)	16(5)	54(9)***	12(4)	7(2)
Hickory trees/ha	47(8)	17(3)***	7(3)	61(9)***	9(3)	9(2)
Coniferous trees/ha	34(14)	73(14)**	221(18)	139(14)***	21(5)	6(1)**
Canopy cover (%)	83.0(1.4)	91.3(0.8)***	82.6(1.8)	91.3(1.0)***	80.0(1.6)	92.2(0.8)***
Tree height (m)	19.9(0.5)	16.7(0.5)***	16.5(0.4)	14.8(0.5)**	16.0(0.4)	17.0(0.3)
Ground cover 0-0.3 m (%)	83.6(2.2)	65.5(3.0)***	72.6(3.2)	50.9(3.1)***	79.9(2.1)	71.9(2.2)**

[1]Significance (*P < 0.05, **P < 0.01, ***P < 0.001) of a Wilcoxon 2-sample test between thin and control.

Table 2. Mean (SE) estimated densities (number per 40.5 ha) and community indices of breeding birds based upon 18 censuses in 1984 and 1985 in three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia.

	Thin 1	Control 1	Thin 2	Control 2	Thin 3	Control 3
Yellow-billed cuckoo	+[1]	+		+		
Downy woodpecker	4(0.9)	1(0.2)***	+	1(0.2)*	1(0.3)	+ *
Hairy woodpecker	1(0.5)	1(0.4)	+	1(0.5)*	1(0.4)	2(0.8)
Pileated woodpecker	2(0.6)	1(0.3)*[2]	1(0.3)	2(0.4)	+	+
Eastern wood-pewee	22(3.4)	10(1.6)**	2(0.9)	+ *	8(1.9)	7(1.5)
Great crested flycatcher	2(0.5)	1(0.4)	1(0.4)	4(0.8)**	2(0.6)	3(0.7)
Blue jay	2(0.7)	2(0.4)	2(0.8)	1(0.5)		
Carolina chickadee	1(0.8)	+	+	+	2(1.0)	+
Tufted titmouse	6(1.4)	4(0.8)*	8(2.2)	8(2.2)	1(0.6)	+ *
White-breasted nuthatch	6(0.7)	2(0.6)***	1(0.4)	1(0.3)	6(1.4)	5(1.1)
Blue-gray gnatcatcher	9(1.6)	7(1.5)*	8(1.2)	11(1.3)	+	+
Wood thrush	7(1.4)	4(0.7)*	4(1.7)	+ *		
Solitary vireo	3(1.7)	+ *			9(2.1)	13(2.0)
Red-eyed vireo	23(3.2)	12(1.6)**	5(1.2)	10(1.7)**	10(2.7)	23(3.8)**
Northern parula				2(0.5)**		
Black-throated blue warbler					6(1.8)	6(1.1)
Blackburnian warbler					9(1.9)	19(3.4)*
Pine warbler	3(1.0)	5(1.2)	4(1.3)	6(1.4)		
Black-and-white warbler	4(1.4)	3(1.0)		2(1.5)	7(2.1)	6(1.8)
Worm-eating warbler	5(1.4)	5(1.3)	3(1.2)	6(1.3)		
Ovenbird	27(3.9)	32(2.2)	17(3.1)	22(2.2)	10(1.8)	14(2.4)
Hooded warbler	7(1.6)	6(1.2)	15(1.7)	7(1.9)**		
Scarlet tanager	15(2.3)	9(1.5)*	2(0.8)	5(1.2)	5(1.2)	8(1.1)
Indigo bunting					4(1.3)	
Rufous-sided towhee	4(1.4)	+ **	3(0.9)	+ **	2(0.6)	
Dark-eyed junco					1(0.6)	+ *
Brown-headed cowbird	+	+	+	+	+	+
Total density	155(12.4)	103(7.1)***	77(8.5)	89(8.3)	86(10.9)	105(9.0)
Diversity (H')	2.54(0.07)	2.23(0.10)	2.26(0.10)	2.37(0.09)	2.59(0.06)	2.18(0.06)
Equitability (J')	0.86	0.76	0.77	0.80	0.92	0.77
Richness (S)	22	22	19	22	20	18

[1]Density < 0.5 birds per 40.5 ha.

[2]*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, t-test between respective thin and control.

Table 3. Correlations of 22 habitat variables with the first three principal components derived from 384 plots in the mixed-hardwood forest, southwestern Virginia, 1984-85.

	Component		
Variable	I	II	III
Tree basal area (m^2/ha)	0.67	0.09	-0.11
Trees 3-8 cm dbh/ha	-0.15	0.59	0.48
Trees 8-15 cm dbh/ha	0.19	0.80	0.00
Trees 15-38 cm dbh/ha	0.33	0.36	-0.38
Trees 38-69 cm dbh/ha	0.49	-0.24	0.17
Snags ≥ 8 cm dbh/ha	0.42	0.35	-0.40
Shrubs/ha	-0.45	-0.04	0.43
Total foliage volume (m^3/ha)	0.59	-0.01	0.42
Foliage volume 0-6 m (m^3/ha)	-0.30	0.51	0.23
Foliage volume 6-18 m (m^3/ha)	0.46	0.15	0.19
Foliage volume > 18 m (m^3/ha)	0.61	-0.42	0.40
Foliage height diversity (H')	0.13	-0.03	0.45
Maple saplings/ha	0.41	0.33	0.25
Maple trees/ha	0.64	0.22	-0.21
Oak saplings/ha	-0.60	0.36	0.24
Oak trees/ha	0.18	0.40	-0.35
Hickory saplings/ha	-0.09	0.06	0.51
Hickory trees/ha	0.08	-0.03	0.49
Coniferous trees/ha	-0.32	0.42	0.23
Canopy cover (%)	0.51	0.52	0.25
Tree height (m)	0.51	-0.60	0.28
Ground cover 0-0.3 m (%)	-0.29	-0.38	-0.08
Percent of total variance	18	14	11
Cumulative % of variance	18	32	43

Table 4. Means (SE) of the first three principal components at three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85.

		Component		
Site	N	I	II	III
Thin 1	58	-0.13(0.09) A[1]	-1.12(0.10) A	0.65(0.11) A
Control 1	68	-0.07(0.11) AC	0.66(0.09) B	0.08(0.10) BD
Thin 2	56	-0.41(0.12) A	0.11(0.12) C	0.43(0.09) AD
Control 2	68	-0.27(0.12) A	0.80(0.10) B	0.64(0.11) A
Thin 3	67	-0.47(0.10) AD	-0.85(0.09) A	-0.91(0.09) C
Control 3	72	1.20(0.06) B	0.20(0.05) C	-0.68(0.08) C

[1]Means with the same capital letter within a component are not significantly different (Tukey's Studentized Range Test, $P < 0.05$).

Table 5. Mean (SE) of habitat variables selected by and results of stepwise discriminant analysis comparing sample plots where selected avian species were present and absent. Data were from 384 plots in three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85.

Species	Variable	Present	Absent	Significance[1]
Wood thrush (WT)[2]	Snags ≥8 cm dbh/ha	57(7)	88(4)	0.03
	Shrubs/ha	8,053(863)	6,314(252)	0.04
	Canopy cover (%)	89.4(1.5)	85.5(0.7)	0.02
	N(%)	38(9.9)	346(90.1)	
	Wilks' lambda	0.97		
	F-statistic[3]	4.17		
	Significance	0.00		
	df	3,380		
Hooded warbler (HW)	Trees 3-8 cm dbh/ha	768(50)	563(17)	0.01
	Trees 15-38 cm dbh/ha	304(17)	304(6)	0.04
	Snags ≥8 cm dbh/ha	54(7)	91(4)	0.00
	Shrubs/ha	10,021(664)	5,794(243)	0.00
	Foliage volume 6-18 m (m^3/ha x10^5)	4.47(0.55)	5.92(0.33)	0.09
	Maple trees/ha	47(7)	101(7)	0.06
	Oak saplings/ha	104(17)	84(7)	0.06
	Hickory saplings/ha	21(4)	35(3)	0.00
	Ground cover 0-0.3 m (%)	79.5(2.3)	68.6(1.4)	0.06
	N(%)	63(16.4)	321(83.6)	
	Wilks' lambda	0.80		
	F-statistic	10.63*		
	Significance	0.00		
	df	9,374		

Table 5. Continued.

Species	Variable	Present	Absent	Significance[1]
Blue-gray gnatcatcher (BGG)	Snags ≥8 cm dbh/ha	61(5)	93(5)	0.03
	Shrubs/ha	7,174(390)	6,264(296)	0.00
	Foliage height diversity (H')	0.55(0.02)	0.49(0.01)	0.02
	Hickory saplings/ha	46(6)	29(3)	0.00
	Ground cover 0-0.3 m (%)	63.2(2.6)	72.7(1.3)	0.01
	N(%)	94(24.5)	290(75.5)	
	Wilks' lambda	0.90		
	F-statistic	8.65*		
	Significance	0.00		
	df	5,378		
Tufted titmouse (TT)	Shrubs/ha	7,879(623)	6,224(262)	0.04
	Hickory trees/ha	44(9)	21(2)	0.00
	Coniferous trees/ha	123(18)	71(6)	0.00
	Ground cover 0-0.3 m (%)	62.6(3.4)	71.9(1.3)	0.01
	N(%)	61(15.9)	323(84.1)	
	Wilks' lambda	0.91		
	F-statistic	8.85*		
	Significance	0.00		
	df	4,379		

Table 5. Continued.

Species	Variable	Present	Absent	Significance[1]
Ovenbird (O)	Trees 15-38 cm dbh/ha	307(9)	301(9)	0.08
	Shrubs/ha	7,492(357)	5,432(313)	0.00
	Oak trees/ha	367(13)	326(10)	0.01
	Coniferous trees/ha	96(9)	61(8)	0.04
	Ground cover 0-0.3 m (%)	68.2(1.8)	72.7(1.6)	0.00
	N(%)	197(51.3)	187(48.7)	
	Wilks' lambda	0.89		
	F-statistic	9.58		
	Significance	0.00		
	df	5,378		
Black-and-white warbler (BWW)	Snags/ha	84(4)	94(12)	0.09
	Shrubs/ha	5,894(796)	6,564(255)	0.09
	Coniferous trees/ha	27(9)	86(7)	0.00
	Ground cover 0-0.3 m (%)	77.1(3.0)	69.5(1.3)	0.07
	N(%)	45(11.7)	339(88.3)	
	Wilks' lambda	0.95		
	F-statistic	4.90*		
	Significance	0.00		
	df	4,379		

Table 5. Continued.

Species	Variable	Present	Absent	Significance[1]
Eastern wood-pewee (EWP)	Trees 8-15 cm dbh/ha	204(11)	266(8)	0.01
	Foliage volume 0-6 m (m^3/ha x10^4)	1.46(0.22)	4.60(0.48)	0.10
	Foliage volume 6-18 m (m^3/ha x10^5)	4.86(0.40)	6.09(0.38)	0.06
	Oak saplings/ha	54(8)	104(8)	0.04
	Coniferous trees/ha	27(6)	105(8)	0.00
	N(%)	127(33.1)	257(66.9)	
	Wilks' lambda	0.84		
	F-statistic	14.55*[2]		
	Significance	0.00		
	df	5,378		
Red-eyed vireo (REV)	Tree basal area (m^2/ha)	28.8(0.7)	26.1(0.5)	0.00
	Trees 8-15 cm dbh/ha	230(11)	256(8)	0.05
	Coniferous trees/ha	50(8)	98(9)	0.00
	N(%)	150(39.1)	234(60.9)	
	Wilks' lambda	0.93		
	F-statistic	9.50		
	Significance	0.00		
	df	3,380		

Table 5. Continued.

Species	Variable	Present	Absent	Significance[1]
Scarlet tanager (ST)	Snags ≥8 cm dbh/ha	97(7)	80(4)	0.09
	Foliage volume 6-18 m (m^3/ha x10^5)	4.87(0.42)	6.05(0.37)	0.06
	Maple saplings/ha	128(11)	168(9)	0.02
	Hickory saplings/ha	40(5)	30(3)	0.05
	Coniferous trees/ha	50(10)	92(8)	0.00
	N(%)	117(30.5)	267(69.5)	
	Wilks' lambda	0.93		
	F-statistic	5.84		
	Significance	0.00		
	df	5,378		
White-breasted nuthatch (WBN)	Tree basal area (m^2/ha)	28.7(1.1)	26.9(0.5)	0.06
	Trees 8-15 cm dbh/ha	192(14)	258(7)	0.01
	Foliage volume >18 m (m^3/ha x10^5)	3.64(0.92)	2.13(0.21)	0.10
	Foliage height diversity (H')	0.55(0.03)	0.49(0.01)	0.04
	Coniferous trees	23(7)	92(7)	0.00
	N(%)	73(19.0)	311(81.0)	
	Wilks' lambda	0.89		
	F-statistic	8.91*		
	Significance	0.00		
	df	5,378		

Table 5. Continued.

Species	Variable	Present	Absent	Significance[1]
Solitary vireo (SV)	Trees 8-15 cm dbh/ha	217(17)	250(7)	0.01
	Trees 38-69 cm dbh/ha	47(6)	47(2)	0.01
	Shrubs/ha	4,132(587)	6,845(261)	0.02
	Maple trees/ha	182(22)	78(6)	0.00
	Oak saplings/ha	24(7)	97(7)	0.03
	Ground cover 0-0.3 m (%)	75.9(2.8)	69.6(1.3)	0.01
	N(%)	51(13.3)	333(86.7)	
	Wilks' lambda	0.82		
	F-statistic	14.21*		
	Significance	0.00		
	df	6,377		
Worm-eating warbler (WEW)	Trees 38-69 cm dbh/ha	60(6)	45(2)	0.08
	Snags ≥8 cm dbh/ha	59(7)	89(4)	0.01
	Maple saplings/ha	204(20)	148(8)	0.10
	Oak saplings/ha	97(16)	86(7)	0.03
	Tree height (m)	18.7(0.6)	16.5(0.2)	0.00
	Ground cover 0-0.3 m (%)	59.0(4.2)	72.1(1.2)	0.00
	N(%)	51(13.3)	333(86.7)	
	Wilks' lambda	0.87		
	F-statistic	9.11		
	Significance	0.00		
	df	6,377		

Table 5. Continued.

Species	Variable	Present	Absent	Significance[1]
Blackburnian warbler (BW)	Snags ≥8 cm dbh/ha	128(12)	77(4)	0.00
	Shrubs/ha	4,364(524)	6,855(266)	0.03
	Foliage volume >18 m (m^3/ha x10^6)	2.31(0.04)	2.43(0.03)	0.07
	Maple trees/ha	174(17)	78(6)	0.01
	Oak saplings/ha	25(7)	99(7)	0.00
	Ground cover 0-0.3 m (%)	76.1(2.6)	69.4(1.3)	0.01
	N(%)	57(14.8)	327(85.1)	
	Wilks' lambda	0.84		
	F-statistic	12.29*		
	Significance	0.00		
	df	6,377		

[1]Test of separation of groups by discriminant function.
[2]Acronyms for species names used in Fig. 1.
[3]Variance-covariance matrix significantly different between present and absent stations (likelihood ratio test, *$\underline{P}$ < 0.05).

Table 6. Regression results for four-variable models selected by stepwise procedure relating density of selected avian species at 0.5-ha plots to 22 habitat variables. Data were collected in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85.

Species	Variable	Standardized regression coefficients (x100) and significance tests
Hooded warbler	Foliage height diversity (H')	4
	Maple saplings/ha	39*[1]
	Oak saplings/ha	-8
	Oak trees/ha	-30*
	Intercept	0.557
	R^2	0.257
	F-statistic	4.07
	Significance	0.007
	df	4,47
Blue-gray gnatcatcher	Foliage height diversity (H')	23
	Hickory saplings/ha	43*
	Canopy cover (%)	-33*
	Ground cover 0-0.3 m (%)	-35*
	Intercept	4.482*
	R^2	0.312
	F-statistic	5.35
	Significance	0.001
	df	4,47
Tufted titmouse	Shrubs/ha	23*
	Foliage height diversity (H')	-13
	Hickory trees/ha	40*
	Coniferous trees/ha	20
	Intercept	0.542*
	R^2	0.288
	F-statistic	7.58
	Significance	0.000
	df	4,75

Table 6. Continued.

