

BIRD RELATIONSHIPS TO HABITAT CHARACTERISTICS CREATED BY TIMBER HARVESTING IN PENNSYLVANIA^a

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ABSTRACT

Bird species richness, abundance, the abundance of individual species, and bird community composition were investigated to determine the impact of recent timber harvesting on 47 forest stands in north-eastern Pennsylvania from 1996-98. Stands were located within northern hardwood and oak-hickory forest types and included mostly non-industrial private forestlands harvested within the past 10 years. Bird community richness and abundance both decreased with increasing retention of overstory cover, residual tree basal area, and litter cover, but both increased with increasing understory plant cover. We identified patterns between bird species richness and abundance, and measures of forest stand characteristics using correlation and correspondence analysis. Threshold levels were evident for tree basal area and understory plant cover above which bird species richness and abundance increased or declined. Bird species richness and abundance

increased sharply when tree basal area for a stand dropped below 18m²/ha. Species richness and abundance of birds declined sharply for stands containing more than 26m²/ha tree basal area. Species richness of birds declined sharply when the understory plant cover in a stand dropped below 45%. Harvest intensity and forest type were the primary factors affecting bird community composition. Axis one of detrended correspondence analysis was characterized by increasing shrub, understory plant, and slash cover and volume of downed woody material, and decreasing conifer, snag, and live tree basal area and overstory, midstory, and litter cover. These vegetative characteristics correspond to heavily harvested versus lightly or nonharvested stands, respectively. Axis two separated northern hardwood and oak-hickory stands. Patterns and threshold levels of species richness and abundance of birds along gradients of forest stand characteristics, as well as the identification of forest stand characteristics preferred by species of management concern, provide natural resource professionals with guidelines for managing bird communities on stands harvested for timber in this region.

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INTRODUCTION

There is growing concern about the maintenance of biodiversity among the public and land managers for all forestlands (O'Connell and Noss 1992, DeCalesta 1994, Thorne et al. 1995, Roberts and Gilliam 1995). Research indicates substantial declines in populations of both migrant and resident eastern songbirds (Brauning 1992, Sauer et al. 1997, Robinson et al. 1995). These declines have been attributed to forest fragmentation and associated increases in edge habitat, habitat loss, and increasing nest predation and parasitism (MacArthur and Wilson 1967, Gates and Gysel 1978, Whitcomb et al. 1981, Brittingham and Temple 1983, Andren and Angelstam 1988, Yahner 1988, Yahner et al. 1989, Paton 1994, Peterjohn and Sauer 1994, Yahner 2000). Declines in some bird populations, especially of Neotropical migrants and area-sensitive species, are due in part to changes in habitat created by timber harvesting (Maurer et al. 1981, Niemi and Hanowski 1984, Yahner 1987, and Yahner 1993). Although the previously mentioned research has identified interactions between bird communities and habitat conditions created by habitat fragmentation and timber harvesting, we address the issue of bird and habitat relationships by presenting thresholds for habitat characteristics above and below which bird communities were significantly different. In addition, nearly all of the previously mentioned research has been conducted on state-owned lands and little is known about bird populations on non-industrial private forests (NIPF). Most commercial forests in the eastern states are NIPF (Widmann 1995). In Pennsylvania, 75% of commercial forestlands were categorized as NIPF, representing over one-half million tracts of land with an average size of only 15 hectares (Widmann 1995). While industry and government forests are often managed by professional foresters, only 20% of harvests on Pennsylvania NIPF lands are guided by foresters or other natural resource professionals, and only 6% of NIPF lands have a written management plan (Birch and Stelter 1993). Determining if current forest practices are sustainable is an important question for this forestland ownership class and is currently a matter of debate for all forest ownership classes (Jones et al. 1995).

As part of a larger study of biodiversity and sustainability in recently harvested NIPF stands (similar studies have been conducted with herpetofauna [Ross et al. 2000] and plants [Fredericksen et al. 1999]), we surveyed breeding bird populations on 47 stands in northeastern Pennsylvania between 1996-1998. We used a retrospective study design, comparing birds' use of stands that had undergone different types and intensities of harvests, ranging from mature forest that has not been harvested for 70 years to clearcut stands with most of the tree basal area removed. Our research objectives were to identify thresholds for habitat characteristics where significant changes in bird communities occur, to

determine assemblages of bird species associated with different habitat conditions following timber harvesting, and to identify forest stand characteristics preferred by species of management concern. Information concerning these relationships between habitat characteristics and bird communities is valuable to non-industrial private forest owners, loggers, and natural resource professionals when developing timber management plans.

