SONGBIRD POPULATION RESPONSE TO SILVICULTURAL PRACTICES IN CENTRAL APPALACHIAN HARDWOODS

H. S. CRAWFORD, Northeastern Forest Experiment Station, USDA Forest Service, Orono, ME 04469
R. G. HOOPER, Southeastern Forest Experiment Station, USDA Forest Service, Charleston, SC 29401
R. W. TITTERINGTON,[1] School of Forest Resources, University of Maine, Orono, ME 04469

Abstract: In central Appalachian hardwood stands songbirds were classified into groups of species that selected territories with similar habitat features. The degree of canopy closure of trees >7.3 m tall and the density of vegetation <1.8 m tall were the most important habitat features. Discriminant analysis was used to separate bird species into 5 groups based on habitat selection: (1) closed-canopy-obligatory species included the ovenbird (*Seiurus aurocapillus*), white-breasted nuthatch (*Sitta carolinensis*), wood thrush (*Hylocichla mustelina*), and American redstart (*Setophaga ruticilla*); (2) species skewed toward closed canopy were the black-and-white warbler (*Mniotilta varia*), Carolina chickadee (*Parus carolinensis*), cardinal (*Cardinalis cardinalis*), hooded warbler (*Wilsonia citrina*), red-eyed vireo (*Vireo olivaceus*), scarlet tanager (*Piranga olivacea*), tufted titmouse (*Parus bicolor*), and blue-gray gnatcatcher (*Polioptila caerulea*); (3) centrally distributed species included the eastern wood pewee (*Contopus virens*) and great crested flycatcher (*Myiarchus crinitus*); (4) species skewed toward open canopy were the Carolina wren (*Thryothorus ludovicianus*), rufous-sided towhee (*Pipilo erythrophthalmus*), and indigo bunting (*Passerina cyanea*); and (5) obligatory open-canopy species included the yellow-breasted chat (*Icteria virens*), field sparrow (*Spizella pusilla*), prairie warbler (*Dendroica discolor*), and eastern bluebird (*Sialia sialis*). Changes in groups can be predicted by the change in configuration of overstory and understory vegetation. Bird succession following cutting generally follows sequentially from open-canopy-obligatory to closed-canopy-obligatory species; however, the initial stage depends upon the degree to which the stand was opened.

J. WILDL. MANAGE. 45(3):680–692

Habitat selection by many bird species depends, in part, on habitat structure (James 1971, Anderson and Shugart 1974, Evans 1978, Titterington et al. 1979). Descriptions of detailed relationships of birds to habitat attributes within an area may be desirable, but would be difficult to apply in land management where all resources must be considered. Conversely, information so broad that it does not distinguish species that occupy different specialized habitats may be of little practical use. Habitat variables designed to benefit land managers should be limited to those usable in management. We determined the response of 5 groups of songbirds to forest cutting practices in western Virginia by combining habitat attributes that can be translated into silvicultural practice. We classified bird species by their use of habitat features, and used discriminant analysis of habitat attributes to group species.

We appreciate the assistance of R. Harlow, C. Dachelet, and R. Conner in field sampling; S. Anderson, R. DeGraaf, and K. Evans made helpful suggestions on manuscript content.

STUDY AREA

The study was in Craig, Montgomery, and Giles counties in western Virginia. This portion of the Appalachian Mountains is made up of a series of parallel ridges separated by narrow valleys that lie along an approximate northeast–southwest axis extending from North Carolina to New England. Our study area was representative of the central portion of this physiographic province, from southwestern Virginia through central Pennsylvania. Elevations ranged from

[1] Present address: Northeastern Forest Experiment Station, Orono, ME 04469.

500 to 750 m. Lower and midslope ridge positions were in the upland oak type, with at least 50% of the basal area composed of *Quercus coccinea*, *Q. velutina*, *Q. prinus*, and *Q. alba*. Associated species included *Acer rubrum*, *Nyssa sylvatica*, *Carya* spp., *Pinus rigida*, *P. pungens*, and *P. virginiana* (Braun 1967:225–242). Site index for upland oaks was 15–21 m height growth in 50 years (Olson 1959).

METHODS

Plots of 6–15 ha totaling 115 ha in 10 plots were located in mature, pole, and regenerating stands 1–90 years old. Plots were gridded and marked at 40-m intervals. Grid points aided in mapping bird territories and served as plot centers for sampling vegetation. Plots were sampled from 1970 through 1974—birds during their breeding season and vegetation within a few weeks thereafter.

Basal coverage of herbaceous, deciduous woody, and coniferous foliage was determined in 24 equal layers to 7.3 m above ground. From each grid point a 20-m tape was placed north, south, east, and west; 24 vertical readings were made at each 2.0-m interval along the tape. A 7.3-m pole, graduated into 24 0.3-m sections and plumbed vertically, was used with the tape to describe 24 0.3×2.0-m vertical planes at each 2.0-m mark along the tape. Thus, 960 vertical planes were described around each grid intersection, 40 in each of the 24 layers. Foliage intersected by the vertical plane was projected downward to the base of the plane. A value of 1 was recorded if foliage covered more than 50% of the base. Within a layer, around a given grid point, the total basal coverage equaled the number of vertical planes with greater than 50% coverage divided by 40.

By sighting along the plumbed pole, any foliage transected by the line of sight in the layer above 7.3 m received a value of 1. These values determined percent canopy cover. Within 20 m of each grid point, the diameters of all live woody stems >6.6 cm were recorded and basal area computed. The number of dead stems and the height of the highest foliage were recorded.

The spot-mapping method (Williams 1936) was used to delineate bird territories on the plots. A minimum of 20 man hours from dawn to midmorning was spent per 5 ha. Special emphasis was placed on simultaneous registrations of conspecific males.