Species	Variable	Standardized regression coefficients (x100) and significance tests
Ovenbird	Trees 8-15 cm dbh/ha	22
	Shrubs/ha	41*
	Oak trees/ha	16
	Hickory saplings/ha	15
	Intercept	-0.739
	R^2	0.328
	F-statistic	9.16
	Significance	0.000
	df	4,75
Eastern wood-pewee	Trees 8-15 cm dbh/ha	-48*
	Maple saplings/ha	25*
	Oaks trees/ha	19
	Coniferous trees/ha	-39*
	Intercept	1.905*
	R^2	0.447
	F-statistic	15.31
	Significance	0.000
	df	4,75
Red-eyed vireo	Trees 15-38 cm dbh/ha	23*
	Foliage volume 6-18 m (m^3/ha)	-25*
	Hickory trees/ha	30*
	Coniferous trees/ha	-51*
	Intercept	4.928*
	R^2	0.333
	F-statistic	9.36
	Significance	0.000
	df	4,75

Table 6. Continued.

Species	Variable	Standardized regression coefficients (x100) and significance tests
Scarlet tanager	Trees 3-8 cm dbh/ha	-62*
	Trees 8-15 cm dbh/ha	-18
	Shrubs/ha	29*
	Canopy cover (%)	47*
	Intercept	0.477
	R^2	0.283
	F-statistic	7.41
	Significance	0.000
	df	4,75
White-breasted nuthatch	Tree basal area (m^2/ha)	38*
	Trees 15-38 cm dbh/ha	-42*
	Coniferous trees/ha	-26*
	Ground cover 0-0.3 m (%)	22*
	Intercept	-0.107
	R^2	0.377
	F-statistic	11.35
	Significance	0.000
	df	4,75
Solitary vireo	Foliage height diversity (H')	-61*
	Maple saplings/ha	73*
	Coniferous trees/ha	43*
	Ground cover 0-0.3 m (%)	36
	Intercept	0.108
	R^2	0.332
	F-statistic	2.86
	Significance	0.046
	df	4,23

Table 6. Continued.

Species	Variable	Standardized regression coefficients (x100) and significance tests
Blackburnian warbler	Oak saplings/ha	-54*
	Hickory trees/ha	47*
	Coniferous trees/ha	48*
	Ground cover 0-0.3 m (%)	47*
	Intercept	-0.989
	R^2	0.563
	F-statistic	7.42
	Significance	0.001
	df	4,23

[1]*Coefficient significant at $\underline{P} < 0.05$.

Table 7. Percent of observations of presence and absence of selected avian species at 178 thinned stations and 208 unthinned stations, respectively, in the mixed-hardwood forest, southwestern Virginia, 1984-85.

	Thinned		Unthinned		
Species	Present	Absent	Present	Absent	Significance[1]
Wood Thrush	14	86	6	94	0.010
Hooded warbler	21	79	13	87	0.028
Blue-gray gnatcatcher	21	79	27	73	0.131
Tufted titmouse	17	83	15	85	0.601
Ovenbird	45	55	56	44	0.044
Black-and-white warbler	13	87	10	90	0.301
Eastern wood-pewee	40	60	27	73	0.005
Red-eyed vireo	38	62	40	60	0.733
Scarlet tanager	32	68	29	71	0.567
White-breasted nuthatch	22	78	16	84	0.099
Solitary vireo	13	87	13	87	0.876
Worm-eating warbler	10	90	16	84	0.096
Blackburnian warbler	11	89	18	82	0.071

[1]χ^2 test of independence on 2x2 contingency table of frequencies of presence and absence at thinned and unthinned stations.

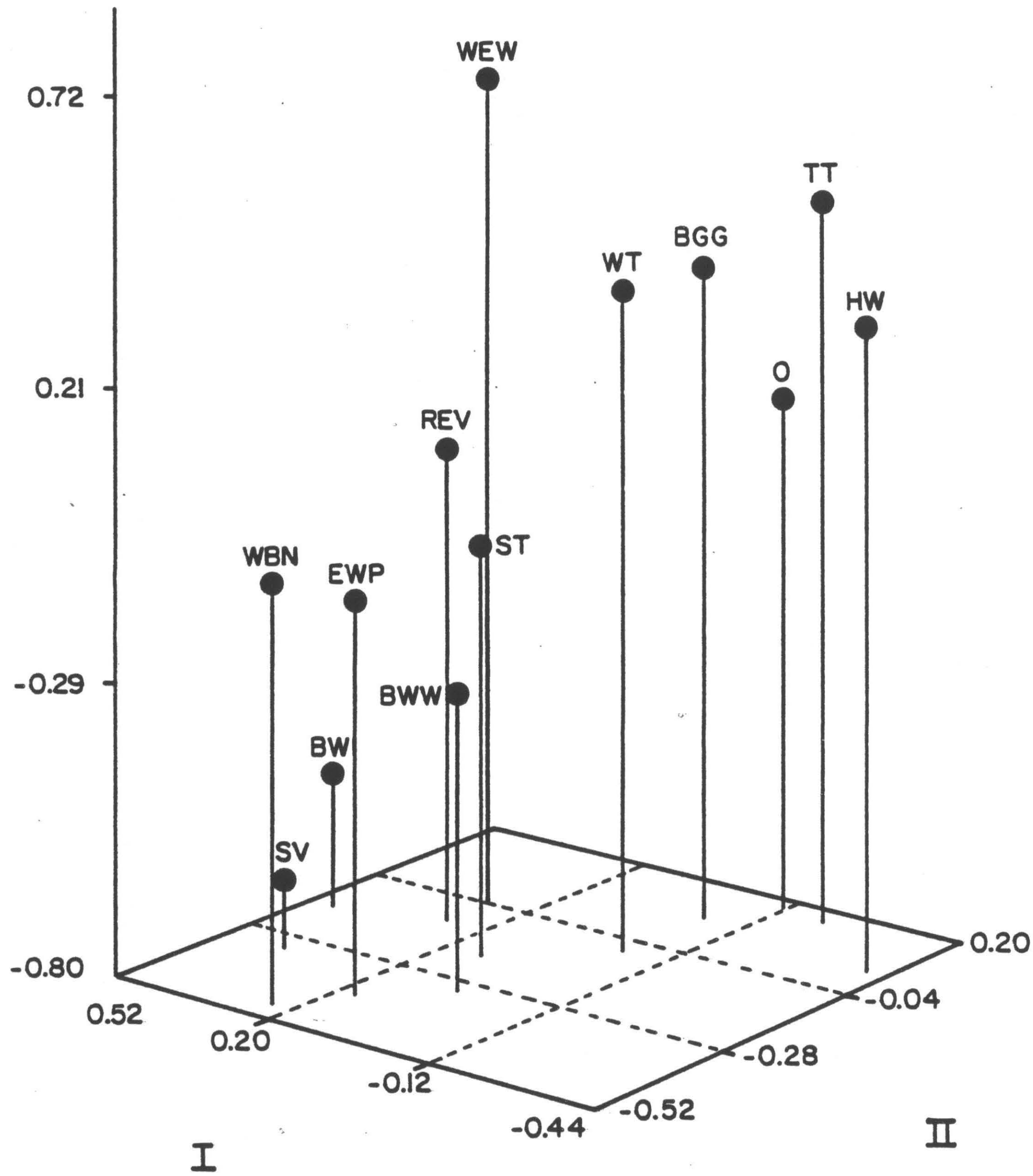

Fig. 1. Three-dimensional ordination of 13 bird species based on mean scores on the first three principal components. Mean scores are the average of vegetation sampling plots where each species was present. The principal components were derived from 384 plots in three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85. See Figs. 2, 3, and 4 for intrepretation of the axes and Table 5 for species' acronyms.

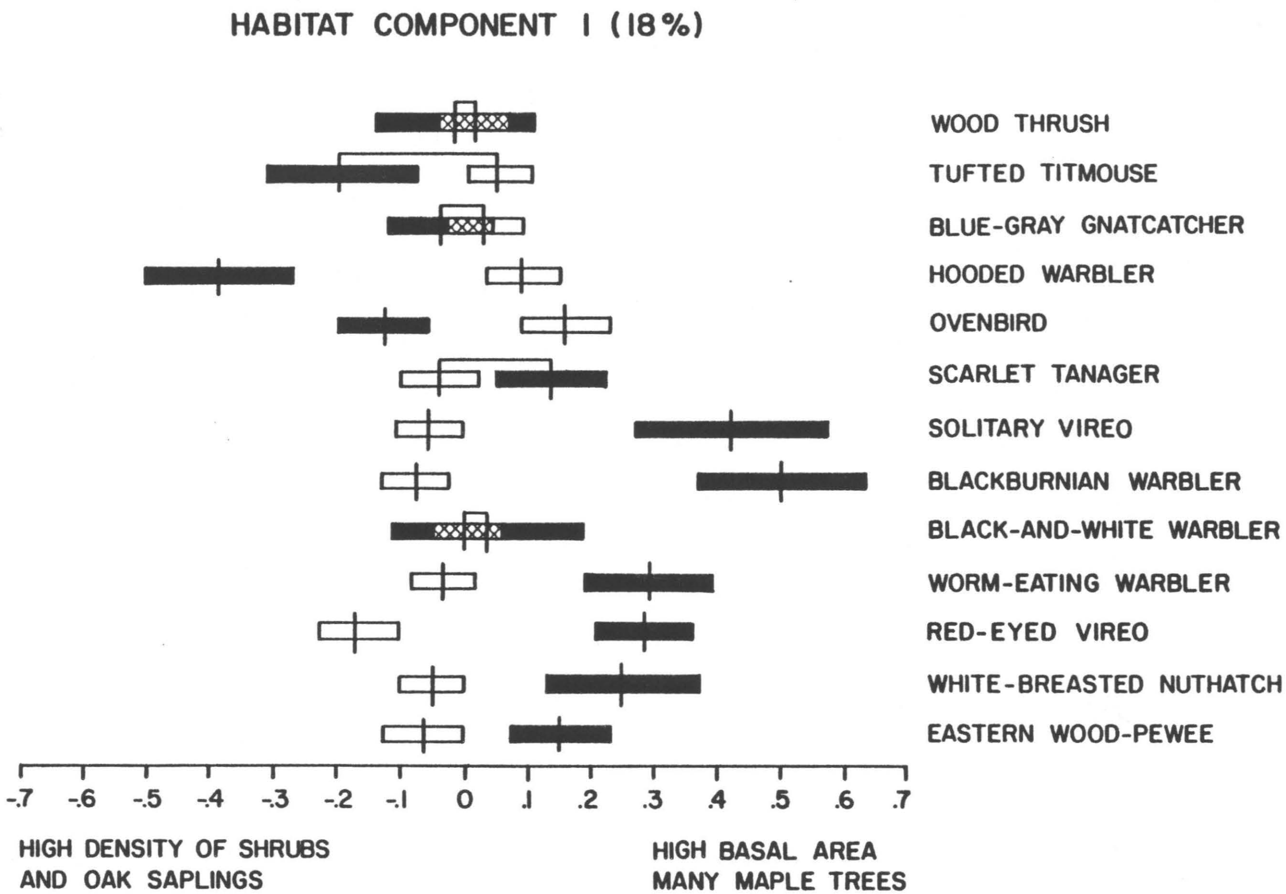

Fig. 2. Distribution of 13 bird species presence and absence along habitat component I. The component was derived from principal components analysis of 384 plots at three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85. Open boxes represent plots where the species was absent and solid boxes represent plots where the species was present. Vertical lines represent the mean value on the gradient; the horizontal bar is 1 SE of the mean. Vertical bars connected by a horizontal line are not significantly different ($\underline{t}$-test, $\underline{P} < 0.05$). Percent of the total variance accounted for by each component is in parentheses.

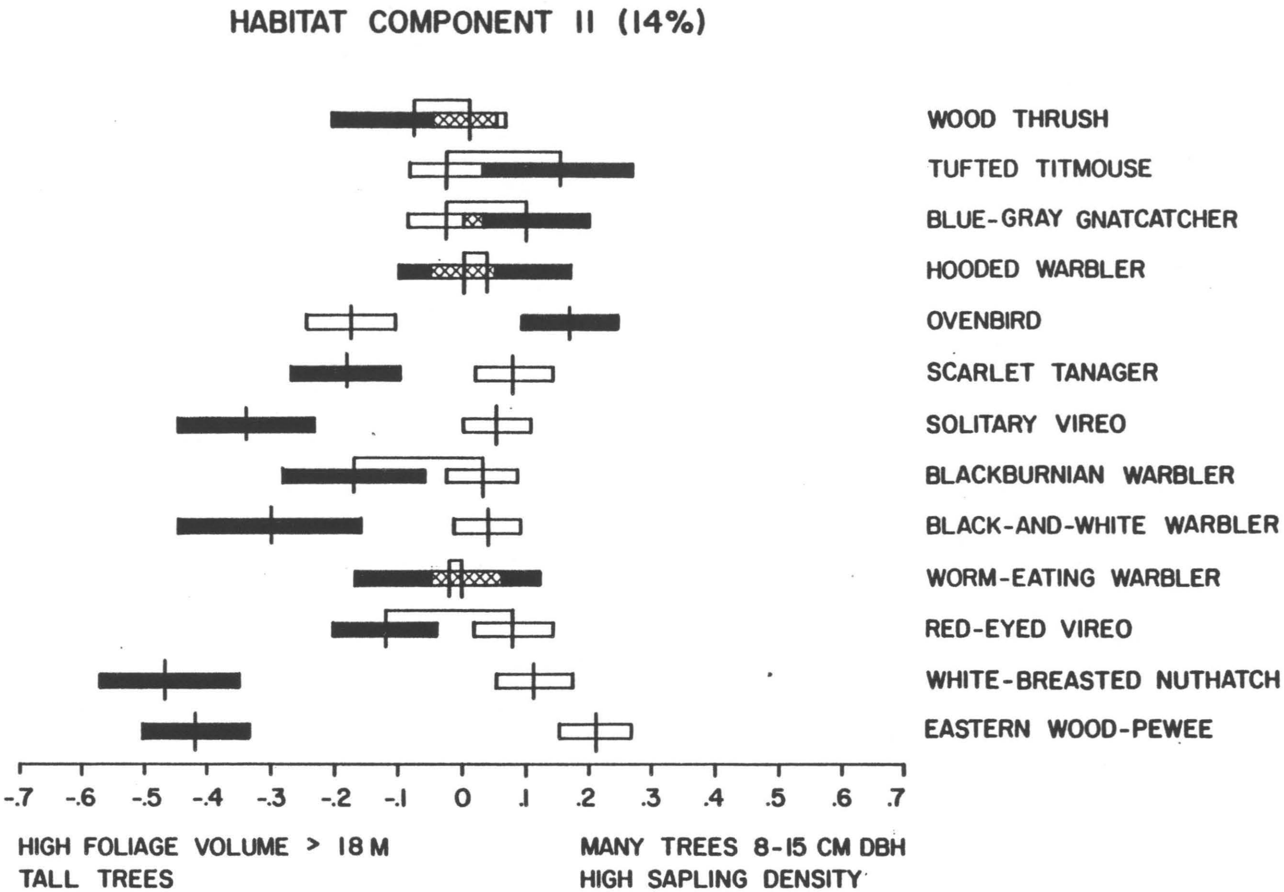

Fig. 3. Distribution of 13 bird species presence and absence along habitat component II. The component was derived from principal components analysis of 384 plots at three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85. Open boxes represent plots where the species was absent and solid boxes represent plots where the species was present. Vertical lines represent the mean value on the gradient; the horizontal bar is 1 SE of the mean. Vertical bars connected by a horizontal line are not significantly different (*t*-test, $P < 0.05$). Percent of the total variance accounted for by each component is in parentheses.