MATERIALS AND METHODS

Study Stands

Study stands were defined as an area of forest with similar age, history, site conditions, and species composition. Our study stands were located in five counties in northeastern Pennsylvania (centered around Latitude 41 25', Longitude 75 25'): Monroe, Pike, Susquehanna, Wayne, and Wyoming. This area lies within the glaciated low plateau and glaciated Pocono Plateau sections of the Allegheny Plateau Physiographic province. Elevations range from 110 to 895 m. Rainfall averages 110 cm per year. Soils are derived from sandstone and siltstone.

Stands were located within the 2 major forest types in Pennsylvania, northern hardwoods ($n = 27$) and oak-hickory ($n = 20$) (Widmann 1995). Dominant tree species on oak-hickory stands included oak (*Quercus* spp.), hickories (*Carya* spp.), sassafras (*Sassafras albidum*), dogwood (*Cornus Florida*), and pitch pine (*Pinus rigida*). Northern hardwood forest stands were composed of basswood (*Tilia americana*), sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula allegheniensis*). Red maple (*Acer rubrum*), white pine (*Pinus strobes*), black birch (*Betula lenta*), and downy serviceberry (*Amelanchier arborea*) occurred on both forest types. The understory of oak-hickory stands was dominated by blueberry (*Vaccinium* spp.) and mountain laurel (*Kalmia latifolia*). Hay-scented fern (*Dennstaedtia punctilobula*) and New York fern (*Thelypteris noveboracensis*) were the most abundant plants in the understory of northern hardwood stands with high amounts of overstory cover, while blackberry and raspberry (*Rubus* spp.) (hereafter referred to as "blackberry") were associated with most northern hardwood stands with low overstory tree cover. As is typical in northeastern Pennsylvania, all stands had been exposed to heavy browsing pressure by white-tailed deer (*Odocoileus virginianus*), and outbreaks of gypsy moth (*Lymantria dispar*) and forest tent caterpillar (*Malacosoma disstria*) within the past 20 years.

Stand sizes ranged from 8-12ha. Thirty-three stands were sampled during 1996 and sampling was repeated in six of these stands in 1997, four of these stands in 1998, and eight of these stands during both 1997 and 1998. In

addition, 14 stands that were not available in 1996 were sampled during 1997 and sampling was repeated in five of these stands in 1998. Of the 47 different stands that were sampled between 1996-98, nine stands had not been harvested for more than 70 years, whereas the remaining 38 stands were harvested 1-10 years before initiation of research (Table 1). Unharvested stands included forested lands owned by NIPF landowners,

Pennsylvania Bureau of Forestry, The Pennsylvania Game Commission, and The Nature Conservancy. Harvested stands were selected from Procter and Gamble harvests on NIPF owned by individuals who were willing to cooperate with our research project. With limited availability of NIPF stands meeting these criteria, we selected stands that had undergone various logging intensities ranging from 0-95% residual, overstory tree cover.

Table 1. Stand characteristics and characteristics of the landscape adjacent to the 47 forest stands sampled in northeastern Pennsylvania between 1996 and 1998