We analyzed the relationships between habitat characteristics and use by breeding birds with 2 multivariate statistical techniques, stepwise discriminant analysis (Eisenbeis and Avery 1972) and stepwise regression analysis (Draper and Smith 1966). Significance was set at the 0.05 level for all statistical tests. The Statistical Package for the Social Sciences (SPSS) computer program (Nie et al. 1975) was used in the analyses. A 40-m^2 plot within a breeding bird's territory was the unit of observation in the discriminant analysis (DA). Each singing male within the plot was associated with vegetation values from the same plot. We used the breeding densities of each individual species as the dependent variables in our regression analyses except where we used the square root of density to correct for a skewed population. The number of different territorial males in each of 44 2-ha plots was tallied for each bird species. We calculated a mean value for each habitat variable using measurements from 12 vegetation sampling plots located within each 2-ha plot. These mean values served as the independent variables in the stepwise regression analyses.

Table 1. Discriminant-function coefficients for separating bird species along habitat gradients.

Habitat feature	DF 1	DF 2
Vegetation <1.8 m tall	0.159	0.264
Shrubs 1.8–4.5 m tall	−0.042	0.349
Shrubs 4.6–6.7 m tall	−0.185	0.206
Percent canopy closure	−0.607	−0.226
Basal area of trees 7–22 cm dbh	−0.036	−0.888
Basal area of trees 22–36 cm dbh	0.008	−0.501
Total basal area	−0.147	1.452

We did not use regression equations for predicting bird densities in other cutover areas, but only to gain further insight into the relative importance of the habitat variables for each bird species. The results of the regression analyses were used as a supplement to the discriminant analysis, not as predictors by themselves.

RESULTS AND DISCUSSION

Discriminant analysis has been used to describe a continuum of bird species along a habitat gradient (James 1971, Smith 1977) and to show grouping of species based on habitat features (Titterington et al. 1979). We found (1) grouping of breeding bird species toward both extremes of a discriminant function of habitat variables, and (2) a continuum of species along the central portion of the axis. Both continuous and discontinuous concepts of classification or ordination were pertinent. For the purpose of making management recommendations we recognized groups of breeding bird species with the realization that response to management actions will be less rigid in some groups than in others. Our groups were selected on the basis of the range and distribution of discriminant scores. The discriminant analysis was not sensitive enough to show exclusive groups, if they exist.

The discriminant analysis indicated that 7 of the habitat variables separated the bird species according to their use of the study areas. Two discriminant functions (DF) were derived using these 7 habitat variables (Table 1).

The first discriminant function (DF 1) explained 79% of the variation in the data, and described a habitat continuum ranging from recently cutover areas at the positive end of the axis to oak stands with dense canopy closure at the negative end (Fig. 1). The most important habitat variables separating the bird species were percent canopy closure and vegetation 4.6–6.7 m tall and <1.8 m tall (Table 1). At one end of the axis we found bird species that were dependent on low, brushy areas with little or no overstory. At the other end were bird species requiring mature stands with large trees and developed understory. In between were species that used some brush, but primarily trees, and species that used brush and trees equally.

The 2nd discriminant function (DF 2) explained an additional 9% of the data variation, and represented a further division of the habitat continuum (Fig. 1). At the negative or dense canopy end of DF 1, a separation of bird species using dense stands of pole-sized (7–22 cm dbh) trees with little understory vs. mature trees with understory was described by DF 2. At the positive or open-canopy end of DF 1, DF 2 separated bird species using areas with scattered large residual trees from species using areas with pole-sized residual trees.

Closed-canopy Obligatory Species

The ovenbird, white-breasted nuthatch, wood thrush, and American redstart were restricted to stands with a closed overstory canopy. These species had a limited distribution along the axis of DF 1 (Fig. 2), showing their depen-