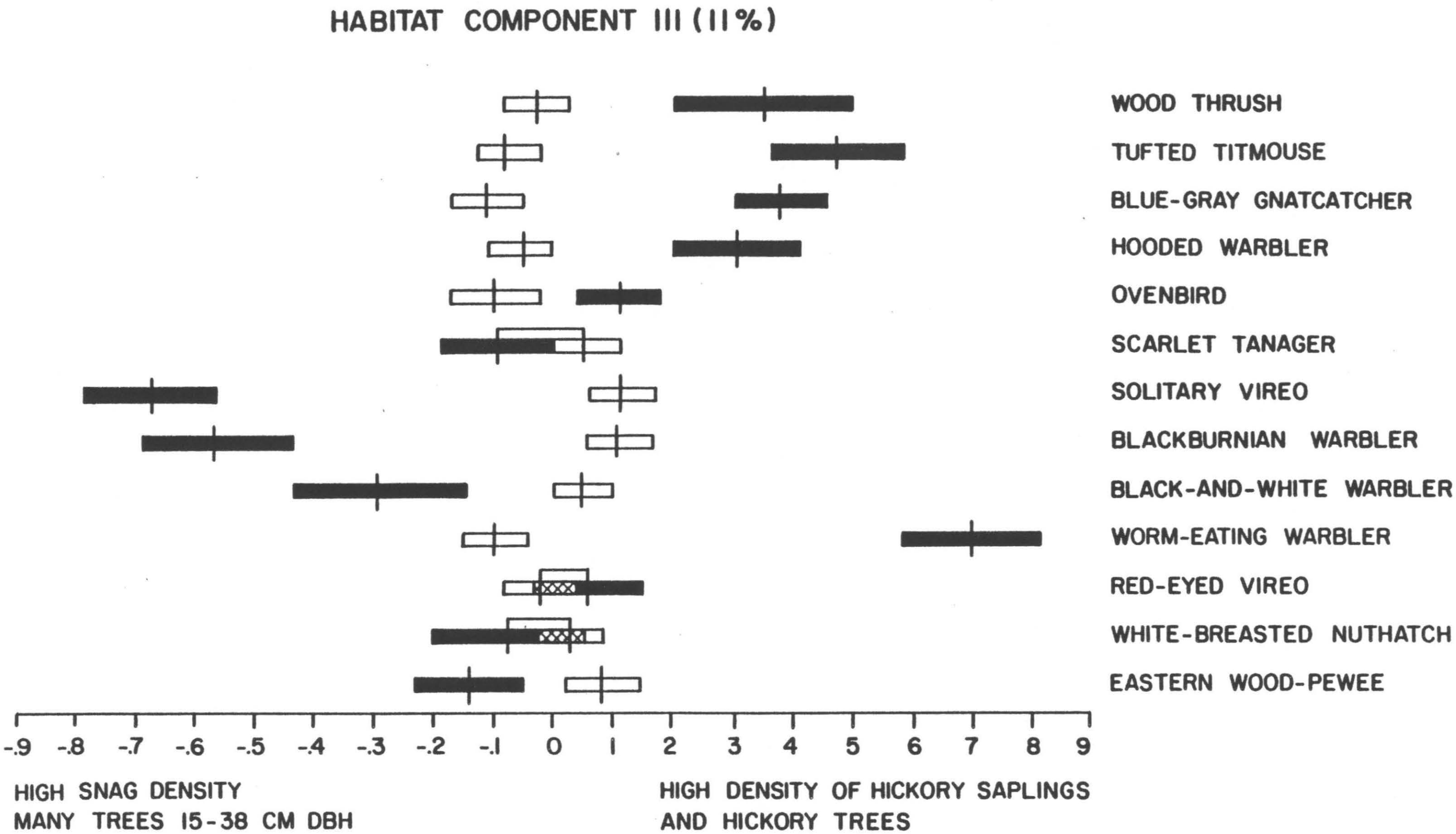

Fig. 4. Distribution of 13 bird species presence and absence along habitat component III. The component was derived from principal components analysis of 384 plots at three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85. Open boxes represent plots where the species was absent and solid boxes represent plots where the species was present. Vertical lines represent the mean value on the gradient; the horizontal bar is 1 SE of the mean. Vertical bars connected by a horizontal line are not significantly different (t-test, $P < 0.05$). Percent of the total variance accounted for by each component is in parentheses.

SECTION III

AVIAN FORAGING ECOLOGY IN THINNED AND UNTHINNED HARDWOOD FORESTS

Many studies have examined the foraging ecology of forest birds. Most of these have concentrated on foraging ecology at the species and community levels (MacArthur 1958, Morse 1968, Stallcup 1968, Jackson 1970, Williamson 1971, Rabenold 1978, Holmes et al. 1979, Conner 1981, Holmes and Robinson 1981, Grubb 1982, Airola and Barrett 1985). Some studies have been done on a number of areas representing different biotic communities (Sabo and Holmes 1983). Cody (1985) and Morse (1985) point out the importance of studying avian habitat use among habitats of different structure. They also state that important insights into the significance of habitat structure in avian habitat use can be gained by studying birds in areas subjected to vegetation manipulation. Franzreb (1978, 1983), Szaro and Balda (1979), Maurer and Whitmore (1981), and Mannan and Meslow (1984) have studied the effects of vegetation changes caused by forestry practices on avian foraging behavior and resource use. These studies have been conducted on stands with considerable differences in their physical structure.

The purpose of this study was to assess differences in avian foraging ecology between thinned and unthinned mixed-hardwood forest stands in the Appalachian mountains, Virginia. In addition, my study examined the influence of subtle differences in vegetation structure on the foraging behavior of Downy Woodpeckers, Eastern Wood-pewees, White-breasted

Nuthatches, Solitary Vireos, Red-eyed Vireos, Blackburnian Warblers, and Scarlet Tanagers.

METHODS

Study Areas

Four study stands were located in the Blacksburg Ranger District, Jefferson National Forest, Montgomery and Giles Counties, southwestern Virginia. The oak (*Quercus* spp.)-hickory (*Carya* spp.) cover type (Burns 1983) dominated the stands which included Appalachian mixed-hardwood and oak-pine (*Pinus* spp.) cover types. The canopy was dominated by white oak (*Q. alba*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), and northern red oak (*Q. rubra*). Other important canopy species were red maple (*Acer rubrum*), pitch pine (*P. rigida*), eastern white pine (*P. strobus*), and various species of hickories.

Two mature stands subjected to different thinning operations were selected along with two unthinned stands that represented pre-thinned conditions. The unthinned stands were as similar as possible to the thinned stands with regard to slope, aspect, slope position, major topographic features, and cover type. Thinned 1 was 6.6 ha and Thinned 3 was 7.9 ha. Unthinned 1 and Unthinned 3 were 8.0 ha each. These stand designations are the same as those in Section II. I did not include Thinned 2 and Unthinned 2 in this analysis because sample sizes were inadequate. Elevations at Thinned 1 and Unthinned 1 were 610-730 m and 1065-1100 m at Thinned 3 and Unthinned 3.

Vegetation Sampling

Transects 100-400 m were established in each stand, and they were spaced 50-m apart and parallel to each other. Vegetation sampling stations were located at 25-m intervals along the transects. Vegetation was sampled using the methods of James and Shugart (1970) and Noon (1981) at 0.04-ha circular plots. Foliage volume (m^3/ha) was estimated for 6-m canopy layers using a modification of the method of Mawson et al. (1976). Basal area (m^2/ha) for dbh classes was estimated by calculating the mean stem density for the dbh class and multiplying that density by a basal area constant for each dbh class. For each tree, ≥8 cm dbh, closest to the station center in each compass quadrant, height (m), crown height (m), and trunk height (m) were measured.

Foraging Observations

Foraging behavior of seven bird species (N = 1,301) was recorded from 6 May-14 August 1984 and 6 May-16 August 1985. The stands were traversed by moving to ten vegetation sampling stations selected from a random numbers table. Observations were recorded for each of seven foraging variables: (1) foraging method (glean, drill, hover, flycatch), (2) substrate part (leaf, branch, trunk, air), (3) location in tree (proximal or distal to trunk), (4) tree species (white oak, scarlet oak, chestnut oak, black oak, northern red oak, red maple, conifer, other), (5) dbh class (3-8 cm, 8-15 cm, 15-23 cm, 23-38 cm, 38-53 cm, >53 cm), (6) height of bird (m) and, (7) height of tree (m). Only one foraging observation was taken per tree. A new observation was made when the bird flew to another tree. Niche breadth (Franzreb 1978, 1983, Conner 1981) based upon 18 independent foraging states (Appendix C) was calculated using

$$H' = -\Sigma(p_i \times \ln p_i)$$

where p_i is the proportion of observations in foraging state $\underline{i}$. Niche breadth of foraging birds for two tree use dimensions was calculated using the proportional similarity index (PSI) (Feinsinger et al. 1981)

$$PSI = 1 - \tfrac{1}{2}\Sigma|p_i - q_i|$$

where p_i is the proportion of foraging observations in niche category $\underline{i}$ and q_i equals the proportion of resource state $\underline{i}$ available. The two tree use dimensions were derived from the eight tree species classes subdivided into: (1) the six dbh classes, or (2) five tree height classes. For each species, these 48- and 40-cell vectors were reduced by deleting cells with no observations. The five tree height classes (0-10.4 m, 10.5-16.4 m, 16.5-22.4 m, 22.5-28.4 m, and ≥28.5 m) were chosen because they best represented the different tree classes (understory, intermediate, codominant, and dominant) that influence the stand structure.

Niche overlap among the species at each stand was calculated for the foraging niche dimension using Euclidean distance (Pielou 1984)

$$d(j,k) = \sum_i (x_{ij} - x_{ik})^2$$

where x_{ij} and x_{ik} are the proportional use of resource state i by species j and k. An average linkage cluster analysis (Dixon 1983) was used to group the species.

Differences in foraging heights and tree heights were tested between the respective thinned and unthinned stands using a t-test. Foraging height and tree height were standardized within a stand by transforming each observation to a z-score

$$z = ((h - \bar{h})/sdh)$$

where h is bird foraging height or tree height, $\bar{h}$ is the mean tree height in a respective stand, and sdh is the standard deviation of the mean tree height. Contingency tables were constructed for categorized variables to test for species differences in resource use between thinned and unthinned stands. Goodness-of-fit tests were used to compare use of a resource state with availability of that resource state.

A χ^2 test of independence was used to test for foraging method differences between the paired thinned and unthinned stands. The G-test of independence and goodness-of-fit test (Sokal and Rohlf 1981) was used to test for differences in use of the tree species classes in the respective stands and tree species use versus availability, respectively. Cells were pooled when the expected values were ≤ 4. The

Kolmogorov-Smirnov test of independence (Sokal and Rohlf 1981) was used to test for differences in use distribution across dbh classes, foliage layers, and tree height classes between the respective thinned and unthinned stands. The Kolmogorov-Smirnov goodness-of-fit test was used to compare observed use of dbh classes, foliage layers, and tree height classes versus expected use based on availability within a stand.

Tests for differences in continuous variables between the respective thinned and unthinned stands were done with a Wilcoxon 2-sample test (SAS 1985). The distribution of proportions of foliage volume and basal area between the respective thinned and unthinned stands were tested with a multivariate analysis of variance (MANOVA)(SAS 1985). Significance was set at $\underline{P} < 0.05$.

RESULTS

Vegetative Differences Between Thinned and Unthinned Stands

A detailed analysis of vegetative differences between the stands is in Section II. Tree height was greater at Thinned 1 than Unthinned 1, but did not differ between Thinned 3 and Unthinned 3 (Table 8). There were more taller trees in Thinned 1 than Unthinned 1, but not between Thinned 3 and Unthinned 3 (Table 8). Density of stems ≥3 cm dbh was lower at Thinned 1 than Unthinned 1, and at Thinned 3 and Unthinned 3 (Table 9). The distribution of stems by dbh class differed between the respective thinnned and unthinned stands (Table 9).

Basal area (m^2/ha) for all stems ≥3 cm dbh was similar at Thinned 1 and Unthinned 1, and basal area was lower at Thinned 3 than Unthinned 3 (Table 10). The distribution of basal area among dbh classes differed between Thinned 1 and Unthinned 1 (MANOVA, F = 16.7, df = 8,117, P < 0.000), and also between Thinned 3 and Unthinned 3 (F = 11.4, df = 7,131, P < 0.00). Most of the basal area was accounted for by stems >23 cm dbh, whereas the highest proportion of density was attributable to stems 3-23 cm dbh.

Most of the tree foliage volume (m^3/ha) occurred from 6-24 m, with the 12-18 m layer contributing approximately 40% of the foliage in each stand (Table 11). Mean foliage volume was not different between Thinned 1 and Unthinned 1, but foliage volume was lower at Thinned 3 than Unthinned 3 (Table 11). The distribution of foliage volume among the layers differed between Thinned 1 and Unthinned 1 (MANOVA, F = 6.1, df = 6,119, P < 0.000), and also between Thinned 3 and Unthinned 3 (F = 4.9, df = 6,132, P < 0.000). There was more chestnut oak at Unthinned 1 than Thinned 1, and there was much more red maple at Unthinned 3 than Thinned 3.

The distribution of stems among the eight tree species classes differed between both Thinned 1 and Unthinned 1 and Thinned 3 and Unthinned 3 (Table 12). The "other" species class accounted for the greatest proportion of stems at three of the stands, while red maple accounted for the greatest proportion of stems at Unthinned 3.

Foraging Behavior

Downy Woodpecker. Downy Woodpeckers used the same foraging methods (drill and glean) equally at Thinned 1 and Unthinned 1 (Fig. 5) (χ^2 = 0.66, df = 1, P = 0.418). Foraging niche breadth was similar in the two stands (Table 13).

Foraging heights differed between the two stands (Table 14), but z-transformed foraging heights did not differ (Table 15). Heights of trees used differed between the two stands (Table 14), and z-transformed tree heights were different between Thinned 1 and Unthinned 1 (Table 15). Downy Woodpeckers used relatively taller trees at Unthinned 1. The distribution of tree heights used was not different between the two stands (Table 16). The distribution of tree heights used by woodpeckers differed from that expected based on availability for Thinned 1 and Unthinned 1 (Table 16). At both stands, Downy Woodpeckers used smaller trees (0-16.4 m) less than expected. Downy Woodpecker foraging height was highly correlated with tree height at both stands (Table 17), and the two coefficients were not different (t = 1.44, df = 56, P = 0.154).

Downy Woodpecker dbh class use was different between Thinned 1 and Unthinned 1 (Table 18). Use of dbh classes compared to availability, based on stem density, was not random in the two stands. Downy Woodpeckers used the smaller dbh classes less than expected and the larger dbh classes more than expected. Based on basal area availability, Downy

Woodpeckers used the dbh classes in the expected proportions (Tables 10, 17).

Downy woodpecker use of foliage layers did not differ between the two stands (Fig. 6, Kolmogorov-Smirnov, $\underline{D} = 0.178$, ns). Foliage layer use differed from that expected for Thinned 1 ($\underline{D} = 0.238$, $\underline{P} < 0.02$), but not for Unthinned 1 ($\underline{D} = 0.209$, ns). Downy Woodpeckers used the 12-18 m layer more than expected at Thinned 1.

Tree species use by Downy Woodpeckers differed between Thinned 1 and Unthinned 1 (Table 19). At both stands, tree species use was different from that expected. Downy Woodpeckers showed higher use of white oak at Thinned 1 and higher use of chestnut oak at Unthinned 1. At both stands, use of the "other" tree species class was much lower than expected. Niche breadth for the tree species foraging dimensions was similar in the two stands (Table 13), indicating that resource use was the same with regard to availability.