Stand	Stand Characteristics				Land-use Types Adjacent to Stands				
	Forest Type ^a	Harvest Method	Time Since Harvest (Years)	Basal Area (m ² /ha)	Mature Forest (%)	Regenerating Forest (%)	Field (%)	Water (%)	Development (%)
1	NH	Clearcut	3	0.0	65	30	2	2	1
2	NH	Clearcut	4	0.5	85	11	3	0	1
3	NH	Diameter-limit	3	5.5	44	0	44	1	11
4	NH	Diameter-limit	8	5.7	84	5	9	1	1
5	NH	Diameter-limit	6	24.6	92	0	4	4	0
6	NH	Selection	2	3.1	90	0	8	2	0
7	NH	Selection	2	8.4	90	4	6	0	0
8	NH	Selection	1	12.7	74	0	24	1	1
9	NH	Selection	5	13.8	80	0	16	2	2
10	NH	Selection	2	15.5	50	17	43	0	0
11	NH	Selection	8	17.3	53	5	39	3	0
12	NH	Selection	7	17.6	80	0	13	3	2
13	NH	Selection	4	18.4	81	0	16	2	1
14	NH	Selection	2	18.6	73	0	15	2	10
15	NH	Selection	5	20.0	90	0	2	1	7
16	NH	Selection	4	20.4	46	0	50	3	1
17	NH	Selection	4	21.6	69	2	23	2	4
18	NH	Selection	3	22.0	73	2	25	0	0
19	NH	Selection	3	22.4	80	13	5	2	1
21	NH	Selection	10	23.2	29	25	45	0	1
22	NH	Selection	5	26.4	74	0	24	1	1
23	NH	None	>70	30.8	89	1	9	0	1
24	NH	None	>70	34.9	38	38	17	2	5
25	NH	None	>70	35.2	60	35	3	2	0
26	NH	None	>70	35.5	35	8	26	31	0
27	NH	None	>70	37.2	59	0	35	2	4
28	OH	Clearcut	6	0.7	93	3	2	0	2
29	OH	Clearcut	3	5.7	81	16	3	1	1
30	OH	Clearcut	3	6.4	91	0	2	2	5
31	OH	Selection	3	3.7	69	30	0	1	0
32	OH	Selection	3	8.7	96	0	0	1	3
33	OH	Selection	3	10.8	92	6	1	1	0
34	OH	Selection	3	11.2	92	0	0	5	3
35	OH	Selection	3	11.8	55	5	5	10	1
36	OH	Selection	8	13.8	48	45	0	5	2
37	OH	Selection	4	14.2	54	40	2	3	1
38	OH	Selection	2	16.3	71	0	27	1	1
39	OH	Selection	8	17.7	58	40	2	0	0
40	OH	Selection	8	18.4	89	0	0	2	9
41	OH	Selection	10	19.5	93	0	0	4	3
42	OH	Selection	10	22.7	97	0	0	1	2
43	OH	Selection	4	22.9	89	10	0	1	0
44	OH	None	>70	22.6	20	75	0	0	5
45	OH	None	>70	23	87	10	3	0	0
46	OH	None	>70	25.9	79	19	0	1	1
47	OH	None	>70	26.6	80	8	10	1	2

^aNH, Northern hardwood; OH, oak-hickory.

Management on the harvested stands included clear-cutting (removing the entire stand at one cutting), diameter-limit (removing timber above a specified diameter), and shelterwood (a series of two or three harvests within the same stand used to regenerate the future forest) and single-tree (removing select trees or small groups of trees to achieve a desired stand structure) selection cuts. Sampling from stands with such a range of variation allowed us to generalize these results across many stands, although precision may be low for any stand type. Thus, the study is a retrospective analysis of the bird species composition, abundance, and species richness associated with varying habitat characteristics resulting from logging. We used this gradient approach to identify trends and thresholds applicable to a variety of stands. This approach was necessary because the size, shape, plant composition and structure, and harvesting type varied widely among stands, negating the effectiveness of a treatment reference approach.

Stand Sampling

Characteristics of forest stands were determined during 1996-98. Stand characteristics and the range of values for the stand characteristics were as follows: live tree basal area (0-37 m²/ha); coniferous tree basal area (0-19 m²/ha); snag basal area (0-7 m²/ha); overstory tree canopy cover (0-95%); midstory tree canopy cover (5-85%); shrub cover (0-50%); slash cover (0-25%); dead and downed woody material (3-110 m³/ha); understory plant cover (20-95%); dominant understory plant cover [i.e., fern (0-70%), blackberry (0-70%), and blueberry (0-90%)]; leaf litter cover (25-98%); and the amount and types of water. Measurements were made on overstory trees, midstory trees, and herbaceous plants in all stands from March through August of 1996, 1997, and 1998. Overstory trees were defined as woody plants being at least 10m in height and 10cm in dbh (diameter-at-breast height, 1.37m). Midstory trees were defined as being between 3-10m in height and at least 10cm dbh. Shrub species included woody plants ranging from 1-5m in height and < 10cm in diameter that were inherently incapable of achieving canopy status. Understory plant cover included woody and herbaceous material < 1m in height. Cover was estimated ocularly at 15 sampling points per stand using 1m² quadrats, except for overstory and midstory cover. Shrub cover was estimated as the percentage of the quadrants between 1-3m in height that contained plant material. Over- and midstory cover was estimated using a transparent grid canopy densiometer. Fifteen sampling points were randomly located using a stratified sampling design. Tree basal area was measured at 20 points within each stand using a 10-factor prism to determine the species composition of live, dead, and coniferous tree basal area. Tree basal area points were located using a stratified random design, and placed along transects of varying