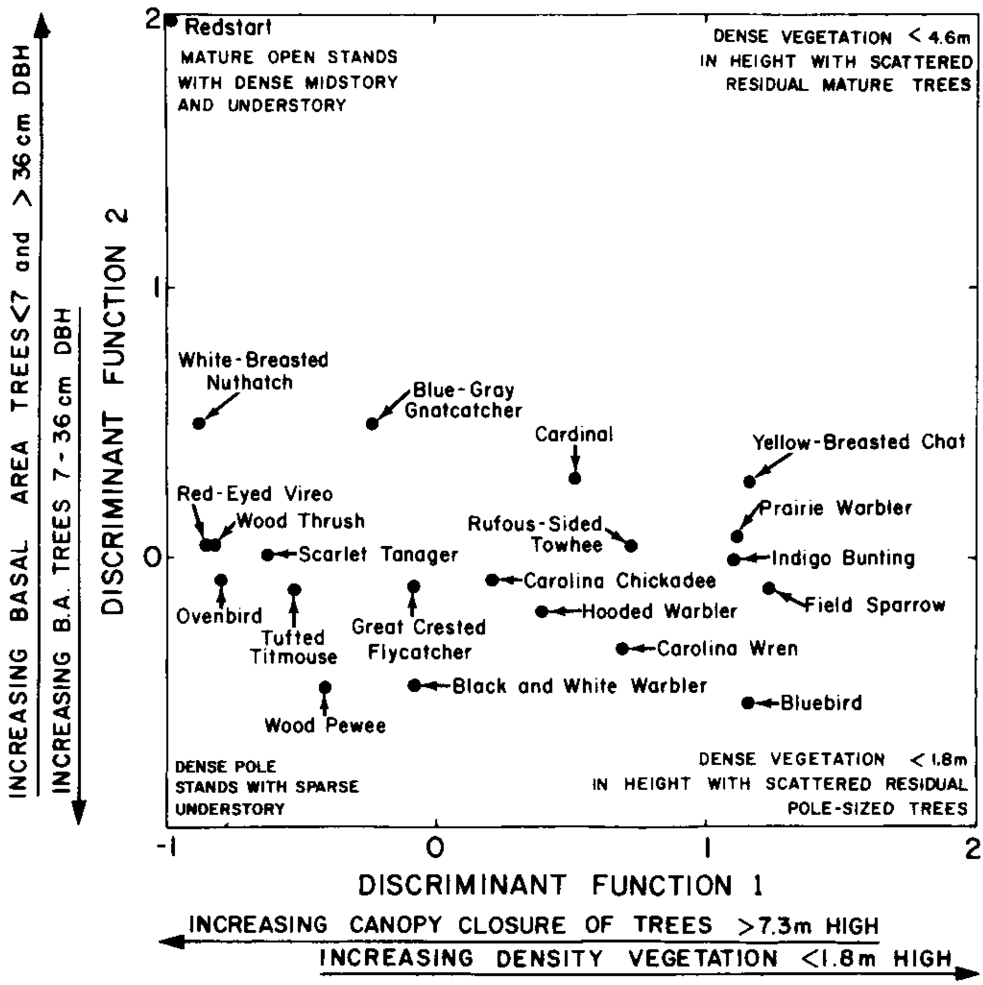

Fig. 1. Mean discriminant scores and habitat features of bird species along the 1st and 2nd discriminant-function axes.

dence on closed-canopy cover during the breeding season. However, they showed a greater latitude along the axis of DF 2, which represents a divergence from pole stands to mature trees.

Ovenbirds and wood thrushes were found more toward open-canopy conditions than were white-breasted nuthatches and redstarts. The number of breeding pairs of ovenbirds and wood thrushes regressed positively with total basal area (Table 2), which represents a canopy cover of pole and mature trees. However, we did not detect significant regressions of numbers of redstarts or nuthatches with habitat variables. Their relationship was that of presence or absence—a strongly discontinuous distribution not detectable by linear regression analyses, but seen in the abrupt right-hand boundary along the axis of DF 1 (Fig. 2). The linear relationship to a habitat variable indicates a less rigorous separation of ovenbirds and wood thrushes into the closed-canopy-

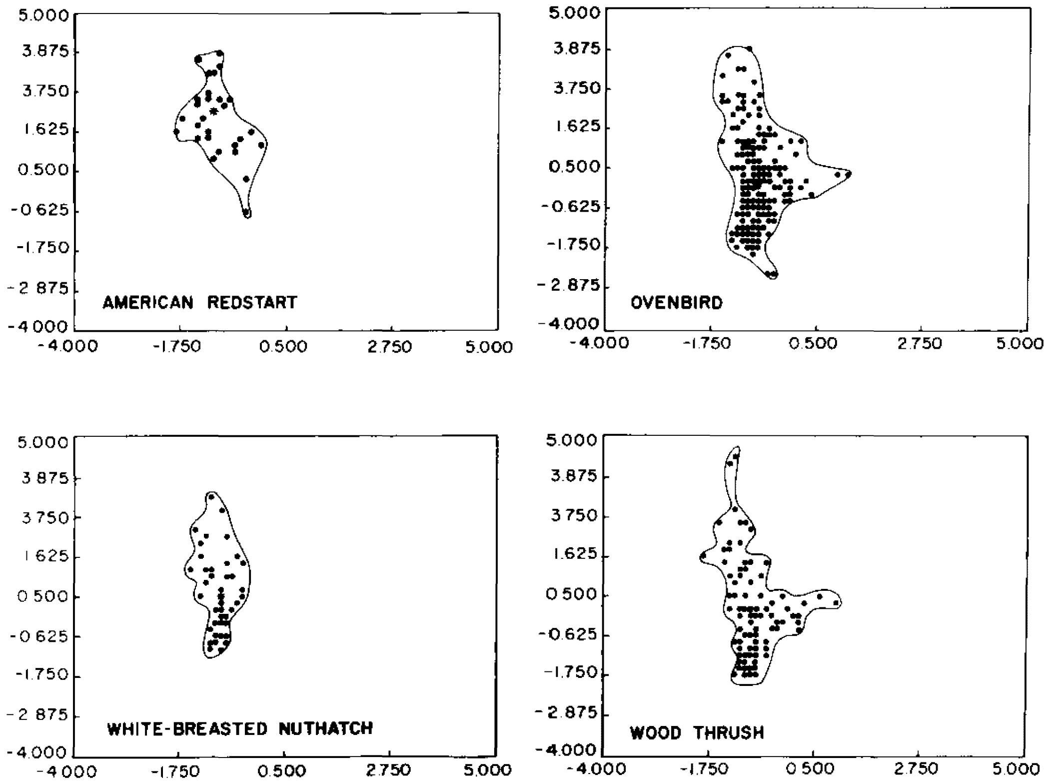

Fig. 2. Closed-canopy species. Plot of DF 1 (horizontal) vs. 2 (vertical); * indicates group mean discriminant score. More than one observation may fall at a point.

obligatory class. However, their pattern of distribution along the axes of DF 1 and 2 shows enough difference from those species classed as skewed toward closed canopy to warrant the separation.

Multiple linear regressions showed that in the presence of a direct relationship to total basal area, wood thrush density was inversely related to basal area of trees 22–36 cm dbh, and ovenbird density was inversely related to basal area of trees >70 cm (Table 2). The relationship of the additional habitat variable in the multiple regression was significant, but not as explanatory as total basal area. Wood thrushes were more abundant when the greatest proportion of total basal area was in trees >36 cm dbh (mature stands) or in trees <22 cm dbh (pole stands). Ovenbirds were more abundant when the greatest proportion of basal area was in trees <70 cm dbh.