Eastern Wood-pewee. Eastern Wood-pewees used the same foraging methods in Thinned 1 and Unthinned 1 (Fig. 5, $\chi^2 = 1.37$, df = 2, $\underline{P} = 0.504$) and Thinned 3 and Unthinned 3 ($\chi^2 = 3.33$, df = 2, $\underline{P} = 0.189$). Flycatching was the major foraging method observed. Foraging niche breadth was essentially the same for pewees in the two pairs of thinned and unthinned stands (Table 13).

Foraging heights of Eastern Wood-pewees did not differ between the two pairs of thinned-unthinned stands (Table 14). Tree heights were different between Thinned 1 and Unthinned 1, but not between Thinned 3 and Unthinned 3 (Table 14). The z-transformed foraging heights and tree heights did not differ between the respective thinned and unthinned stands (Table 15), indicating similarity in relative foraging and tree heights.

The distribution of tree heights used by Eastern Wood-pewees differed between the two pairs of thinned and unthinned stands (Table 16). Pewees foraged more frequently from trees ≥22.5 m at Thinned 1 and Unthinned 3 than Unthinned 1 and Thinned 3, respectively. Tree heights used by pewees differed from that expected at all four stands. At Unthinned 3, pewees used the 16.5-22.4 m height class less than expected, and pewees used the 10.5-16.4 m height class less than expected at the other stands (Tables 8, 16).

Eastern Wood-pewee foraging height was highly correlated with tree height (Table 17). There were no differences in the correlations between the respective thinned and unthinned stands (Table 17, $\underline{P} > 0.05$). The correlation coefficients were higher at Thinned 3 and Unthinned 3 than at Thinned 1 and Unthinned 1, indicating a closer relationship between foraging height and tree height.

The distribution of dbh class use by Eastern Wood-pewees differed between Thinned 1 and Unthinned 1, but not between Thinned 3 and Unthinned 3 (Table 18). Pewees used larger dbh (≥23 cm) trees more often at Thinned 1 than Unthinned 1. Pewees used the smaller dbh classes (3-23 cm) less than expected based on stem density availability at all stands (Tables 9, 18). Use of dbh classes did not differ from expected use based on basal area availability (Tables 10, 18).

Eastern Wood-pewees used foliage layers similarly between the respective thinned and unthinned stands (Figs. 6, 7, Thinned 1 vs. Unthinned 1, $\underline{D} = 0.064$, ns; Thinned 3 vs. Unthinned 3, $\underline{D} = 0.129$, ns).

The distribution of foliage layers used by pewees was different from that expected based on availability (Thinned 1, *D* = 0.492, $P < 0.01$; Unthinned 1, *D* = 0.306, $P < 0.01$; Thinned 3, *D* = 0.399, $P < 0.01$; Unthinned 3, *D* = 0.409, $P < 0.01$). Pewees made greater use of the lower foliage layers (0-12 m) which had the lowest proportions of foliage and more open conditions.

Tree species use by pewees differed between the respective thinned and unthinned stands (Table 19). Pewee use of tree species was different from that expected based on availability (Thinned 1, *G* = 156.9, df = 6, $P < 0.001$; Unthinned 1, *G* = 56.7, df = 5, $P < 0.001$; Thinned 3, *G* = 81.8, df = 6, $P < 0.001$; Unthinned 3, *G* = 21.9, df = 3, $P < 0.001$). Pewees made greater use than expected of oaks, which tended to have large branches and open, lower foliage layers more suitable for perching and flycatching. Niche breadth for the two tree species dimensions were similar between the respective thinned and unthinned stands (Table 13).

White-breasted Nuthatch. White-breasted Nuthatches used similar foraging methods in the respective stand pairs (Fig. 5, Thinned 1 vs. Unthinned 1, $\chi^2 = 1.74$, df = 2, $P = 0.419$; Thinned 3 vs. Unthinned 3, $\chi^2 = 2.65$, df = 3, $P = 0.448$). Gleaning and drilling were the most frequent foraging methods. Foraging niche breadths in the four stands were similar (Table 13).

Nuthatch foraging heights and heights of trees used differed between the respective thinned and unthinned stands (Table 14) The z-transformed foraging heights did not differ between the paired thinned and unthinned stands (Table 15). The z-transformed tree heights differed between Thinned 1 and Unthinned 1, but not between Thinned 3 and Unthinned 3

(Table 15). Nuthatches were using trees much taller than average at Unthinned 1.

The distribution of tree heights used by nuthatches did not differ between the two stand pairs (Table 16). The distribution of tree heights used by nuthatches was different than expected based on tree height availability. Nuthatches used the shorter trees (0-16.4 m) less than expected and the taller trees (≥22.5 m) more than expected. The greatest differences in use versus availability occurred in the 22.5-28.4 m height class at Thinned 1 and Unthinned 1, and in the 10.5-16.4 m height class at Thinned 3 and Unthinned 3.

White-breasted Nuthatch foraging height was correlated with tree height at the four stands (Table 17). The correlation coefficients were not different between the respective thinned and unthinned stands (Thinned 1 vs. Unthinned 1, $\underline{t}$ = 0.419, df = 124, $\underline{P}$ = 0.674; Thinned 3 vs. Unthinned 3, $\underline{t}$ = 0.377, df = 200, $\underline{P}$ = 0.704). Nuthatches had some of the lowest correlation coefficients among the species, indicating a relatively weak association between bird height and tree height.

The distribution of dbh classes used by nuthatches differed between Thinned 1 and Unthinned 1, but not between Thinned 3 and Unthinned 3 (Table 18). Nuthatches used the 15-23 cm dbh class more at Unthinned 1 than at Thinned 1. Nuthatches used the smaller dbh classes (3-15 cm) less than expected based on stem density availability (Tables 9, 18). Use of dbh classes by nuthatches was different from expected use based on basal area availability at Thinned 3, but not at the other stands (Tables 10, 18). At Thinned 3, nuthatches used the 23-38 cm dbh class less than expected.

White-breasted Nuthatch use of foliage layers was similar between the paired thinned and unthinned stands (Figs. 6, 7, Thinned 1 vs. Unthinned 1, $\underline{D}$ = 0.192, ns; Thinned 3 vs. Unthinned 3, $\underline{D}$ = 0.198, $\underline{P}$ < 0.1). The use of foliage layers by nuthatches was different from that expected based on availability (Thinned 1, $\underline{D}$ = 0.240, $\underline{P}$ < 0.01; Unthinned 1, $\underline{D}$ = 0.183, $\underline{P}$ < 0.01; Thinned 3, $\underline{D}$ = 0.221, $\underline{P}$ < 0.01; Unthinned 3, $\underline{D}$ = 0.215, $\underline{P}$ < 0.01). At all stands, nuthatches made greater use than expected of the 6-18 m layers. Nuthatches used the lower portions of the tree which had larger trunk and branch surface areas and less foliage.

Tree species use by nuthatches differed between the respective thinned and unthinned stands, and use of tree species differed from expected use (Tables 12, 19). Nuthatches made greater use than expected of the oaks, and less use of red maple. Niche breadth for the tree species × dbh class dimension were similar between the respective thinned and unthinned stands (Table 13). The tree species × height niche breadth was lower at Unthinned 3 than Thinned 3, indicating more concentrated resource use in less abundant resource classes).

Solitary Vireo. Solitary Vireos used the same foraging methods in similar proportions in Thinned 3 and Unthinned 3 (Fig. 5, χ^2 = 1.67, df = 2, $\underline{P}$ = 0.434). Gleaning and hovering were the most frequent foraging methods used. Foraging niche breadth was essentially the same in the two stands (Table 13).

Solitary Vireo foraging height did not differ between Thinned 3 and Unthinned 3, and heights of trees used were the same in the two stands (Table 14). The z-transformed foraging heights and tree heights did not differ between Thinned 3 and Unthinned 3 (Table 15). The distribution of observations among tree heights did not differ between Thinned 3 and Unthinned 3 (Table 16). At both stands, Solitary Vireos used tree heights differently than expected based on availability (Tables 8, 16). Solitary Vireos used the 10.5-16.4 m class less and the 22.5-28.4 m class more than expected at Thinned 3, and the 16.5-22.4 m class less than expected at Unthinned 3. Solitary Vireo foraging height was highly correlated with tree height (Table 17), and the correlation coefficients did not differ between Thinned 3 and Unthinned 3 (t = 0.20, df = 54, P = 0.892).

Solitary Vireo dbh class use did not differ between Thinned 3 and Unthinned 3 (Table 18). Solitary Vireos used the smaller dbh classes less than expected based on stem density availability at Thinned 3 and Unthinned 3 (Tables 9, 18). Use of dbh classes by Solitary Vireos did not differ from that expected based on basal area availability at both stands (Tables 10, 18).

Solitary Vireo use of foliage layers differed between Thinned 3 and Unthinned 3 (Fig. 7, D = 0.343, P < 0.05). The greatest difference was in the higher use of the 6-12 m layer at Thinned 3. There was no difference in use of the foliage layers by Solitary Vireos and expected use (Thinned 3, D = 0.111, ns; Unthinned 3, D = 0.200, ns).

Use of tree species by Solitary Vireos differed between Thinned 3 and Unthinned 3 (Table 19). Solitary Vireos showed greater use of northern red oak and less use of scarlet oak at Unthinned 3 than Thinned 3. Tree species use was different than expected use at Unthinned 3, but use was equal to expected use at Thinned 3 (Tables 12, 19). The tree species niche breadths were similar in the two stands, although the tree species

× dbh niche breadth was lower at Thinned 3 than at Unthinned 3, indicating more concentrated use in proportion to availability (Table 13).

Red-eyed Vireo. Red-eyed Vireos used the same foraging methods in equivalent proportions at the respective stand pairs (Fig. 5, Thinned 1 vs. Unthinned 1, $\chi^2 = 0.55$, df = 2, $P = 0.760$; Thinned 3 vs. Unthinned 3, $\chi^2 = 0.54$, df = 2, $P = 0.762$). Gleaning and hovering were the most common foraging methods observed. Foraging niche breadth was similar between the respective stand pairs (Table 13).

Red-eyed Vireo foraging heights and heights of trees used differed between each thinned-unthinned stand pair (Table 14). The z-transformed foraging heights and tree heights did not differ between the respective thinned-unthinned stands (Table 15). The distribution of tree heights used by Red-eyed Vireos did not differ between the respective stands (Table 16). Red-eyed Vireos used tree heights different from that expected based on availability (Tables 8, 16). They used the intermediate trees (10.4-16.4 m) less than expected and the dominant trees (≥22.5 m) more than expected. Red-eyed Vireo foraging height was highly correlated with tree height at the four stands (Table 17). The correlation coefficients were the same between Thinned 1 and Unthinned 1 ($t = 0.93$, df = 108, $P = 0.352$) and Thinned 3 and Unthinned 3 ($t = 0.19$, df = 138, $P = 0.850$).

Red-eyed Vireo use of dbh classes did not differ between the respective thinned-unthinned stands (Table 18). Red-eyed Vireos used the smaller dbh classes (3-15 cm) less and the larger dbh classes (≥23 cm) more than expected, based on stem density availability (Tables 9, 18). Use of dbh classes by Red-eyed Vireos did not differ from expected use based on basal area availability (Tables 10, 18).

Red-eyed Vireo use of foliage layers did not differ between either stand pairs (Figs. 6, 7, $\underline{P} > 0.05$). Foliage layer use by Red-eyed Vireos did not differ from expected use based on availability (Thinned 1, $\underline{D}$ = 0.065, ns; Unthinned 1, $\underline{D}$ = 0.128, ns; Thinned 3, $\underline{D}$ = 0.095, ns; Unthinned 3, $\underline{D}$ = 0.026, ns). Red-eyed Vireos concentrated most of their foraging activities in the mid-canopy (12-24 m), where most of the foliage is located.

Tree species use by Red-eyed Vireos differed between Thinned 3 and Unthinned 3, but not between Thinned 1 and Unthinned 1 (Table 19). Red-eyed Vireos differed most in their use of red maple, white oak, scarlet oak, and red oak at Thinned 3 and Unthinned 3. Red-eyed Vireo tree species use differed from expected use at three stands, but not Unthinned 3. At these stands, use of white oak by Red-eyed Vireos was greater than expected. Niche breadth for the tree species dimensions were fairly similar between the respective thinned-unthinned stands (Table 13).

Blackburnian Warbler. Blackburnian Warblers did not differ in the proportion of foraging methods at Thinned 3 and Unthinned 3 (Fig. 5, χ^2 = 4.52, df = 2, $\underline{P}$ = 0.105). Gleaning and hovering were the most frequent foraging methods observed. Foraging niche breadth was higher at Unthinned 3 than Thinned 3 reflecting use of a wider variety of foraging methods.

Blackburnian Warbler foraging heights differed between Thinned 3 and Unthinned 3, and tree heights used were also different (Table 14). The z-transformed foraging and tree heights did not differ between the stands

(Table 15). The positive z-transformed foraging height at Unthinned 3 indicates that Blackburnian Warblers were foraging above the average tree height in the stand. Blackburnian Warblers were similar in use of tree height classes between Thinned 3 and Unthinned 3, and use of tree heights was different from expected use based on availability (Table 16). Blackburnian Warblers foraged on the intermediate trees (10.5-16.4 m) less and the dominant trees (≥22.5 m) more than expected. Foraging height was highly correlated with tree height at Thinned 3 and Unthinned 3 (Table 17), and the correlation coefficients approached significance between the two stands ($\underline{t}$ = 1.82, df = 58, $\underline{P}$ = 0.069).

The distribution of dbh class use by Blackburnian Warblers did not differ between Thinned 3 and Unthinned 3 (Table 18). At both stands, they used the smaller dbh classes (3-23 cm) less and the larger dbh classes (≥23 cm) greater than expected based on stem density availability (Tables 9, 18). Use of dbh classes by Blackburnian Warblers did not differ from expected use, based on basal area (Tables 10, 18).

Blackburnian Warbler use of foliage layers did not differ between Thinned 3 and Unthinned 3 (Fig. 7, $\underline{D}$ = 0.270, ns). Use of foliage layers did not differ from expected use based on foliage availability (Thinned 3, $\underline{D}$ = 0.171, ns; Unthinned 3, $\underline{D}$ = 0.145, ns). Blackburnian Warblers concentrated most of their foraging in the 12-24 m mid- to upper-canopy layers.

There was no difference in tree species use by Blackburnian Warblers between Thinned 3 and Unthinned 3, and use did not differ from that expected based on availability at Thinned 3 (Table 19). However, at Unthinned 3, tree species use differed from availability. At Unthinned

3, Blackburnian Warblers had low use of red maple and high use of white oak, compared to availability.

Scarlet Tanager. Scarlet Tanager foraging methods were similar in Thinned 1 and Unthinned 1 (Fig. 5, $\chi^2 = 2.20$, df = 2, $\underline{P} = 0.333$) and Thinned 3 and Unthinned 3 ($\chi^2 = 1.59$, df = 2, $\underline{P} = 0.452$). Gleaning and hovering were the most common foraging methods observed. Foraging niche breadth was similar between the two thinned-unthinned stand pairs (Table 13).