lengths so that all sections of the stand were equally sampled. Woody debris was sampled along 20 randomly located 40m-long transects by measuring and recording the diameters of all logs > 5cm in diameter that intersected the transect. We determined log volume from the measurements of woody debris using a formula described by Harvey and Finley (1995). An index was also developed to quantify the relative abundance of temporary and permanent water sources inside of and/or proximal to each stand. Index scores for water ranged from 1-5 for each stand as follows: 1 = no known source of water in or near the stand; 2 = one source of water adjacent to study stand, but none within the stand; 3 = more than one water source adjacent to stand, but none within the stand; 4 = one water source within the stand; 5 = more than one water source within the stand. Average percent slope and aspect of all stands were recorded using a clinometer and compass, respectively.

In addition to measuring within stand characteristics, we measured the percent of mature forest, regenerating forest, field, water, and development that bordered each stand using aerial photos accompanied by ground-truthing the results obtained from the aerial photos.

Bird Surveys

Breeding songbirds were surveyed on stands during May and June 1996-98 using 40-m fixed-radius circular plots. Each stand contained 4-6 plots with each plot depending upon stand size (approximately one plot for every 2ha of stand area). Plots were randomly located using a stratified sampling design. Each plot was located > 50m from the edge of the stand and plot centers were located > 80m apart. Four, 5-min counts were conducted at each plot per year. All counts were conducted within 5 hours of sunrise on mornings with no precipitation and wind < 25km/hr. The species, sex, and observation method (e.g., song, visual) were recorded for each bird detected. All birds detected were included in the data analyses.

Data Analyses

The experimental unit for statistical analyses was the stand. For each stand, species richness was calculated as number of different species of birds detected within a stand. An index of bird abundance (hereafter referred to as abundance) was calculated as the number of birds per hectare. Mean richness, total bird abundance, and abundance of individual species were used for stands surveyed during more than one breeding season, because there were no significant differences ($P > 0.10$) in bird richness or abundance between years.

Simple product-moment correlation analysis was used to test for significant relationships between total bird abundance, the abundance of individual species, and species richness of birds and forest stand characteristics.

Transformations were performed in cases of non-linear relationships before conducting linear correlation. Statistical relationships were considered significant at $P < 0.05$. Based on relationships identified during correlation analysis, we plotted bird species richness and abundance with forest stand characteristics to identify potential thresholds in dependent and independent variables.

Best subset regression analysis was used to determine if bird species richness or abundance could be predicted from the set of forest characteristics. Variables were considered significant if $P < 0.05$. We do not present regression results for individual bird species because bird-habitat relationships could be explained using few simple correlations.

Ordination of stands and species was conducted using detrended correspondence analysis (DCA) (Hill 1979, Hill and Gauch 1980) to determine changes in species composition with variations in the habitat characteristics associated with differing degrees of logging intensity. This technique orders stands along gradients according to their similarity in species composition. Species responses are also ordered so that stand-species associations can be detected. Only species that occurred on 3 or more stands were used in correlation and DCA to avoid including single observations of bird species and/or transient species not breeding within northeastern Pennsylvania.

RESULTS

Correlation, Thresholds, and Regression Analyses

Bird community richness decreased with increases in overstory cover and litter cover, and increased with increases in blackberry cover ($r = 0.36$, $P = 0.01$) (Table 2). Bird abundance decreased with increases in overstory cover, conifer and snag basal area, and litter cover, and increased with increases in understory plant cover, in particular blackberry cover ($r = 0.36$, $P = 0.01$) (Table 2). We identified threshold values for tree basal area and understory plant cover above and below which bird species richness and litter cover, and increased with increases in understory plant cover, in particular blackberry cover ($r = 0.36$, $P = 0.01$) (Table 2). We identified threshold values for tree basal area and understory plant cover above and below which bird species richness and abundance were significantly different. Species richness and abundance of birds increased sharply when tree basal area on stands dropped below $18\text{m}^2/\text{ha}$ (Table 3 and Figure 1). Bird species richness and abundance declined sharply for stands containing more than $26\text{m}^2/\text{ha}$ tree basal area (Table 3 and Figure 1). Species richness of birds declined sharply when the understory plant cover in a stand dropped below 45% (Table 3 and Figure 2). Bird abundance and species richness were not signifi-

cantly ($P > 0.05$) associated with land-use types adjacent to the study stands.