The white-breasted nuthatch has been reported as a species of mature stands with open understory (James 1971, Anderson and Shugart 1974, Smith 1977). Our data supported these studies, but showed a distribution along the axis of DF 2 that indicated only slightly less tolerance of pole-sized stands than in the ovenbird or wood thrush. The redstart showed the least tolerance of this group toward pole-sized stands and the greatest grouping of any species in the mature-stand position of both discriminant-function axes. Our sample for the redstart was

Table 2. Regressions of bird numbers on habitat features ($P < 0.05$, $N = 44$).

Number of territorial males by species (Y)	a	b	X variable	Cumulative R^2
Wood thrush	−0.039	0.745	Total basal area	0.354
		−0.010	Basal area of stems 22–36 cm dbh	0.428
Ovenbird	−0.016	0.954	Total basal area	0.688
		−0.889	Basal area of stems >70 cm dbh	0.738
Black-and-white warbler	0.851	−0.018	Trees and shrubs 1.8–4.5 m tall	0.214
Hooded warbler	0.339	0.018	Trees and shrubs 1.8–4.5 m tall	0.230
		0.122	Basal area of stems 36–60 cm dbh	0.344
		−0.023	Total canopy cover, %	0.455
Scarlet tanager	0.156	0.098	Basal area of stems 22–36 cm dbh	0.367
Red-eyed vireo	−1.406	0.062	Basal area of stems 7–22 cm dbh	0.252
		0.305	Number of dead snags	0.444
Wood pewee	0.910	0.062	Basal area of stems 7–22 cm dbh	0.252
		−0.034	Trees and shrubs 4.6–7.3 m tall	0.348
		−0.148	Number of dead snags	0.424
Rufous-sided towhee[a]	1.732	−0.031	Total canopy cover, %	0.670
		0.030	Basal area of stems 22–36 cm dbh	0.699
Indigo bunting[a]	1.187	−0.014	Total canopy cover, %	0.509
Prairie warbler	2.397	−0.052	Total canopy cover, %	0.699
		−0.053	Trees and shrubs 4.6–7.3 m tall	0.727
		0.018	Trees and shrubs 1.8–4.5 m tall	0.758
Yellow-breasted chat	0.211	0.004	Vegetation <1.8 m tall	0.379
		0.042	Trees and shrubs 1.8–4.5 m tall	0.483
		−0.060	Trees and shrubs 4.6–7.3 m tall	0.720

[a] Square root transformation used.

limited ($N = 31$), and the species may not be as restricted to these conditions as our study indicates. Studies in more northerly latitudes (Webb et al. 1977, Crawford and Titterington 1979) indicate a different habitat. However, our classification is similar to that of James (1971), who worked at a latitude similar to ours. Her work would place the redstart slightly to the right of the other species along the axis of DF 1 rather than slightly to the left (Fig. 1), or more toward open-canopy conditions.

Closed-canopy-obligatory species will tolerate uneven-age management of forest stands. Single-tree selection (removal of mature trees as scattered individuals throughout the stand) and thinning understory trees that compete for root space will create favorable conditions for these species. Light diameter-limit cutting that removes only the best trees from the stand would be tolerated. Any intermediate or harvest cutting that opens the canopy will probably decrease populations of these birds.

Species Skewed Toward Closed Canopy

Eight species bracketed a central portion of the DF 1 axis, but were skewed toward closed-canopy stands (Fig. 3). Thus, these species are often found where overstory canopy is closed, but tolerate a moderately open canopy with a low vegetative layer.

The black-and-white warbler and Carolina chickadee were more strongly skewed toward pole stands than mature stands. Regression analysis indicated that the black-and-white warbler was responding inversely to the density of shrubs in the 1.8–4.5-m layer (Table 2). This component is largely lacking in pole stands, but is present in mature stands, as shown by DF 2 (Fig. 1). The avoidance of understory appeared only as the overstory increased in coverage. Anderson and Shugart (1974) found Carolina chickadees more frequently in areas with open, sparse understory.

The cardinal and hooded warbler showed avoidance of pole stands and preference for mature stands on both discriminant-function axes (Fig. 3). Additionally, numbers of hooded warblers were related ($P < 0.05$) to increases in (1) density of the 1.8–4.5-m-tall shrub layer that is sparse in pole stands, and (2) the basal area of 36–60-cm-dbh trees, which are components of mature stands (Table 2). A significant 3-variable regression for the hooded warbler included an inverse relationship with crown canopy when evaluated in the presence of increasing basal area of trees 36–60 cm dbh. This situation occurs as dominant trees increase in number while intermediate trees decrease, resulting in canopy opening; this condition is common to overstocked, overmature stands. This is also a characteristic of plots that border cut and uncut areas and have features of each. The number of cardinals was directly related to total vegetation <1.8 m tall. This vegetative stratum is commonly found with open canopy or under mature stands, but to a much lesser extent under pole stands. Others have shown the relation of cardinals to dense understory vegetation (Anderson and Shugart 1974).

The red-eyed vireo, scarlet tanager, tufted titmouse, and blue-gray gnatcatcher displayed a wide latitude in habitats used. They were tolerant of differences in canopy closure, as shown by their distribution along the axis of DF 1, but they were also widely distributed along the axis of DF 2, showing a tolerance of pole or mature stands. Using regression analyses, we found that the number of scarlet tanagers was directly related to basal area of intermediate-sized trees 22–36 cm dbh (Table 2).