Scarlet Tanager foraging heights differed between Thinned 1 and Unthinned 1, but not between Thinned 3 and Unthinned 3 (Table 14). Tree heights used by Scarlet Tanagers were different between Thinned 1 and Unthinned 1, and approached significance between Thinned 3 and Unthinned 3 (Table 14). The z-transformed foraging heights and tree heights did not differ between the respective thinned-unthinned stands (Table 15). Use of tree height classes by Scarlet Tanagers differed between Thinned 1 and Unthinned 1, but not between Thinned 3 and Unthinned 3 (Table 16). There was greater use of the 10.5-16.4 m class and less use of the 16.5-22.4 m class in Thinned 3 than Unthinned 3. Scarlet Tanager use of tree height classes differed from expected use based on availability at Thinned 1 and Unthinned 3, but not at Unthinned 1 and Thinned 3 (Tables 8, 16). Scarlet Tanagers used the 10.5-16.4 m trees less and the 22.5-28.4 trees more than expected at Thinned 1 and Unthinned 3. Foraging height was highly correlated with tree height at all stands (Table 17). The correlation coefficients were different between Thinned 3 and Unthinned 3 ($\underline{t} = 2.33$, df = 103, $\underline{P} = 0.020$), but not between Thinned 1 and Unthinned 1 ($\underline{t} = 0.55$, df = 109, $\underline{P} = 0.582$). The relationship between

Scarlet Tanager foraging height and tree height was stronger at Thinned 3 than Unthinned 3.

Scarlet Tanager use of dbh classes differed between Thinned 1 and Unthinned 1, but not between Thinned 3 and Unthinned 3 (Table 18). Tanagers showed more use of the 15-23 cm class and less use of the 38-53 cm class at Unthinned 1 than Thinned 1. Tanagers used the smaller dbh classes (3-15 cm) less and the larger dbh classes (≥23 cm) more than expected based on stem density availability (Tables 9, 18). Use of dbh classes by Scarlet Tanagers did not differ from expected use based on basal area at three stands (Tables 10, 18). At Unthinned 3, Scarlet Tanagers used the 23-38 cm dbh class more that expected, based on basal area availability.

Scarlet Tanager use of foliage layers differed between Thinned 1 and Unthinned 1 (Fig. 6, $\underline{D} = 0.283$, $\underline{P} < 0.025$), but not between Thinned 3 and Unthinned 3 (Fig. 7, $\underline{D} = 0.159$, ns). Scarlet Tanagers used the 6-12 m layer more and the 12-18 m layer less at Unthinned 1 than Thinned 1. Use of foliage layers by Tanagers was different from expected use based on availability of foliage at Unthinned 1 ($\underline{D} = 0.179$, $\underline{P} < 0.05$), but not at the other three stands (Thinned 1, $D = 0.154$, ns; Thinned 3, $\underline{D} = 0.100$, ns; Unthinned 3, $\underline{D} = 0.101$, ns). Scarlet Tanagers concentrated their foraging in the 6-18 m mid-canopy foliage layers.

Tree species use by Scarlet Tanagers was different between the respective thinned-unthinned stands, and use of tree species differed from expected use at all four stands (Table 19). At Thinned 1 and Unthinned 1, Scarlet Tanagers showed high use of white oak and chestnut oak and low use of red maple compared to availability. At Thinned 3, Tanagers had high use of scarlet oak and red oak, and at Unthinned 3, Tanagers had high use of white oak and chestnut oak compared to availability.

Species Relationships. The species relationships along the foraging niche dimension as determined by cluster analysis were essentially the same between Thinned 1 and Unthinned 1 and between Thinned 3 and Unthinned 3 (Fig. 8). The Eastern Wood-pewee was unique among species due to it flycatching habits. The White-breasted Nuthatch and Downy Woodpecker were grouped together at Thinned 1 and Unthinned 1 due to their bark-foraging habits. The Solitary Vireo, Red-eyed Vireo, Blackburnian Warbler, and Scarlet Tanager were clustered together because of their foliage-gleaning habits (Fig. 8).

DISCUSSION

There were no differences in the foraging methods or niche breadth of a species or the foraging dimension relationships among the species between the thinned and unthinned stands. The foraging methods and their proportions I observed for each species were similar to those reported elsewhere (Morse 1968, Jackson 1970, Williamson 1971, James 1976, 1979, Conner 1981, Maurer and Whitmore 1981, Grubb 1982, Robinson and Holmes 1982, Airola and Barrett 1985). Maurer and Whitmore (1981) noted no differences in the foraging patterns of Acadian Flycatchers (Empidonax virescens), Red-eyed Vireos, Black-throated Green Warblers (D. virens), and Scarlet Tanagers between a 30-year-old stand and a 90-year-old stand in the deciduous forest of West Virginia. American Redstarts (Setophaga ruticilla) hovered more in the 30-year-old and hawked more in the 90-year-old stand, which they attributed to denser foliage in the young stand. Franzreb (1983) reported no differences in the foraging methods of Yellow-bellied Sapsuckers (Sphyrapicus varius) and Yellow-rumped Warblers (D. coronata) between an unlogged stand and an intensively thinned stand in the mixed-coniferous forest of Arizona. White-breasted Nuthatches did more hammering-tearing in a lightly thinned stand and an unlogged stand than in a heavily thinned stand and a strip cut stand in Arizona (Szaro and Balda 1979).

Species' foraging heights and tree heights differed between the thinned and unthinned stands. However, when these two variables were standardized to account for variations in tree height within a stand, there were few differences. The bark-foraging White-breasted Nuthatch and Downy Woodpecker appeared to utilize taller than average trees in shorter stands; e.g., Unthinned 1. These taller trees have more bark surface area on which to forage. Foraging height was highly correlated with tree height, and most species used the taller trees in proportion to availability while showing little use of the more abundant smaller (≤10.4 m) trees. These relationships were consistent in thinned and unthinned stands. Maurer and Whitmore (1981) noted little difference in the foraging heights of Scarlet Tanagers and Red-eyed Vireos, and different foraging heights of Black-throated Green Warblers between two stands.

The relationship of avian foraging behavior to foliage volume and layering is well documented (MacArthur 1958, Williamson 1971, Holmes et al. 1979, Szaro and Balda 1979, Robinson and Holmes 1984). In my study, bird use of foliage layers was consistent in the thinned and unthinned stands. However, I found differences in use of foliage layers between stands for Solitary Vireos and Scarlet Tanagers. These differences were parallel to foliage layering differences between the respective thinned and unthinned stands.

The White-breasted Nuthatch, Downy Woodpecker, and Eastern Wood-Pewee consistently used the lower, more open foliage layers. These lower layers consisted of tree trunks, large branches, and low foliage volumes, all habitat characteristics suitable for feeding by bark-foragers and flycatchers. Solitary Vireos, Red-eyed Vireos, Blackburnian Warblers, and Scarlet Tanagers consistently used the intermediate and upper canopy layers. Most of the foliage was concentrated in these layers creating favorable foraging conditions for foliage-gleaning birds. Szaro and Balda (1979) and Maurer and Whitmore (1981) reported similar results.

Few studies have been done on foraging bird use of tree diameter in relation to availability. Travis (1977), Jackson (1979), Raphael and White (1984), and Morrison et al. (1985) reported the use of medium to large diameter trees by foraging birds. The dbh class use pattern was similar among all species. Use was equal to availability based on basal area, and use was not equal to availability based on stem density. Birds consistently avoided the smaller (3-23 cm) diameter trees, which occurred in the highest density. There was consistent use of the larger (>23 cm) diameter trees, which occurred in the lowest density, but accounted for most of the basal area. Most of the foliage and bark surface area is concentrated on these larger, taller trees. Therefore, bird use of dbh classes is the result of a multi-dimensional foraging response to a combination of resource states of which tree diameter is an indicator. Tree diameter is related to tree height, foliage volume, and bark surface area, all of which are cues for foraging birds.

Preferential use of certain tree species by foraging birds has been well documented (Franzreb 1978, 1983, Szaro and Balda 1979, Conner 1981, Holmes and Robinson 1981, Maurer and Whitmore 1981, Robinson and Holmes 1984, Airola and Barrett 1985, Morrison et al. 1985). I found no consistent pattern in tree species use between the thinned and unthinned stands. In general, white oak, chestnut oak, and scarlet oak were used most frequently. Northern red oak replaced scarlet oak at higher elevations. Red maple and conifers had consistently low use compared to availability. At Unthinned 3, Scarlet Tanagers frequently used red maple (22%), and conifers were used by Blackburnian Warblers at Thinned 3 (13%) and Unthinned 3 (9%). Red maple accounted for 42% of the stems at Unthinned 3, and conifers accounted for 4% and 1% of the stems, respectively, at Thinned 3 and Unthinned 3. Holmes and Robinson (1981) and Morse (1985) noted the preference for coniferous trees by Blackburnian Warblers. Maurer and Whitmore (1981) noted no differences in tree species use between a young stand and a mature stand for Red-eyed Vireos, Black-throated Green Warblers, and differences for Acadian Flycatchers and Scarlet Tanagers.

This study tested the null hypothesis that foraging behavior and resource use of selected bird species was not different between thinned and unthinned forest stands. My study failed to reject this general hypothesis, and I concluded that thinning mixed-hardwood forest stands had little impact on avian foraging ecology. Any differences noted in resource use between thinned and unthinned stands are generally the result of birds consistently using or not using the available resources. These differences are not due to ecological or ethological compensation to habitat changes caused by thinning. Therefore, foraging differences noted between the respective thinned and unthinned stands were the result of the vegetation differences between the stands. These vegetative differences were due, in part, to thinning (see Section II).

My results suggest that foraging birds utilize habitat resources in a consistent manner and respond to changes in resource availability. There is little evidence to suggest that birds are compensating for loss of resources by altering their foraging ecology. Franzreb (1978, 1983) and Maurer and Whitmore (1981) came to the same general conclusions.

The ability of forest birds to opportunistically utilize available resources indicates that thinning practices of the magnitude studied here have little negative impact on the foraging ecology of selected bird species in Appalachian mixed-hardwood forests. Removal of small diameter (3-23 cm), overtopped and intermediate (≤16.4 m) trees, particularly red maples and conifers, and retaining the larger diameter (≥23 cm), taller (≥16.5 m) oaks will leave stands in a suitable state for use by foraging birds.

Table 8. Distribution of trees among five tree height classes and mean tree height in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

	Percent of Observations			
	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Tree height (m)	(n=232)	(n=272)	(n=268)	(n=288)
0-10.4	10.8	16.5	14.9	10.1
10.5-16.4	20.7	33.5	34.3	34.0
16.5-22.4	32.8	32.0	45.5	43.1
22.5-28.4	25.0	14.0	4.5	11.8
≥28.5	10.8	4.0	0.7	1.0
Significance[1]	0.001		ns	
Mean (SE)	19.9(0.5)	16.7(0.5)	16.0(0.4)	17.0(0.3)
Significance[2]	0.001		0.096	

[1]Significance level of Kolmogorov-Smirnov test-of-independence on distribution of frequencies among tree height classes between respective thinned and unthinned stands.

[2]Significance level of Wilcoxon 2-sample test on mean tree heights between respective thinned and unthinned stands.

Table 9. Distribution of trees among six dbh classes and mean stem density in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

	Percent of Observations			
	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
dbh class	(n=2,066)	(n=3,626)	(n=1,818)	(n=3,323)
3-8 cm	51.1	49.3	42.0	40.9
8-15 cm	13.0	23.1	19.0	24.1
15-23 cm	10.9	15.0	10.6	15.6
23-38 cm	18.1	10.9	23.2	13.8
38-53 cm	5.5	1.4	4.6	4.5
>53 cm	1.3	0.2	0.5	0.9
Significance[1]	0.001		0.001	
Mean (SE)	912(13) (n=58)	1,398(40) (n=68)	717(24) (n=67)	1,237(24) (n=72)
Significance[2]	0.001		0.001	

[1]Significance level of Kolmogorov-Smirnov test-of-independence on distribution of dbh classes between respective thinned and unthinned stands.
[2]Significance level of Wilcoxon 2-sample test on stem density between respective thinned and unthinned stands.

Table 10. Distribution of relative basal area (m^2/ha) among six dbh classes and mean basal area in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

	Percent of Total Basal Area			
	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
dbh class	(n=58)	(n=68)	(n=67)	(n=72)
3-8 cm	3.8	6.3	3.1	3.5
8-15 cm	4.2	12.7	6.2	8.9
15-23 cm	9.5	22.6	9.4	15.7
23-38 cm	40.9	42.3	52.8	35.8
38-53 cm	27.8	12.5	23.5	26.2
>53 cm	13.8	3.7	5.0	9.9
Mean (SE)	29.5(1.3)	26.3(0.8)	23.0(0.9)	34.9(0.7)
Significance[1]	0.102		0.001	

[1]Significance of Wilcoxon 2-sample test on basal area between respective thinned and unthinned stands.

Table 11. Distribution of foliage volume (m^3/ha) among six height layers and mean foliage volume in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

	Percent of Total Volume			
	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Height layer	(n=58)	(n=68)	(n=67)	(n=72)
0-6 m	2.2	6.6	5.5	4.1
6-12 m	15.6	36.2	37.1	24.7
12-18 m	40.5	36.3	46.8	46.3
18-24 m	29.7	15.6	9.4	22.1
24-30 m	10.0	4.0	1.2	2.7
>30 m	2.1	1.4	0.0	0.0
Mean foliage volume ($x10^5$)(SE)	7.84(0.75)	9.58(0.99)	6.24(0.94)	8.49(0.66)
Significance[1]	0.268		0.001	

[1]Significance level of Wilcoxon 2-sample test on foliage volume between respective thinned and unthinned stands.

Table 12. Relative proportions of eight tree species in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

Tree species	Percent of Observations			
	Thinned 1 (n=2,066)	Unthinned 1 (n=3,626)	Thinned 3 (n=1,818)	Unthinned 3 (n=3,323)
Conifer	4.9	6.2	4.1	0.8
Red maple	17.3	17.2	11.1	41.8
White oak	17.3	19.9	16.0	5.4
Scarlet oak	5.0	6.4	4.7	0.6
Chestnut oak	8.6	20.0	19.6	9.6
Northern red oak	1.1	1.0	9.0	14.3
Black oak	4.2	2.2	7.0	1.0
Other	41.6	27.2	28.5	26.6
G-statistic[1]	1,676		955	
Significance	0.001		0.001	

[1]Test statistic and significance level of G test-of-independence comparing distribution of tree species groups between respective thinned and unthinned stands, df = 7.

Table 13. Niche breadth values for insectivorous birds at two thinned and two unthinned stands in mixed-hardwood forest, southwestern Virginia, 1984-85.

	Niche breadth(SD)			
Species	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Downy woodpecker				
Foraging[1]	1.81(0.11)	1.90(0.17)		
Tree species x dbh[2]	0.30(0.04)	0.23(0.00)		
Tree species x height[3]	0.50(0.05)	0.51(0.07)		
Eastern wood-pewee				
Foraging	0.94(0.13)	0.93(0.14)	1.04(0.12)	0.98(0.12)
Tree species x dbh	0.38(0.03)	0.41(0.03)	0.54(0.03)	0.60(0.07)
Tree species x height	0.60(0.05)	0.63(0.04)	0.68(0.04)	0.56(0.06)
White-breasted nuthatch				
Foraging	1.97(0.12)	1.92(0.09)	1.96(0.08)	1.95(0.11)
Tree species x dbh	0.25(0.02)	0.32(0.04)	0.39(0.04)	0.29(0.04)
Tree species x height	0.53(0.06)	0.50(0.04)	0.53(0.04)	0.36(0.02)
Solitary vireo				
Foraging			2.05(0.17)	1.96(0.15)
Tree species x dbh			0.43(0.08)	0.62(0.08)
Tree species x height			0.55(0.09)	0.51(0.07)
Red-eyed vireo				
Foraging	1.99(0.09)	2.00(0.13)	2.07(0.10)	1.91(0.12)
Tree species x dbh	0.30(0.01)	0.35(0.05)	0.58(0.04)	0.44(0.03)
Tree species x height	0.60(0.02)	0.45(0.06)	0.75(0.05)	0.67(0.06)

Table 13. Continued.