Best Subsets regression between bird species richness and all forest characteristics was fairly weak (adjusted $R^2 = 0.24$) but significant ($P = 0.002$). Species richness was higher on oak-hickory stands ($P = 0.02$), increased with blackberry cover ($P = 0.007$), but decreased with leaf litter cover ($P = 0.02$). There was a moderate (adjusted $R^2 = 0.50$) and significant ($P < 0.001$) relationship between total bird abundance and forest characteristics: bird abundance was higher on oak-hickory stands ($P = 0.006$), increased with blackberry cover ($P < 0.001$) and temporary water ($P = 0.003$), but decreased with tree basal area ($P = 0.01$) and fern cover ($P = 0.02$).

Eleven bird species were associated with oak-hickory stands and 6 species were associated with northern hardwood forests (Table 2). There were >10 significant correlations between the abundance of individual bird species and 10 measures of forest structure (Table 2). Significant positive and negative correlations were similar (within 2) for conifer and snag basal area and midstory cover. Negative correlations were dominant for overstory cover (21 negative, 7 positive correlations), basal area (20 negative, 10 positive), and litter cover (17 negative, 3 positive). Positive correlations were dominant for shrub (11 positive, 3 negative) and understory plant cover (16 positive, for overstory cover (21 negative, 7 positive correlations), basal area (20 negative, 10 positive), and litter cover (17 negative, 3 positive). Positive correlations were dominant for shrub (11 positive, 3 negative) and understory plant cover (16 positive, 10 negative).

Besides the relationships between bird communities and characteristics of the forest stands, there were several significant ($P \leq 0.001$) correlations between forest stand characteristics. Overstory cover and tree basal area were highly correlated ($r = 0.90$). Over- and midstory cover was associated with several measures of understory plant-level cover. Understory plant and slash cover decreased with increasing overstory (r 's = -0.61 and -0.45 , respectively) and midstory (r 's = -0.75 and -0.57 , respectively). Leaf litter cover increased with increasing overstory ($r = 0.49$) and midstory cover ($r = 0.58$). No other relationships between variables exceeded $r = 0.5$.

Bird Communities Associated With Forest Stand Characteristics

Detrended correspondence analysis (DCA) identified 1 major and 2 minor axes. Axis 1 accounted for 67% of explainable variation in the data set (Table 4). Axis 1 was characterized by increasing shrub, understory plant, and slash cover and volume of downed woody material and decreasing conifer, snag, and live tree basal area and overstory, midstory, and litter cover. The first axis may be related to harvest intensity since more heavily harvested stands were associated with higher values of

Table 2. Simple correlation between bird variables and forest characteristics on 47 forest sites, northeastern Pennsylvania, 1996-98. Significant correlations are shown ($r \geq 0.29$, $P < 0.05$; $r \geq 0.32$, $P < 0.01$). Birds are presented in taxonomic order by detrended correspondence analysis (DCA) species groupings.