Red-eyed vireos were directly related to total canopy and dead snags, both indicative of fully stocked to overstocked stands. This explains why the mean of discriminant score (centroid) of the scarlet tanager is below and to the right of that of the red-eyed vireo (Fig. 1). The distribution of discriminant scores for the tufted titmouse was skewed toward pole stands (Fig. 3). The centroid of the blue-gray gnatcatcher was located toward the mature stand, but we did not find a clustering of observations in any quadrant of the discriminant-function display. Our findings for these 4 species agree with those of Anderson and Shugart (1974).

Birds of this group tolerate a fairly broad range of silvicultural practices. Large clear-cuts would not maintain populations of these species, nor would intensive site preparation such as burning, disking, or any common method for seeding or planting. However, the latitude shown by these birds for openings in the canopy would permit group selection (removal of small groups of mature trees throughout the stand), small or narrow clear-cuts, thinning to remove overmature trees, cutting trees larger than a specified diameter limit, or single-tree selection. Group selection to create a mosaic of even-aged patches would provide the habitat variety to support the greatest number of birds in this group. Thinning overmature trees would benefit cardinals and hooded warblers, but may tend to lessen numbers of black-and-white warblers and Carolina chickadees if there is an increase in density of shrubs 1.8–4.5 m tall. Thinning understory trees would tend to favor the latter 2 species. Leaving dead stems standing is recommended.

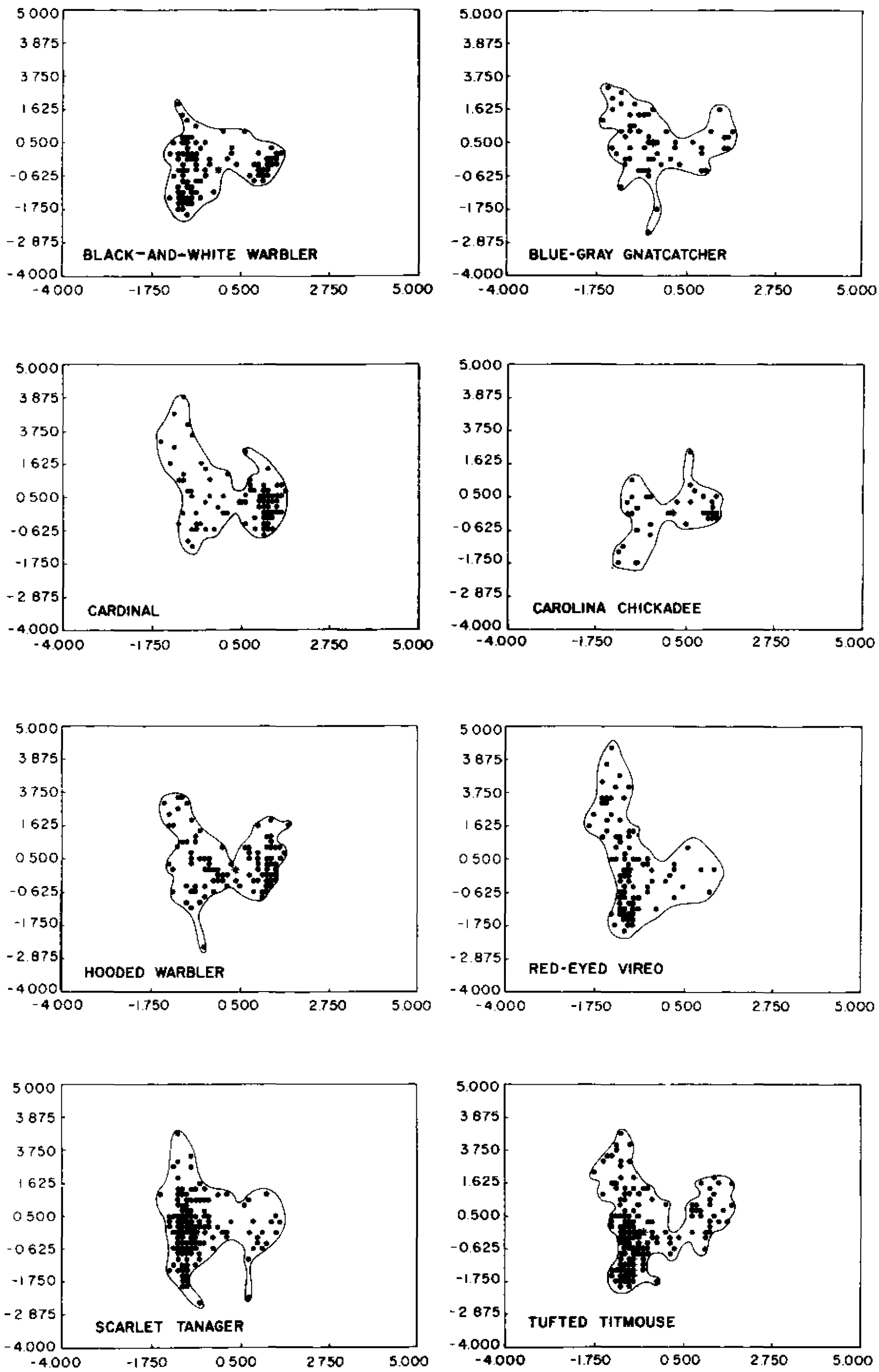

Fig. 3. Species skewed toward closed canopy. Plot of DF 1 (horizontal) vs. 2 (vertical); * indicates group mean discriminant score. More than one observation may fall at a point.