	Niche breadth(SD)			
Species	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Blackburnian warbler				
Foraging			1.67(0.18)	1.92(0.16)
Tree species x dbh			0.45(0.06)	0.33(0.03)
Tree species x height			0.55(0.08)	0.51(0.08)
Scarlet tanager				
Foraging	2.13(0.08)	2.01(0.11)	1.93(0.12)	2.01(0.10)
Tree species x dbh	0.41(0.04)	0.39(0.05)	0.35(0.06)	0.53(0.05)
Tree species x height	0.67(0.04)	0.62(0.04)	0.46(0.07)	0.64(0.06)

[1]Breadth (H') based on distribution of observations among 18 foraging behavior classes.

[2]Breadth (PSI) based on distribution of foraging observations among eight tree species classes and seven dbh classes.

[3]Breadth (PSI) based on distribution of foraging observations among eight tree species classes and five tree height classes.

Table 14. Mean ± SE (n) heights of foraging birds and of trees foraged upon in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

Bird species	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Downy woodpecker				
Bird height	15.2±0.6 (34)	12.6±0.8 (21)*[1]		
Tree height	24.8±0.9 (39)	22.1±1.0 (23)*		
Eastern wood-pewee				
Bird height	11.8±0.5 (91)	10.5±0.5 (75)ns	9.8±0.3 (79)	10.6±0.6 (56)ns
Tree height	22.2±0.6 (97)	18.6±0.8 (79)***	18.0±0.5 (80)	19.5±1.0 (56)ns
White-breasted nuthatch				
Bird height	14.7±0.7 (41)	12.3±0.4 (78)***	11.3±0.3 (120)	12.6±0.5 (60)**
Tree height	25.9±0.8 (45)	22.4±0.6 (78)***	20.2±0.4 (122)	22.5±0.6 (60)***
Solitary vireo				
Bird height			12.6±0.9 (28)	15.0±1.0 (40)ns
Tree height			19.4±1.0 (28)	20.3±1.0 (40)ns
Red-eyed vireo				
Bird height	18.4±0.7 (69)	14.6±0.9 (39)***	13.2±0.5 (77)	15.5±0.6 (61)**
Tree height	24.0±0.6 (74)	20.3±0.9 (40)***	17.9±0.5 (80)	21.0±0.6 (61)***

Table 14. Continued.

Bird species	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Blackburnian warbler				
Bird height			14.2±1.1 (27)	17.2±0.7 (33)*
Tree height			18.7±0.8 (31)	21.5±0.7 (33)**
Scarlet tanager				
Bird height	16.6±0.8 (58)	13.2±0.7 (51)***	13.0±0.6 (37)	14.1±0.6 (68)ns
Tree height	22.3±0.7 (68)	18.5±0.7 (61)***	18.4±0.8 (38)	19.8±0.6 (68)ns

[1]Significance (*$P < 0.05$, **$P < 0.01$, $P < 0.001$) of Wilcoxon 2-sample test on heights between respective thinned and unthinned stands.

Table 15. Mean ± SE (n) of z-transformed heights of foraging birds in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

Bird species	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Downy woodpecker				
Bird height	-0.66±0.09 (35)	-0.88±0.17 (21)ns[1]		
Tree height	0.70±0.14 (35)	1.28±0.22 (21)*		
Eastern wood-pewee				
Bird height	-1.13±0.07 (91)	-1.32±0.10 (75)ns	-1.32±0.07 (79)	-1.23±0.12 (56)ns
Tree height	0.32±0.08 (91)	0.39±0.17 (79)ns	0.45±0.11 (80)	0.50±0.19 (56)ns
White-breasted nuthatch				
Bird height	-0.71±0.10 (41)	-0.95±0.09 (78)ns	-1.00±0.07 (120)	-0.85±0.10 (61)ns
Tree height	0.86±0.12 (41)	1.22±0.13 (78)*	0.92±0.08 (120)	1.05±0.11 (60)ns
Solitary vireo				
Bird height			-0.73±0.19 (28)	-0.38±0.19 (40)ns
Tree height			0.74±0.22 (28)	0.64±0.20 (40)ns
Red-eyed vireo				
Bird height	-0.20±0.10 (69)	-0.49±0.19 (40)ns	-0.58±0.11 (77)	-0.29±0.12 (61)ns
Tree height	0.58±0.10 (69)	0.69±0.20 (40)ns	0.47±0.11 (77)	0.77±0.12 (61)ns

Table 15. Continued.

Bird species	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Blackburnian warbler				
Bird height			-0.38±0.23 (27)	0.05±0.13 (33)ns
Tree height			0.58±0.20 (27)	0.87±0.14 (33)ns
Scarlet tanager				
Bird height	-0.46±0.11 (58)	-0.77±0.15 (51)ns	-0.63±0.13 (37)	-0.56±0.12 (68)ns
Tree height	0.39±0.11 (68)	0.56±0.15 (61)ns	0.56±0.17 (37)	0.54±0.11 (68)ns

[1]Significance (*$P < 0.05$) of t-test on heights between respective thinned and unthinned stands.

Table 16. Relative proportions of foraging birds in five tree height categories in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

	Percent of Observations						
	Tree height (m)						
Species	0-10.4	10.5-16.4	16.5-22.4	22.5-28.4	≥28.5	Between[1]	U/A[2]
Downy woodpecker							
Thinned 1 (n=39)	0.0	5.0	35.0	37.5	22.5	ns	**
Unthinned 1 (n=23)	0.0	8.7	52.2	17.4	21.7		**
Eastern wood-pewee							
Thinned 1 (n=97)	3.1	9.3	38.1	38.1	11.3	*	**
Unthinned 1 (n=79)	15.2	13.9	44.3	21.5	5.1		**
Thinned 3 (n=80)	5.0	26.3	55.0	13.8	0.0	*	*
Unthinned 3 (n=56)	17.9	12.5	30.4	30.4	8.9		*

Table 16. Continued.

	Percent of Observations						
	Tree height (m)						
Species	0-10.4	10.5-16.4	16.5-22.4	22.5-28.4	≥28.5	Between	U/A
White-breasted nuthatch							
Thinned 1 (n=45)	0.0	0.0	28.9	48.9	22.2	ns	**
Unthinned 1 (n=78)	1.3	14.1	38.5	30.8	15.4		**
Thinned 3 (n=122)	0.8	16.4	57.4	20.5	4.9	ns	**
Unthinned 3 (n=62)	0.0	8.1	54.8	25.8	11.3		**
Solitary vireo							
Thinned 3 (n=28)	7.1	14.3	46.4	32.1	0.0	ns	**
Unthinned 3 (n=40)	12.5	17.5	17.5	50.0	2.5		**
Red-eyed vireo							
Thinned 1 (n=74)	1.4	5.4	29.7	48.6	14.9	ns	**
Unthinned 1 (n=41)	9.8	14.6	34.1	39.0	2.4		*
Thinned 3 (n=80)	8.8	23.8	51.3	16.3	0.0	ns	*
Unthinned 3 (n=61)	1.6	13.1	50.8	31.1	3.3		**

Table 16. Continued.

	Percent of Observations						
	Tree height (m)						
Species	0-10.4	10.5-16.4	16.5-22.4	22.5-28.4	≥28.5	Between	U/A
Blackburnian warbler							
Thinned 3 (n=31)	6.5	12.9	58.1	22.6	0.0	ns	**
Unthinned 3 (n=33)	0.0	6.1	48.5	42.4	3.0		**
Scarlet tanager							
Thinned 1 (n=68)	2.9	10.3	35.3	41.2	10.3	*	*
Unthinned 1 (n=61)	4.8	37.1	32.3	22.6	3.2		**
Thinned 3 (n=38)	0.0	36.8	39.5	23.7	0.0	ns	ns
Unthinned 3 (n=68)	4.3	18.6	50.0	24.3	2.8		ns

[1]Significance (*P < 0.05, **P < 0.01) of Kolmogorov-Smirnov test-of-independence by species on distribution of observations across tree height classes between respective thinned and unthinned stand.

[2]Significance (*P < 0.05, **P < 0.01) of Kolmogorov-Smirnov goodness-of-fit test by species on observed use and expected use of tree height classes within a stand.

Table 17. Spearman correlation coefficients (r) of bird foraging height and tree height in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia. All coefficients significant at $\underline{P} < 0.0005$.

Bird species	Thinned 1	Unthinned 1	Thinned 3	Unthinned 3
Downy woodpecker	0.58	0.79		
Eastern wood-pewee	0.49	0.46	0.70	0.77
White-breasted nuthatch	0.54	0.60	0.47	0.43
Solitary vireo			0.83	0.89
Red-eyed vireo	0.77	0.69	0.78	0.77
Blackburnian warbler			0.82	0.57
Scarlet tanager	0.67	0.73	0.83[1]	0.60

[1]Correlation coefficient different between respective thinned and unthinned stand, $\underline{t}$-test, $\underline{P} < 0.02$.

Table 18. Distribution of foraging bird observations among six dbh classes in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

	Percent of Observations								
	DBH class (cm)								
Species	3-8	8-15	15-23	23-38	38-53	>53	Between[1]	U/A[2]	U/A[3]
Downy woodpecker									
Thinned 1 (n=39)	0.0	0.0	7.7	35.9	56.4	0.0	*	**	ns
Unthinned 1 (n=23)	0.0	0.0	21.7	60.9	17.4	0.0		**	ns
Eastern wood-pewee									
Thinned 1 (n=97)	1.0	7.2	10.3	43.3	35.1	3.1	**	**	ns
Unthinned 1 (n=79)	5.1	13.9	34.2	34.2	11.4	1.3		**	ns
Thinned 3 (n=80)	2.5	7.5	22.5	51.3	11.2	5.1	ns	**	ns
Unthinned 3 (n=56)	7.1	21.4	16.1	26.8	17.9	10.8		**	ns

Table 18. Continued.

Species	DBH class (cm)								
	3-8	8-15	15-23	23-38	38-53	>53	Between	U/A	U/A
White-breasted nuthatch									
Thinned 1 (n=45)	0.0	0.0	4.4	46.7	37.8	11.1	*	**	ns
Unthinned 1 (n=78)	0.0	9.0	21.8	46.2	15.4	7.7		**	ns
Thinned 3 (n=122)	0.0	3.3	9.8	45.9	27.1	13.9	ns	**	**
Unthinned 3 (n=60)	0.0	5.0	6.7	45.0	38.3	5.0		*	*
Solitary vireo									
Thinned 3 (n=28)	3.6	7.1	14.3	39.3	21.4	14.3	ns	**	ns
Unthinned 3 (n=40)	15.5	20.0	5.0	47.5	15.0	0.0		**	ns
Red-eyed vireo									
Thinned 1 (n=74)	1.4	0.0	10.8	46.0	39.2	2.7	ns	**	ns
Unthinned 1 (n=40)	7.5	5.0	10.0	55.0	17.5	5.0		**	ns
Thinned 3 (n=80)	3.8	11.2	10.0	51.3	22.5	1.2	ns	**	ns
Unthinned 3 (n=61)	0.0	6.6	27.9	37.7	27.9	0.0		**	ns

Table 18. Continued.

Species	DBH class (cm)								
	3-8	8-15	15-23	23-38	38-53	>53	Between	U/A	U/A
Blackburnian warbler									
Thinned 3 (n=31)	0.0	3.2	25.8	41.9	22.6	6.5	ns	**	ns
Unthinned 3 (n=33)	0.0	6.1	9.1	54.6	27.3	3.0		**	ns
Scarlet tanager									
Thinned 1 (n=68)	1.5	8.8	11.8	45.6	29.4	2.9	**	**	ns
Unthinned 1 (n=61)	1.6	14.8	37.7	34.4	9.8	1.6		**	ns
Thinned 3 (n=38)	0.0	10.5	18.4	34.2	26.3	10.5	ns	**	ns
Unthinned 3 (n=68)	2.9	11.8	29.4	41.2	8.8	5.9		**	**

[1]Significance (*_P_ < 0.05, **_P_ < 0.01) of Kolmogorov-Smirnov test-of-independence on distribution of observations across dbh classes between respective thinned and unthinned stands.

[2]Significance (*_P_ < 0.05, **_P_ < 0.01) of Kolmogorov-Smirnov goodness-of-fit test on observed use and expected use based on stem density availability within a stand.

[3]Significance (*_P_ < 0.05, **_P_ < 0.01) of Kolmogorov-Smirnov goodness-of-fit test on observed use and expected use based on basal area availability within a stand.

Table 19. Distribution of foraging bird observations among eight tree species classes in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia.

Species	Percent of Observations									
	Tree species									
	Red maple	Conifer	White oak	Scarlet oak	Chestnut oak	Red oak	Black oak	Other	Between[1]	U/A[2]
Downy woodpecker										
Thinned 1 (n=39)	0.0	0.0	48.7	25.6	12.8	2.6	5.1	5.1	*	***
Unthinned 1 (n=23)	0.0	4.4	30.4	8.7	52.2	0.0	4.4	0.0		***
Eastern wood-pewee										
Thinned 1 (n=97)	1.0	3.1	48.5	26.8	11.3	0.0	4.1	5.2	***	***
Unthinned 1 (n=79)	2.5	1.3	39.2	8.9	38.0	1.3	2.5	6.3		***
Thinned 3 (n=80)	3.8	2.5	23.8	26.3	20.0	12.5	0.0	10.0	***	***
Unthinned 3 (n=56)	25.0	0.0	8.9	5.4	28.6	21.4	0.0	10.7		***

Table 19. Continued.

	Percent of Observations									
	Tree species									
Species	Red maple	Conifer	White oak	Scarlet oak	Chestnut oak	Red oak	Black oak	Other	Between	U/A
White-breasted nuthatch										
Thinned 1 (n=45)	0.0	2.2	28.9	24.4	15.6	0.0	26.7	2.2	***	***
Unthinned 1 (n=78)	2.6	6.4	29.5	2.6	48.7	7.7	0.0	2.6		***
Thinned 3 (n=122)	2.5	0.0	36.9	21.3	12.3	10.7	1.6	14.8	**	***
Unthinned 3 (n=62)	1.7	0.0	26.7	0.0	40.0	8.3	10.0	13.3		***
Solitary vireo										
Thinned 3 (n=28)	0.0	3.6	21.4	17.9	14.3	17.9	14.3	10.7	*	ns
Unthinned 3 (n=40)	27.5	0.0	12.5	2.5	12.5	35.0	0.0	10.0		**

Table 19. Continued.

	Percent of Observations									
	Tree species									
Species	Red maple	Conifer	White oak	Scarlet oak	Chestnut oak	Red oak	Black oak	Other	Between	U/A
Red-eyed vireo										
Thinned 1 (n=74)	1.4	0.0	39.2	18.9	13.5	1.4	13.5	12.2	ns	***
Unthinned 1 (n=40)	5.0	0.0	45.0	7.5	25.0	2.5	2.5	12.5		***
Thinned 3 (n=80)	7.5	1.3	31.3	16.3	16.3	8.7	13.7	5.0	***	***
Unthinned 3 (n=62)	27.9	0.0	11.5	3.3	19.7	31.2	1.6	4.9		ns
Blackburnian warbler										
Thinned 3 (n=31)	3.2	12.9	25.8	25.8	9.7	9.7	9.7	3.2	ns	ns
Unthinned 3 (n=33)	12.1	9.1	24.2	6.1	21.2	15.2	6.1	6.1		***

Table 19. Continued.

Species	Red maple	Conifer	White oak	Scarlet oak	Chestnut oak	Red oak	Black oak	Other	Between	U/A
	Percent of Observations									
	Tree species									
Scarlet tanager										
Thinned 1 (n=68)	2.9	1.5	30.9	16.2	20.6	5.9	11.8	10.3	*	***
Unthinned 1 (n=61)	3.3	0.0	49.2	4.9	31.2	1.6	1.6	8.2		***
Thinned 3 (n=38)	0.0	0.0	18.4	26.3	5.3	31.6	2.6	15.8	***	***
Unthinned 3 (n=68)	22.1	0.0	19.1	2.9	19.1	14.7	10.3	11.8		***

[1]Significance (**P* < 0.05, ***P* < 0.01, ****P* < 0.001) of G test-of-independence by species comparing frequency of observations among tree species classes between respective thinned and unthinned stands.