Bird Species	FT ^a	OC ^a	BA ^a	MC ^a	CBA ^a	SBA ^a	SC ^a	GC ^a	LC ^a
Species Richness	—	-0.37	-0.40	—	—	—	—	0.27 ^b	-0.36
Bird Abundance	—	-0.47	-0.53	—	-0.32	-0.32	—	0.38	-0.30
DCA Species Group A - Birds associated with mature oak-hickory forest									
Red-bellied Woodpecker <i>Melanerpes cauirolmus</i>	0.27 ^b	—	—	—	—	—	—	—	—
Great-crested Flycatcher <i>Myiarchus crinitus</i>	0.32	0.31	—	0.44	—	—	—	-0.42	0.38
Tufted Titmouse <i>Baeolophus bicolor</i>	—	—	—	—	—	—	—	—	—
White-breasted Nuthatch <i>Sitta carolinensis</i>	0.30	—	—	0.39	—	—	—	-0.31	—
Blue-gray Gnatcatcher <i>Poliophla caerulea</i>	0.65	—	—	0.39	—	—	—	—	-0.28 ^b
Hermit Thrush <i>Catharus guttatus</i>	—	—	—	0.32	—	—	—	-0.41	—
Cerulean Warbler <i>Dendroica cerulea</i>	0.32	—	—	—	—	—	—	—	—
American Redstart <i>Setophaga rutacilla</i>	0.32	—	—	—	0.39	—	—	—	—
DCA Species Group B - Birds associated with mature northern hardwood and oak-hickory forest									
Downy Woodpecker <i>Picoides pubescens</i>	—	—	—	—	—	—	—	—	—
Eastern Wood-Pewee <i>Contopus virens</i>	—	—	—	—	—	—	-0.34	—	—
Acadian Flycatcher <i>Empidonax virens</i>	—	—	—	0.29	—	—	—	—	—
Red Red-eyed Vireo <i>Vireo olivaceus</i>	—	0.35	0.45	0.42	—	—	—	-0.37	—
Black-capped Chickadee <i>Poecile atricapilla</i>	—	—	0.33	0.42	0.30	—	—	-0.43	—
Brown Creeper <i>Certhia americana</i>	—	0.39	0.43	—	0.29	0.52	—	—	0.29
Wood Thrush <i>Hylocichla mustelina</i>	—	—	—	0.37	0.31	—	—	-0.32	—
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	—	—	—	—	—	—	—	—	—
Pine Warbler <i>Dendroica pinus</i>	0.29	—	—	—	—	—	—	—	—
Ovenbird <i>Seiurus aurocapillus</i>	0.31	0.35	0.37	0.66	—	—	—	-0.56	0.40
Scarlet Tanager <i>Piranga olivacea</i>	—	0.31	0.35	0.44	—	—	-0.31	-0.45	—
DCA Species Group C - Birds associated with mature northern hardwood forest									
Blue-headed Vireo <i>Vireo solitarius</i>	—	0.35	0.53	0.32	0.66	0.42	—	-0.44	—
American Crow <i>Corvus brachyrhynchos</i>	—	—	0.34	—	—	—	—	—	—
Winter Wren <i>Troglodytes troglodytes</i>	—	—	—	—	—	—	—	—	—
Magnolia Warbler <i>Dendroica magnolia</i>	—	—	—	—	—	—	—	—	—
Blackburnian Warbler <i>Dendroica fusca</i>	—	—	—	—	—	—	—	—	—
Black-throated Green Warbler <i>Dendroica virens</i>	—	—	0.37	0.30	0.49	—	—	-0.36	—

Table 2. Continued.

Bird Species	FT ^a	OC ^a	BA ^a	MC ^a	CBA ^a	SBA ^a	SC ^a	GC ^a	LC ^a
Black-throated Green Warbler <i>Dendroica virens</i>	—	—	0.37	0.30	0.49	—	—	-0.36	—
Canada Warbler <i>Wilsonia canadensis</i>	—	—	—	0.30	0.30	—	—	—	—
Dark-eyed Junco <i>Junco hyemalis</i>	—	—	—	—	—	0.38	—	—	—
DCA Species Group D - Birds associated with oak-hickory forest exposed to various intensities of logging									
Least Flycatcher <i>Empidonax minimus</i>	—	—	—	—	—	—	—	—	—
Yellow-throated Vireo <i>Vireo flavifrons</i>	0.53	—	—	—	—	—	—	—	—
American Robin <i>Turdus migratorius</i>	—	-0.27 ^b	0.31	-0.41	—	—	—	—	-0.56
DCA Species Group E - Birds associated with northern hardwood and oak-hickory forest exposed to various intensities of logging									
Wild Turkey <i>Meleagris gallopavo</i>	—	—	—	—	—	—	—	—	—
Ruffed Grouse <i>Bonasa umbellus</i>	—	—	—	—	—	—	—	—	—
Yellow-billed Cuckoo <i>Coccyzus americanus</i>	—	—	—	—	—	—	—	—	—
Black-billed Cuckoo <i>Coccyzus erythrophthalmus</i>	—	—	—	—	—	-0.29	—	—	—
Ruby-throated Hummingbird <i>Archilochus colubris</i>	—	-0.41	-0.41	—	—	—	—	0.32	-0.42
Northern Flicker <i>Colaptes auratus</i>	—	0.30	—	—	—	—	—	—	—
Hairy Woodpecker <i>Dendrocopos villosus</i>	—	—	0.29	—	—	0.42	—	—	—
Warbling Vireo <i>Vireo gilvus</i>	—	—	—	—	—	—	—	—	—
Blue Jay <i>Cyanocitta cristata</i>	—	—	—	—	—	—	—	—	—
Veery <i>Catharus fuscescens</i>	—	—	—	0.35	—	—	—	—	—
Cedar Waxwing <i>Bombicilla cedrorum</i>	—	0.33	-0.32	-0.47	—	—	—	0.35	—
Chestnut-sided Warbler <i>Dendroica pensylvanica</i>	—	0.54	-0.56	-0.47	0.34	—	0.32	0.64	—
Black-and-White Warbler <i>Mniotilta varia</i>	0.61	-0.46	-0.43	—	-0.37	-0.35	0.62	—	—
Common Yellowthroat <i>Geothlypis trichas</i>	—	-0.68	-0.63	-0.60	-0.29	—	0.33	0.76	-0.35
Eastern Towhee <i>Pipilo erythrophthalmus</i>	0.32	-0.59	-0.56	-0.47	-0.33	-0.34	0.37	0.46	—
Chipping Sparrow <i>Spizella passerina</i>	—	—	—	—	—	—	—	—	—
White-throated Sparrow <i>Zonotrichia albicollis</i>	—	—	—	—	—	—	—	—	—
Rose-breasted Grosbeak <i>PS7eucticus ludovicianus</i>	-0.41	—	—	—	—	—	—	—	-0.43
Northern Cardinal <i>Cardinalis cardinalis</i>	—	—	—	—	—	—	—	—	-0.58
Common Grackle <i>Quiscalus quiscula</i>	—	—	—	—	—	—	0.30	—	—
Brown-headed Cowbird <i>Molothrus ater</i>	—	-0.31	-0.27	—	—	—	—	—	—
Baltimore Oriole <i>Icterus galbula</i>	-0.35	—	—	-0.53	—	—	—	0.41	-0.56
American Goldfinch <i>Spinus tristis</i>	—	-0.49	-0.39	—	—	—	0.32	—	-0.45