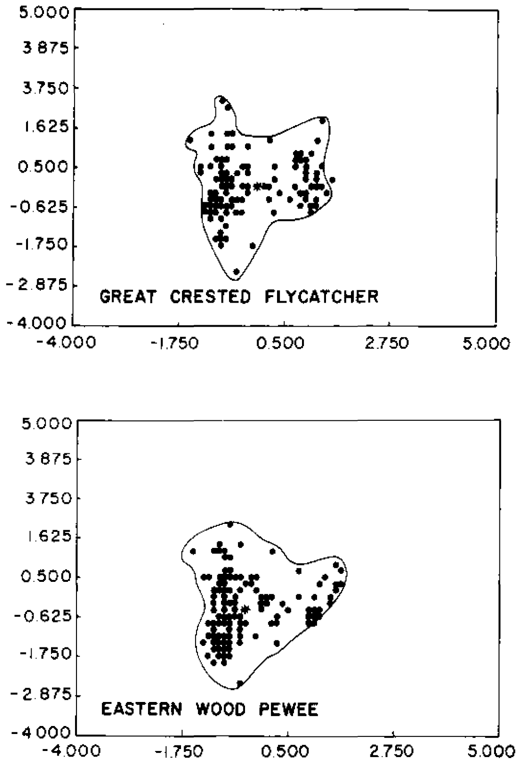

Fig. 4. Centrally distributed species. Plot of DF 1 (horizontal) vs. 2 (vertical; * indicates group mean discriminant score. More than one observation may fall at a point.

Centrally Distributed Species

The eastern wood pewee and great crested flycatcher are located approximately in the center of each discriminant-function axis, and have an essentially uniform distribution (Fig. 4). They represent intermediate canopy closure and intermediate-sized trees. Multiple regression analysis for the pewee showed numbers of birds responded (1) directly to basal area of trees 7–22 cm dbh (intermediate-sized trees), (2) inversely to the density of shrubs 4.6–7.3 m tall found in younger stands, and (3) inversely to the number of dead snags, which represent mature and overstocked stands (Table 2). Distributions of these birds do not reach the extremes of habitat conditions similar to birds exhibiting skewed distributions on the discriminant axes. Thus, although found in a variety of conditions, they are generally less common as conditions change. They do not have as much latitude in response to changes in habitats as do the skewed groups.

The extremes of harvest systems, light selection of only the largest trees or large clear-cuts, would probably decrease numbers of these 2 species. Any practice encouraging intermediate-sized stands would retain their representation. Diameter-limit cutting to remove many large stems, group selection, or scattered clear-cuts of moderate size (~10 ha) should maintain their habitat. Thinning to remove overmature trees or to remove trees less than 7 cm dbh would help create satisfactory habitat.

Species Skewed Toward Open Canopy

The Carolina wren, rufous-sided towhee, and indigo bunting were found primarily in stands with open canopy and dense understory, but also in areas where canopy closure was more complete.

The towhee displayed a strong inverse relationship with canopy cover. This relationship between the square root of the number of towhees and total canopy accounted for 67% of the variation in the regression equation (Table 2). The indigo bunting showed the same relationship, but the fit of the regression was not as good as that for the towhee. The distribution toward closed canopy was not as continuous as that for the towhee (Fig. 5). The Carolina wren showed a definite preference for brushland conditions, where it nested in brush piles. However,

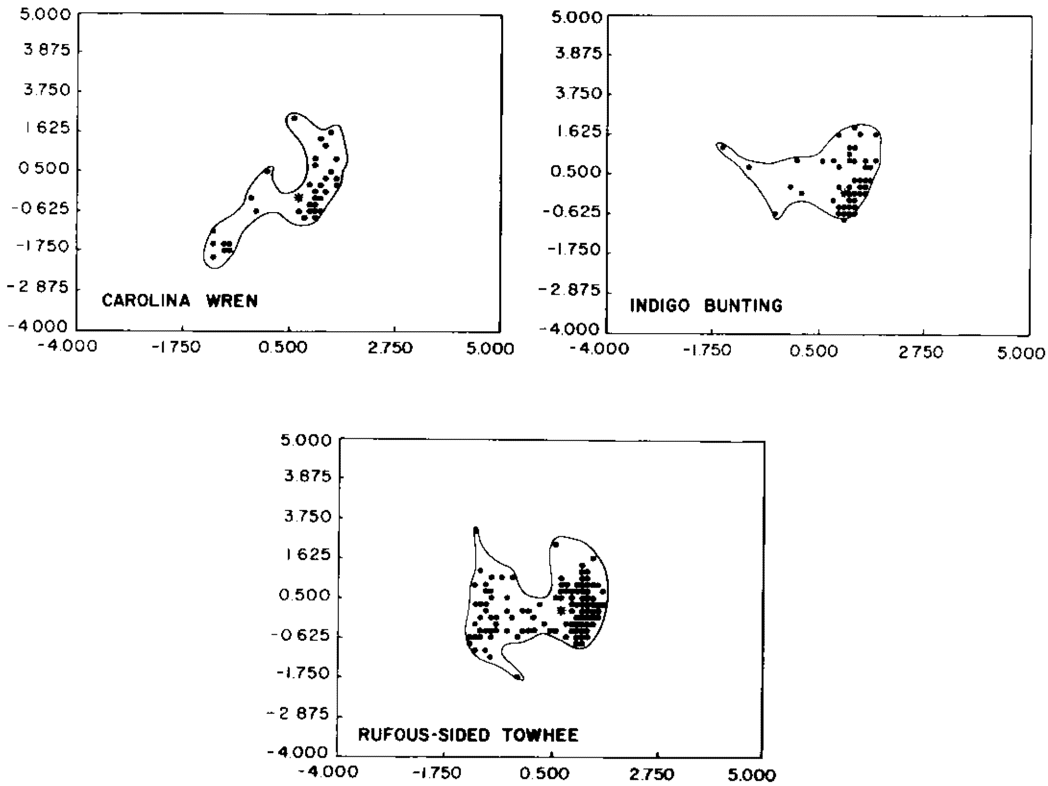

Fig. 5. Species skewed toward open canopy. Plot of DF 1 (horizontal) vs. 2 (vertical); * indicates group mean discriminant score. More than one observation may fall at a point.

it was also tolerant of pole stands with closed canopy (Fig. 5).