[2]Significance (**P* < 0.05, ***P* < 0.01, ****P* < 0.001) of G goodness-of-fit test comparing frequency of use of tree species classes against expected use by bird species within a stand.

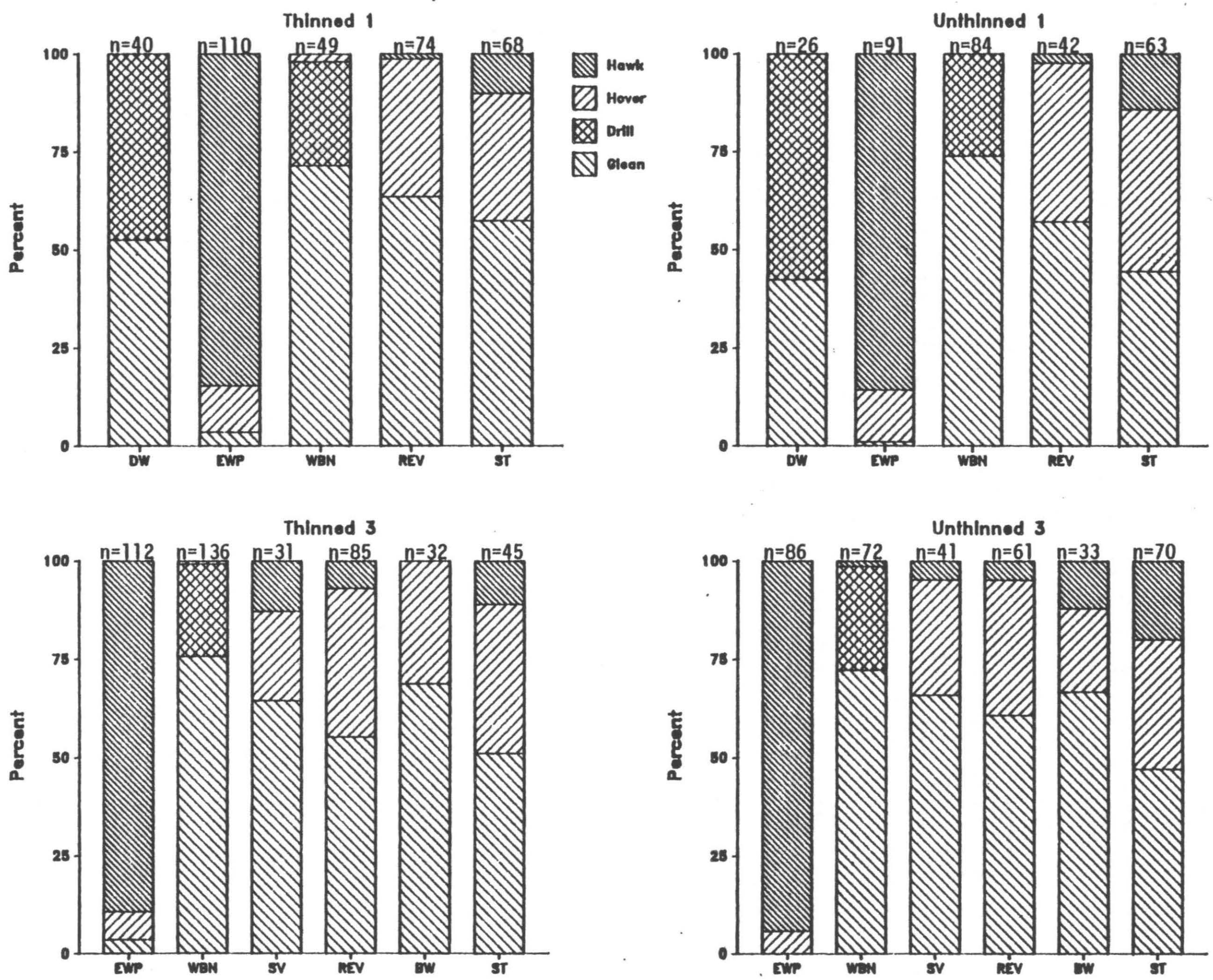

Fig. 5. Foraging methods used by birds in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia. Species acronyms are: Downy Woodpecker (DW), Eastern Wood-pewee (EWP), White-breasted Nuthatch (WBN), Solitary Vireo (SV), Red-eyed Vireo (REV), and Scarlet Tanager (ST).

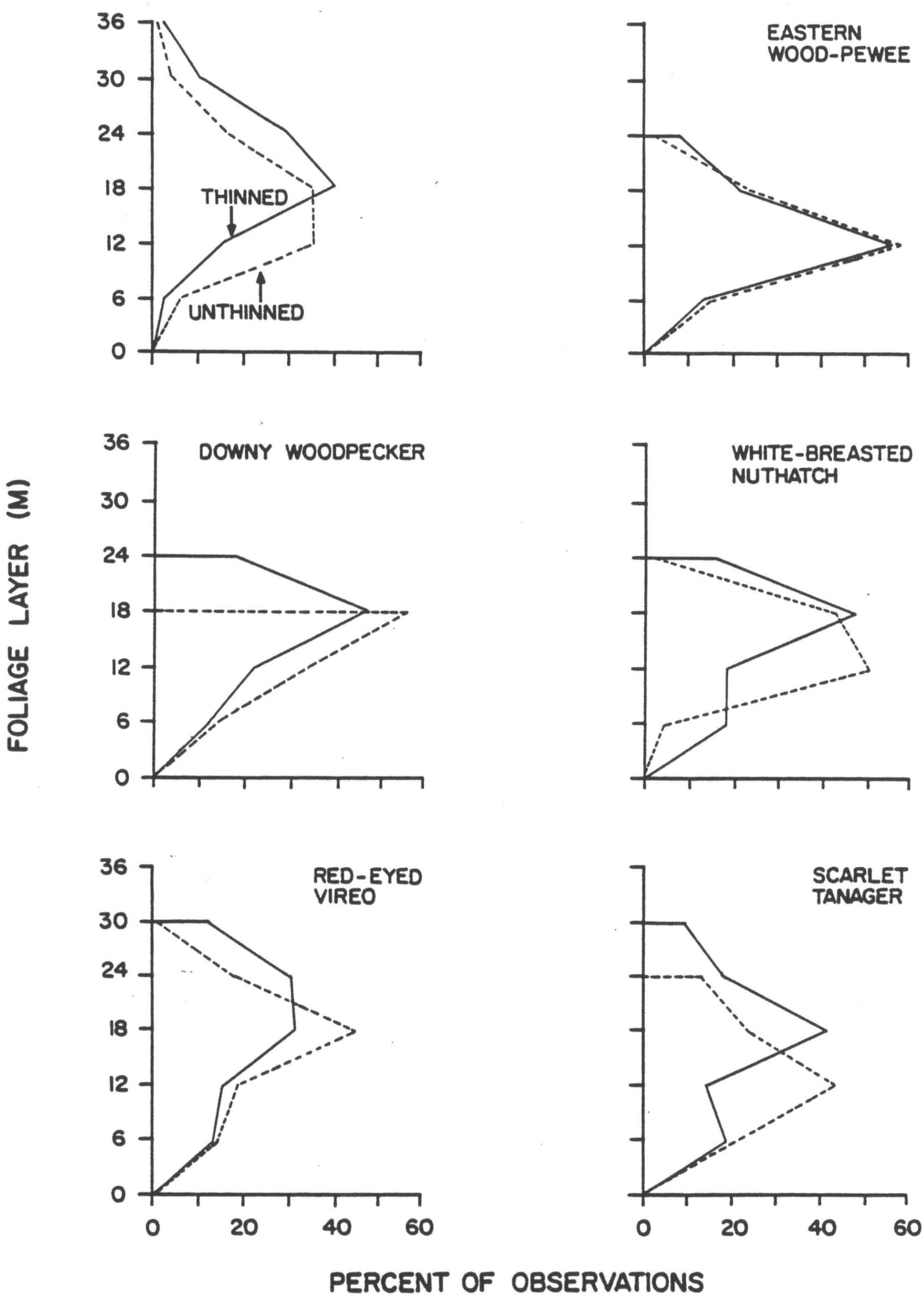

Fig. 6. Foliage layer profile and distribution of foraging observations by bird species among 6 foliage layers at stands Thinned 1 (solid line) and Unthinned 1 (broken line), mixed-hardwood forest, southwestern Virginia.

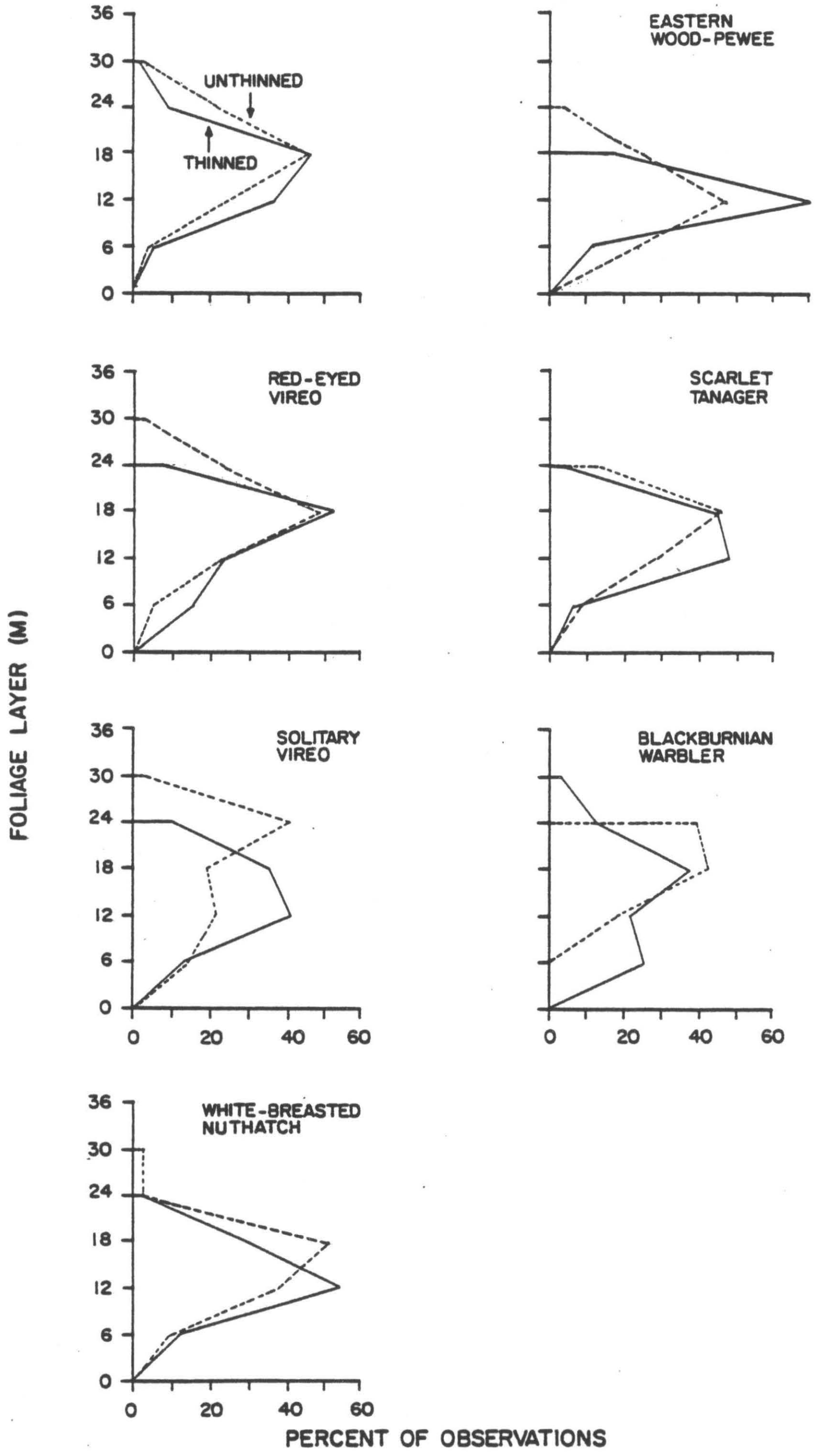

Fig. 7. Foliage layer profile and distribution of foraging observations by bird species among 6 foliage layers at stands Thinned 3 (solid line) and Unthinned 3 (broken line), mixed-hardwood forest, southwestern Virginia.

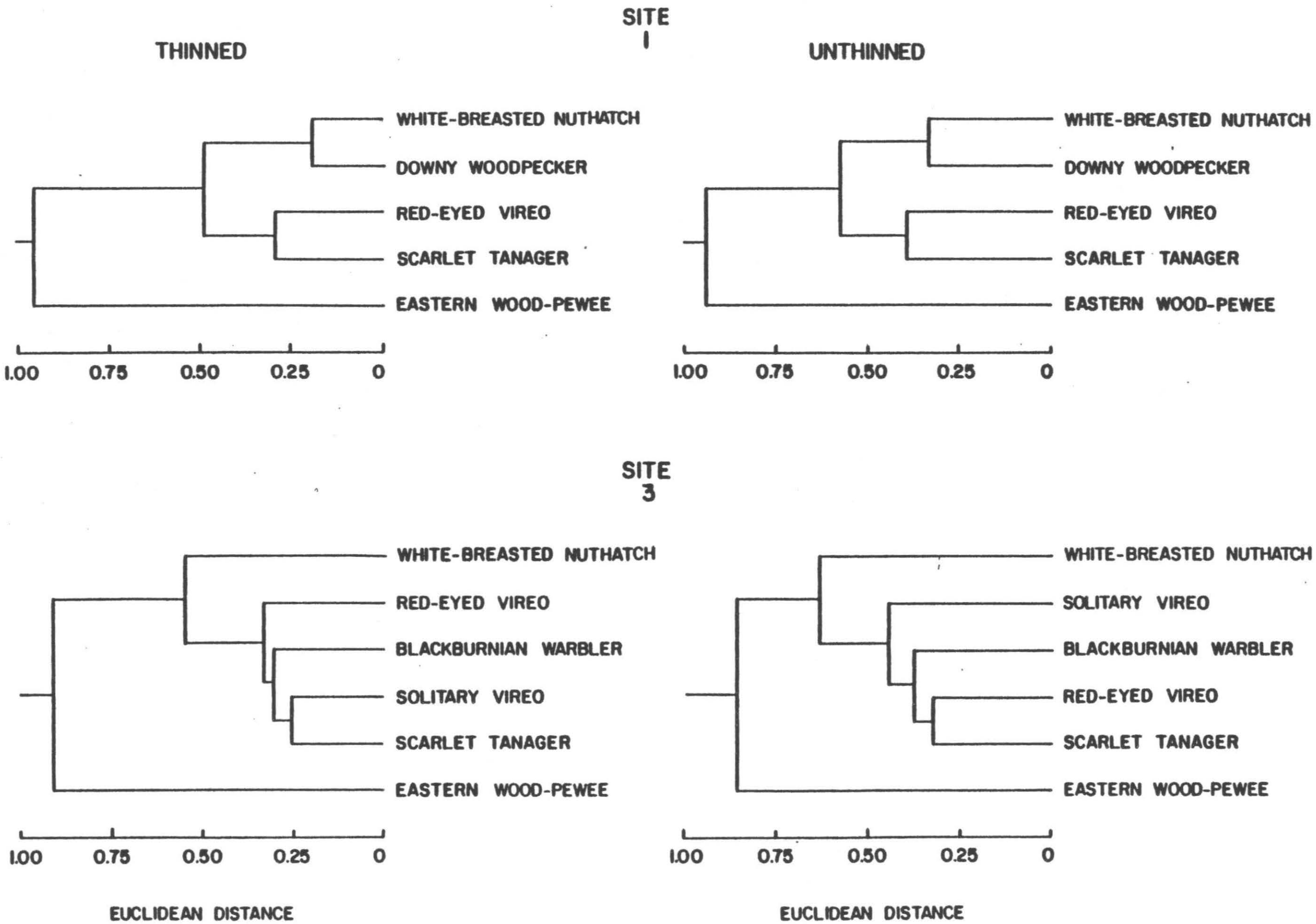

Fig. 8. Dendrogram based on Euclidean distances of similarities in 18 foraging states for birds in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia. See Appendix C for description of the foraging states.