Table 2. Continued.

Bird Species	FT ^a	OC ^a	BA ^a	MC ^a	CBA ^a	SBA ^a	SC ^a	GC ^a	LC ^a
DCA Species Group F - Birds associated with northern hardwood forest exposed to various intensities of logging									
Yellow-bellied Sapsucker <i>Sphyrapicus varius</i>	-0.57	0.31	0.38	—	—	0.54	-0.39	—	—
Indigo Bunting <i>Passerina cyanea</i>	-0.36	-0.33	-0.32	-0.32	—	—	—	0.34	—
DCA Species Group G - Birds associated with heavily harvested oak-hickory forest									
Blue-winged Warbler <i>Vermivora pinus</i>	—	0.37	-0.32	0.27 ^b	—	-0.32	—	0.32	-0.48
Golden-winged Warbler <i>Vermivora chrysoptera</i>	0.47	-0.46	-0.42	—	—	—	0.49	—	—
Yellow-breasted Chat <i>Icteria wrens</i>	—	-0.31	-0.30	—	—	—	0.40	—	-0.53
DCA Species Group H - Birds associated with heavily harvested northern hardwood and oak-hickory forest									
House Wren <i>Troglodytes aedon</i>	-0.33	-0.48	-0.46	-0.62	—	—	—	0.44	-0.60
Gray Catbird <i>DumetelBa carolinensis</i>	—	-0.63	-0.62	-0.57	—	—	0.50	0.52	-0.59
Yellow warbler <i>Dendroica petechia</i>	—	-0.61	-0.57	-0.49	—	-0.34	0.55	0.39	-0.53
Mourning Warbler <i>Oporornis Philadelphia</i>	-0.27 ^b	—	—	0.33	—	—	—	0.33	-0.37
Song Sparrow <i>Melospiza melodia</i>	-0.32	-0.55	-0.50	-0.56	—	—	0.28 ^b	0.45	-0.75
DCA Species Group I - Birds associated with heavily harvested northern hardwood forest									
Mourning Dove <i>Zenaida macroura</i>	—	—	—	—	—	—	—	—	—
Field Sparrow <i>Spizella pusilla</i>	—	0.44	-0.41	-0.37	—	-0.29	—	0.31	—
^a Habitat variables include forest type (FT), percent overstory tree cover (OC), tree basal area in m ² /ha (BA), percent midstory tree cover (MC), coniferous tree basal area in m ² /ha (CBA), snag basal area in m ² /ha (SBA), percent shrub cover (SC), percent plant understory plant cover (GC), and percent leaf litter cover (LC). ^b Correlations are significant at ($P = 0.06$).									