These species are adapted to clear-cutting because they can occupy recently cut areas and remain as woodland succession proceeds into pole stands. Small as well as large clear-cuts will support these species, but smaller cuts with a greater proximity of other age stands will provide for a greater variety of birds. Large group-selection cuts (1–2 ha) will also support good nesting populations, and intensive thinning of the overstory will create favorable conditions. Burning or disking for site preparation would eliminate the slash component necessary for nesting and foraging cover for towhees and Carolina wrens. Light thinning in mature stands, single-tree selection, or other practices that fail to open the canopy will not benefit these birds.

Open-canopy Obligatory Species

The yellow-breasted chat, field sparrow, prairie warbler, and eastern bluebird preferred open overstory and brushy understory, and showed a narrow range of tolerance for other vegetative conditions.

Bluebirds were found in open stands with small, residual trees. Their nests were located in dead snags in recently

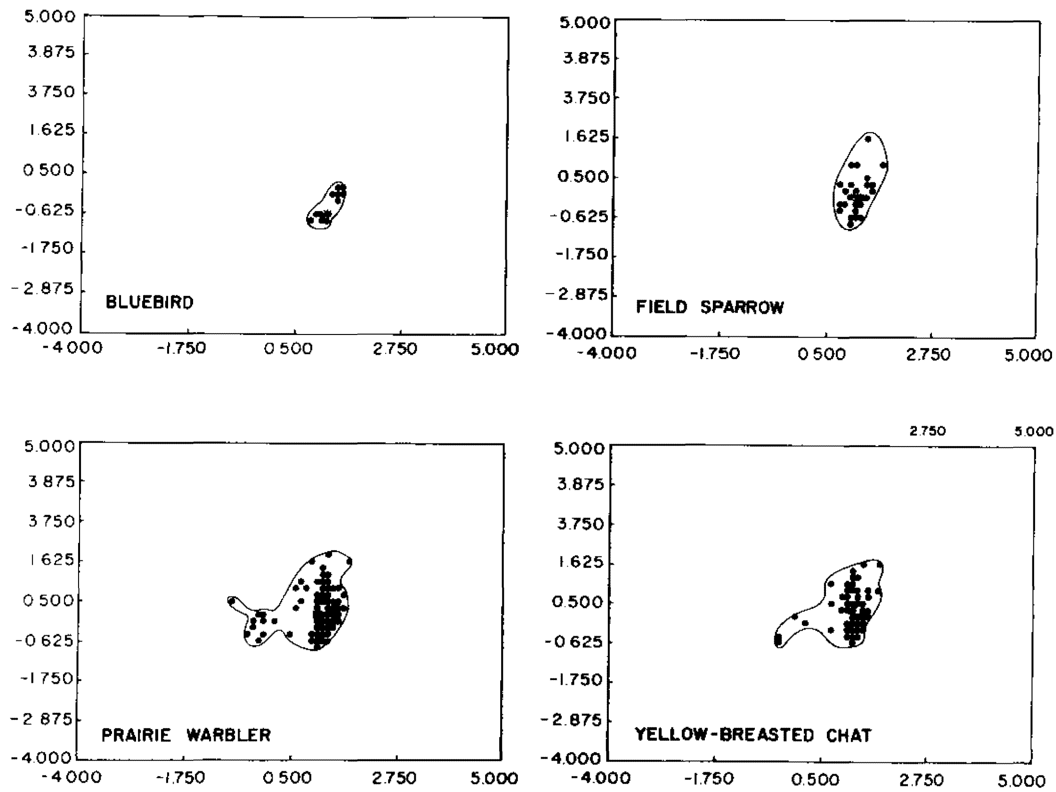

Fig. 6. Open-canopy species. Plot of DF 1 (horizontal) vs. 2 (vertical); * indicates group mean discriminant score. More than 1 observation may fall at a point.

clear-cut stands. The distribution pattern of scores for bluebirds along the axes of DF 1 and 2 was related to open overstory and dense vegetation 0–1.8 m tall with small residual trees (Fig. 6).

The field sparrow was equally restricted in distribution along the canopy-closure axis (DF 1), but had greater tolerance for size of residual trees (DF 2). In comparison, the yellow-breasted chat and prairie warbler had a broader tolerance for canopy cover than either the field sparrow or bluebird, as shown by the spread of scores along the axis of DF 1. Their tolerance extended toward canopy cover in pole stands but not mature stands (Fig. 6).

Nesting populations of the field sparrow and bluebird were strongly discontinuous; they favored only brushy stands with little or no overstory. However, populations of the prairie warbler and yellow-breasted chat were more continuous, but strongly favored open canopy and dense understory (Table 2). Increasing amounts of cover >4.5 m tall reduced ($P < 0.05$) populations of prairie warblers and chats, whereas total vegetation <1.8 m tall showed a positive relationship with numbers of these birds. Populations of yellow-breasted chats were directly related to shrub density to a height of 4.5 m. The 3-variable regressions for each species accounted for a surprisingly large percentage of the variation in nesting populations (Table 2).