SECTION IV

CONCLUSIONS

The purpose of this study was to assess the impact of thinning practices on avifauna in Appalachian mixed-hardwood forests. I tested the general hypothesis that differences in vegetation structure and composition between thinned and unthinned stands did not result in differences in avian population densities, habitat use, and foraging ecology. Thinning alters vegetation structure, and it is the differences in stand structure that should result in differences in avian population densities and habitat use.

Thinned stands differed from unthinned stands in several respects. Thinned stands generally had higher densities of shrubs, more ground cover, and more diverse foliage than unthinned stands. Thinned stands also had lower densities of snags, saplings, and trees of all dbh classes than unthinned stands. Canopy cover and foliage volumes were lower in thinned stands.

Three vegetation gradients were important in ordinating the sampling stations. The first gradient represented a continuum from sites with low basal areas and maple tree densities and a dense shrub/sapling layer to sites with high basal areas and maple tree densities and an open shrub/sapling layer. The second gradient ordinated the stations from those with tall trees and dense upper canopies with open understories to areas with short trees, relatively open upper canopies and dense understories. The third gradient represented a continuum from sites with high densities of snags and medium-sized trees with low hickory densities to those with high hickory densities and low snag and medium-sized tree densities.

Most bird species had either no population density differences or inconsistent differences between thinned and unthinned stands. These species were at low, medium, and high densities. Population densities were higher at thinned stands than unthinned stands for most understory species, as well as eastern wood-pewees and wood thrush. Blackburnian warbler population density was lower at one thinned stand compared to one unthinned stand.

Thirteen bird species were placed in three general habitat use groups based on similarities in population differences and results of principal components, discriminant function, and multiple linear regression analyses. The shrub/conifer group used areas with high densities of shrubs and conifers and open ground cover. The generalist group were found in a variety of deciduous sites with low conifer densities, moderate shrub densities, and dense upper canopies. The mature/deciduous species were present at sites with tall deciduous trees, high basal areas, moderate shrub densities, open subcanopies, and closed upper canopies. The habitat variables most consistently significant in separating species presence and absence were conifer density, shrub density, snag density, and ground cover.

I found no differences in the foraging methods used or foraging niche breadth of selected species in thinned or unthinned stands. There were no differences in the species' foraging niche overlap betweeen thinned and unthinned stands. I detected differences in heights of trees used and bird foraging height between stands. However, these differences were due to tree height differences between the stands. White-breasted nuthatches and downy woodpeckers used taller than average tree in stands with relatively short trees.

For most species, resource use for foraging was equal to availability of foliage volume, dbh class basal area, and tree height classes. I found differences in resource class use between thinned and unthinned stands. However, I attributed these differences to inherent vegetation differences between thinned and unthinned stands, and not ecological or ethological compensation by foraging birds.

Short, small diameter trees were rarely used for foraging. White oak, chestnut oak, scarlet oak, and northern red oak were most frequently used, often in greater proportion than their availability. Red maple and conifers had consistently low use compared to availability.

Based on these results, I concluded that: (1) thinning of the magnitude studied had little negative impact on the foraging ecology of selected species, (2) in thinned stands, most species did not have different population densities than in unthinned stands, (3) shrub/understory species had higher population densities in thinned stands, (4) canopy-dwelling species had inconsistent density differences between thinned and unthinned stands, and careful consideration must be given to their populations when planning thinning activities, and (5) habitat preferences of a species dictates whether a particular silvicultural practice in a given habitat will result in a population change.

Thinning provides forest managers many opportunities to manipulate forest vegetation to improve avian habitat. However, these habitat improvements are temporary because thinning is done prior to regeneration harvests which revert the stand to a seedling stage. By creating a diversity of mature forest cover types, forest managers can maintain populations and diversity of avifauna dependent on late-successional vegetational stages.

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APPENDICES

Appendix A. Common and scientific names of breeding birds in the mixed-hardwood forest, Montgomery and Giles Counties, Virginia, 1984-85. An asterisk (*) indicates that breeding was verified with either an active nest found or adults observed feeding dependent young.

Common name	Scientific name
Black vulture	Coragyps atratus
Turkey vulture	Cathartes aura
Sharp-shinned hawk	Accipiter striatus
Cooper's hawk	Accipiter cooperii
Red-shouldered hawk	Buteo lineatus
Broad-winged hawk	Buteo platypterus
Red-tailed hawk	Buteo jamaicensis
Ruffed grouse*	Bonasa umbellus
Wild turkey*	Meleagris gallopavo
Mourning dove*	Zenaida macroura
Yellow-billed cuckoo	Coccyzus americanus
Black-billed cuckoo	Coccyzus erythropthalmus
Eastern screech-owl	Otus asio
Great horned owl	Bubo virginianus
Barred owl	Strix varia
Whip-poor-will*	Caprimulgus vociferus
Chimney swift	Chaetura pelagica
Ruby-throated hummingbird*	Archilochus colubris
Belted kingfisher	Ceryle alcyon
Red-bellied woodpecker	Melanerpes carolinus
Downy woodpecker*	Picoides pubescens
Hairy woodpecker*	Picoides villosus
Northern flicker*	Colaptes auratus
Pileated woodpecker*	Dryocopus pileatus
Eastern wood-pewee*	Contopus virens
Acadian flycatcher	Empidonax virescens
Eastern phoebe*	Sayornis phoebe
Great crested flycatcher*	Myiarchus crinitus
Eastern kingbird	Tyrannus tyrannus
Blue jay	Cyanocitta cristata
American crow	Corvus brachyrhynchos
Common raven	Corvus corax

Appendix A. Continued.

Common name	Scientific name
Black-capped chickadee	_Parus atricapillus_
Carolina chickadee	_Parus carolinensis_
Tufted titmouse*	_Parus bicolor_
White-breasted nuthatch*	_Sitta carolinensis_
Carolina wren*	_Thryothorus ludovicianus_
Blue-gray gnatcatcher*	_Polioptila caerulea_
Eastern bluebird*	_Sialia sialis_
Wood thrush*	_Hylocichla mustelina_
American robin*	_Turdus migratorius_
Gray catbird	_Dumetella carolinensis_
Brown thrasher	_Toxostoma rufum_
Cedar waxwing	_Bombycilla cedrorum_
European starling*	_Sturnus vulgaris_
White-eyed vireo*	_Vireo griseus_
Solitary vireo*	_Vireo solitarius_
Yellow-throated vireo*	_Vireo flavifrons_
Red-eyed vireo*	_Vireo olivaceus_
Golden-winged warbler	_Vermivora chrysoptera_
Northern parula	_Parula americana_
Chestnut-sided warbler	_Dendroica pensylvanica_
Black-throated blue warbler	_Dendroica caerulescens_
Blackburnian warbler*	_Dendroica fusca_
Pine warbler*	_Dendroica pinus_
Prairie warbler*	_Dendroica discolor_
Cerulean warbler	_Dendroica cerulea_
Black-and-white warbler*	_Mniotilta varia_
American redstart*	_Setophaga ruticilla_
Worm-eating warbler*	_Helmitheros vermivorus_
Ovenbird*	_Seiurus aurocapillus_
Louisiana waterthrush*	_Seiurus motacilla_
Kentucky warbler	_Oporornis formosus_
Hooded warbler*	_Wilsonia citrina_
Canada warbler	_Wilsonia canadensis_
Yellow-breasted chat*	_Icteria virens_

Appendix A. Continued.

Common name	Scientific name
Scarlet tanager*	*Piranga olivacea*
Northern cardinal*	*Cardinalis cardinalis*
Rose-breasted grosbeak*	*Pheucticus ludovicianus*
Indigo bunting*	*Passerina cyanea*
Rufous-sided towhee*	*Pipilo erythrophthalmus*
Field sparrow*	*Spizella pusilla*
Dark-eyed junco*	*Junco hyemalis*
Brown-headed cowbird*	*Molothrus ater*
Red crossbill	*Loxia curvirostra*
American goldfinch	*Carduelis tristis*

Appendix B. Mean (SE) of 22 habitat variables from stations where selected avian species where present in three thinned and three unthinned mixed-hardwood forest stands, southwestern Virginia, 1984-85.

Variable	Eastern wood-pewee N=128	Tufted titmouse N=61	White-breasted nuthatch N=73	Blue-gray gnatcatcher N=94	Wood thrush N=38	Solitary vireo N=51	Red-eyed vireo N=151
Tree basal area (m^2/ha)	27.6(0.8)	26.4(1.0)	28.7(1.1)	27.7(0.8)	27.3(1.4)	28.1(1.2)	28.8(0.7)
Trees 3-8 cm dbh/ha	492(24)	687(45)	461(25)	646(29)	614(54)	443(36)	547(23)
Trees 8-15 cm dbh/ha	204(11)	263(18)	192(14)	250(14)	239(18)	217(17)	230(11)
Trees 15-38 cm dbh/ha	292(12)	298(15)	290(14)	303(10)	276(21)	312(15)	310(10)
Trees 38-69 cm dbh/ha	52(4)	41(5)	59(5)	47(4)	51(7)	47(6)	54(4)
Snags ≥8 cm dbh/ha	89(7)	61(7)	86(10)	61(5)	57(7)	115(13)	87(7)
Shrubs/ha	6,200(444)	7,879(623)	5,731(560)	7,174(390)	8,053(863)	4,132(587)	5,918(381)
Total foliage volume (m^3/ha $x10^5$)	7.56(0.58)	8.12(0.96)	10.29(1.68)	8.45(0.77)	7.08(0.82)	7.40(0.64)	9.28(0.89)
Foliage volume 0-6 m (m^3/ha $x10^4$)	1.46(0.22)	3.26(0.64)	3.17(0.86)	3.37(0.56)	2.00(0.39)	2.05(0.63)	3.51(0.59)
Foliage volume 6-18 m (m^3/ha $x10^5$)	4.86(0.40)	5.29(0.63)	6.33(0.84)	5.25(0.51)	4.73(0.64)	5.45(0.53)	5.59(0.45)
Foliage volume >18 m (m^3/ha $x10^5$)	2.55(0.34)	2.51(0.53)	3.64(0.92)	2.87(0.47)	2.15(0.44)	1.74(0.33)	3.34(0.54)
Foliage height diversity (H')	0.49(0.02)	0.54(0.03)	0.55(0.03)	0.55(0.02)	0.53(0.04)	0.48(0.03)	0.53(0.02)
Maple saplings/ha	147(14)	150(16)	137(14)	168(14)	151(18)	166(28)	179(13)
Maple trees/ha	97(11)	56(9)	113(16)	64(8)	74(14)	182(22)	116(11)
Oak saplings/ha	54(8)	110(16)	59(10)	89(9)	61(14)	24(7)	62(7)
Oak trees/ha	346(14)	327(24)	332(16)	351(16)	322(27)	309(16)	345(13)
Hickory saplings/ha	34(5)	41(7)	27(5)	46(6)	40(8)	11(4)	40(5)
Hickory trees/ha	23(4)	44(9)	23(4)	33(5)	33(8)	8(3)	32(5)
Coniferous trees/ha	27(6)	123(18)	23(7)	102(13)	84(21)	17(6)	50(8)
Canopy cover (%)	84.5(1.0)	87.8(1.3)	85.2(1.4)	87.7(1.2)	89.4(1.5)	83.9(1.9)	87.0(0.9)
Tree height (m)	17.7(0.3)	16.9(0.5)	17.7(0.5)	17.2(0.4)	17.1(0.6)	16.8(0.4)	17.5(0.3)
Ground cover 0-0.3 m (%)	72.2(1.9)	62.6(3.4)	74.7(2.3)	63.2(2.6)	66.1(4.2)	67.3(2.0)	67.3(2.0)

Appendix B. Continued.

Variable	Black-and-white warbler N=45	Worm-eating warbler N=51	Blackburnian warbler N=57	Ovenbird N=197	Hooded warbler N=63	Scarlet tanager N=118
Tree basal area (m^2/ha)	27.6(1.3)	29.0(1.2)	29.6(1.0)	26.9(0.6)	26.4(1.1)	28.1(0.8)
Trees 3-8 cm dbh/ha	499(43)	681(44)	455(28)	649(25)	768(50)	512(27)
Trees 8-15 cm dbh/ha	217(19)	249(17)	242(15)	264(10)	252(16)	229(11)
Trees 15-38 cm dbh/ha	299(19)	275(16)	321(16)	307(9)	304(17)	310(11)
Trees 38-69 cm dbh/ha	47(6)	60(6)	53(4)	44(3)	39(4)	49(4)
Snags ≥8 cm dbh/ha	94(12)	59(7)	128(12)	80(5)	54(7)	97(7)
Shrubs/ha	5,894(796)	7,169(562)	4,364(524)	7,492(357)	10,021(664)	6,164(416)
Total foliage volume (m^3/ha x10^5)	6.47(0.67)	10.41(0.93)	8.08(0.84)	8.12(0.52)	7.16(0.73)	7.73(0.61)
Foliage volume 0-6 m (m^3/ha x10^4)	1.61(0.55)	3.91(1.16)	2.50(0.66)	4.41(0.58)	3.77(0.95)	2.91(0.51)
Foliage volume 6-18 m (m^3/ha x10^5)	4.50(0.43)	5.79(0.60)	5.52(0.56)	5.73(0.40)	4.47(0.55)	4.87(0.42)
Foliage volume >18 m (m^3/ha x10^5)	1.81(0.41)	4.23(0.76)	2.31(0.44)	1.95(0.22)	2.31(0.38)	2.57(0.38)
Foliage height diversity (H')	0.47(0.03)	0.57(0.02)	0.47(0.03)	0.50(0.02)	0.54(0.03)	0.50(0.02)
Maple saplings/ha	137(21)	204(20)	151(15)	157(10)	161(15)	128(11)
Maple trees/ha	101(20)	85(14)	174(17)	77(8)	47(7)	104(13)
Oak saplings/ha	84(19)	97(16)	25(7)	108(10)	104(17)	74(10)
Oak trees/ha	368(25)	307(23)	331(16)	367(13)	336(23)	350(15)
Hickory saplings/ha	27(6)	37(7)	25(9)	38(4)	21(4)	40(5)
Hickory trees/ha	23(6)	39(9)	14(5)	25(4)	17(4)	29(5)
Coniferous trees/ha	27(9)	81(15)	32(11)	96(9)	124(17)	50(10)
Canopy cover (%)	84.8(1.8)	89.1(1.7)	85.7(1.7)	86.9(0.8)	86.0(1.3)	86.7(1.0)
Tree height (m)	17.3(0.5)	18.7(0.6)	17.0(0.5)	16.3(0.3)	17.0(0.5)	17.4(0.3)
Ground cover 0-0.3 m (%)	77.1(3.0)	59.0(4.2)	76.1(2.6)	68.2(1.8)	79.4(2.3)	72.2(2.2)

Appendix C. Resource states used to calculate foraging niche breadth and niche overlap for birds in thinned and unthinned mixed-hardwood forest stands, southwestern Virginia. The foraging states were derived by combining the 4 foraging methods with substrate parts and/or tree locations to create a vector of 18 mutually exclusive categories.

Foraging States	
Hawk tree	Drill wood proximal
Glean trunk	Hover wood distal
Drill trunk	Hover wood proximal
Hover trunk	Hover leaf distal
Glean wood distal	Hover leaf proximal
Glean wood proximal	Glean snag
Glean leaf distal	Drill snag
Glean leaf proximal	Hover snag
Drill wood distal	Hawk snag

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