With the possible exception of the bluebird, which nested in the numerous small snags, all species in this group were dependent on dense coppice regrowth after clear-cutting, and were not as tolerant of successional change as the previous group of birds. Scarification, cutting of small stems, and fire will create favorable nesting habitat. These species probably prefer regeneration areas >2 ha and generally are not found in smaller areas. As soon as tree canopy exceeds a height of 4.5 m, bird numbers will decline. Thus, the period of time that birds are abundant will depend on the quality of the site, i.e., how fast trees will grow. On exceptionally good sites, bluebirds and field sparrows may nest for only 3–5 years, and yellow-breasted chats and prairie warblers will remain in decreasing numbers until small pole stands develop at 5–10 years. On poorer sites, the population may not decrease for as long as 10–15 years. Moderate-sized (10–12 ha) clear-cuts will ensure variety in stand conditions throughout the area and a corresponding variety in birds.

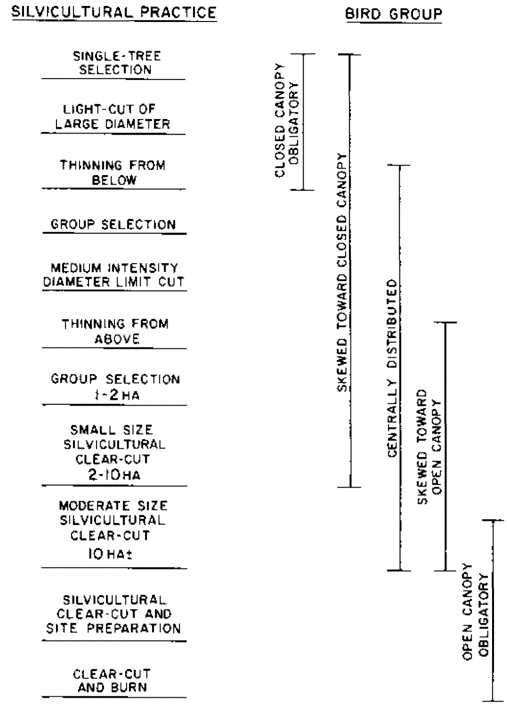

Fig. 7. Generalized schematic of the relationship between silvicultural practices and bird group.

CONCLUSIONS

Silvicultural practices cannot be categorically described as beneficial or detrimental to birds. A certain silvicultural practice may change the habitat enough to decrease the populations of birds occupying the area. However, other species will occupy the site following change, because they are better adapted to the modified habitat. Each habitat has a characteristic group of bird species. Changes in bird groups can be predicted based on a knowledge of the change in configuration of overstory and understory vegetation in the forest stand.

Bird succession following substantial stand disturbance would generally follow sequentially from open-canopy-obligatory to closed-canopy-obligatory species. The initial stage, however, depends upon the degree to which the stand was opened. Open-canopy-obligatory species would occupy sites following moderate to large clear-cuts. Sapling stages would favor species classed as skewed toward open canopy and that would remain in pole-sized stands. Centrally distributed species would also be represented in pole stands. As pole-sized stands develop a closed upper canopy and progress into sawlog sizes, the 2 groups of birds associated with closed-canopy stands would become more prevalent.

Light harvests that leave an intact overstory canopy favor the closed-canopy-obligatory species. Single-tree selection, thinning in the understory, and a light selection cut of the largest trees would favor this group of birds (Fig. 7). Single-tree selection would probably not be used in long-term management for mid-tolerant hardwoods, because the trees would eventually be replaced by more tolerant species. These same silvical practices, plus group selection, thinning the overstory, small clear-cuts, strip clear-cuts, and medium-sized diameter-limit cuts, would favor many of the species classed as skewed toward closed canopy.

Diameter-limit cutting to remove many large stems, group selection, thinning, and small to moderate clear-cuts should favor the birds that were centrally distributed with respect to canopy closure. Clear-cutting, large group-selection cuts, and intensive thinning from above favor species that are skewed toward open-canopy stands. Large to moderate clear-cuts and site preparation practices such as prescribed burning would favor those species dependent on an open overstory.

LITERATURE CITED

ANDERSON, S. H., AND H. H. SHUGART, JR. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55:828–837.

BRAUN, E. L. 1967. Deciduous forests of eastern North America. Hafner Publ. Co., New York, N.Y. 596pp.

CRAWFORD, H. S., AND R. W. TITTERINGTON. 1979. Effects of silvicultural practices on bird communities in upland spruce-fir stands. Pages 110–119 *in* R. M. DeGraaf and K. E. Evans, eds. Workshop proceedings, management of northcentral and northeastern forests for nongame birds. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC51.

DRAPER, N. R., AND H. SMITH. 1966. Applied regression analysis. John Wiley & Sons, Inc., New York, N.Y. 407pp.

EISENBEIS, R. A., AND R. B. AVERY. 1972. Discriminant analysis and classification procedures. Lexington Books, D. C. Heath & Co., Lexington, Mass. 254pp.

EVANS, K. E. 1978. Forest management opportunities for songbirds. Trans. North Am. Wildl. and Nat. Resour. Conf. 43:69–77.

JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences, 2nd ed. McGraw-Hill Book Co., New York, N.Y. 675pp.

OLSON, D. J. 1959. Site index curves for upland oak in the Southeast. U.S. Dep. Agric. For. Serv., Southeast. For. Exp. Stn. RN125. 2pp.

SMITH, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810–819.

TITTERINGTON, R. W., H. S. CRAWFORD, AND B. N. BURGASON. 1979. Songbird response to commercial clearcutting in Maine spruce-fir forests. J. Wildl. Manage. 43:602–609.

WEBB, W. L., D. F. BEHREND, AND B. SAISORN. 1977. Effect of logging on songbird populations in a northern hardwood forest. Wildl. Monogr. 55. 35pp.

WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6:319–408.

Received 3 March 1980.
Accepted 5 September 1980.