Table 3. Differences in mean abundance and species richness of birds above and below threshold values for tree basal area and understory plant cover on 47 forest stands, northeastern Pennsylvania, 1996-98.

Thresholds	Bird Species Richness				Index of Abundance (no. individuals/ha)			
	Mean	C.I. ^a	<i>t</i> -static	<i>P</i> -value	Mean	C.I. ^a	<i>t</i> -static	<i>P</i> -value
Tree basal area < 18.5 m ² /ha	30.2	28.4 - 32.0	2.61	0.01	13.7	12.5 - 14.9	3.90	0.0003
Tree basal area > 18.5 m ² /ha	26.4	23.9 - 28.9			10.3	9.0 - 11.6		
Tree basal area < 26 m ² /ha	29.5	27.9 - 31.1	3.66	0.0007	12.8	11.8 - 13.8	3.89	0.0003
Tree basal area > 26 m ² /ha	22.8	21.0 - 24.6			8.3	7.5 - 9.1		
Understory Plant Cover ≤ 45%	24.4	21.9 - 26.9	2.59	0.01	—	—	—	—
Understory Plant Cover > 45%	29.3	27.6 - 31.0			—	—		

^a C.I. represents the 95% confidence interval around the mean.

shrub and understory plant cover and lower values of tree and litter cover. Axis 2 (21% of explainable variation) generally separated northern hardwood and oak-hickory stands. Northern hardwood forest stands were positively associated with blackberry ($r=0.54$, $P < 0.001$), fern ($r = 0.48$, $P < 0.001$) and conifer cover ($r = 0.40$, $P < 0.006$), whereas oak-hickory stands were positively associated with blueberry cover ($r = 0.70$, $P < 0.001$).

The third axis accounted for 12% of the variation, and separated dry, oak associated with blueberry cover ($r = 0.70$, $P < 0.001$). The third axis accounted for 12% of the variation, and separated dry, oak-hickory stands with abundant shrub cover from unharvested or lightly cut northern hardwood stands that contained temporary and permanent water sources.

Plotting the bird species on the two DCA axes showed

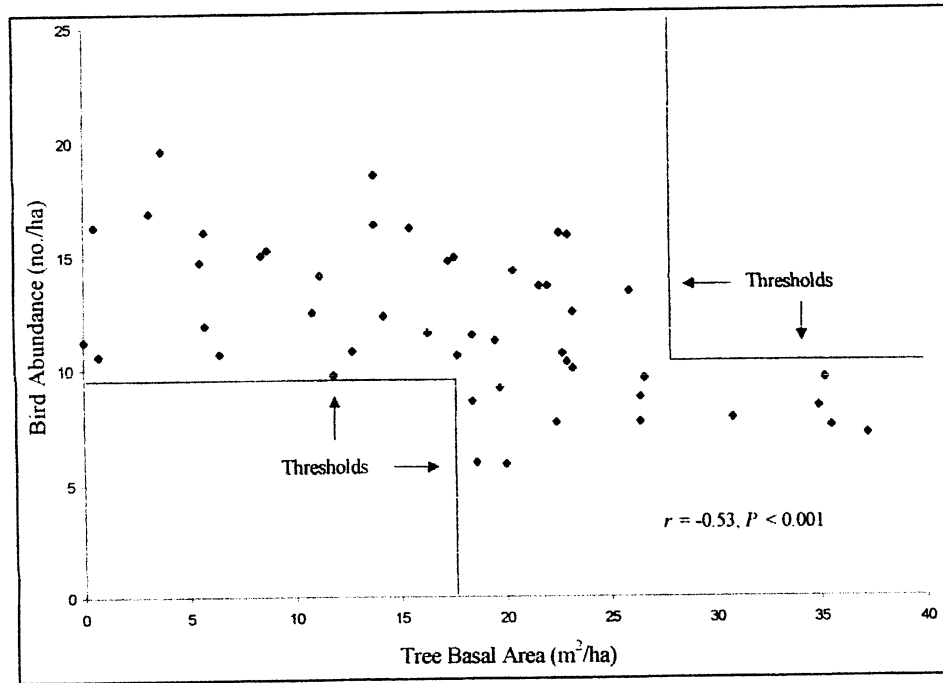


FIGURE 1. Relationship between bird abundance and residual tree basal area for 47 forest sites in northeastern Pennsylvania during 1996-98.

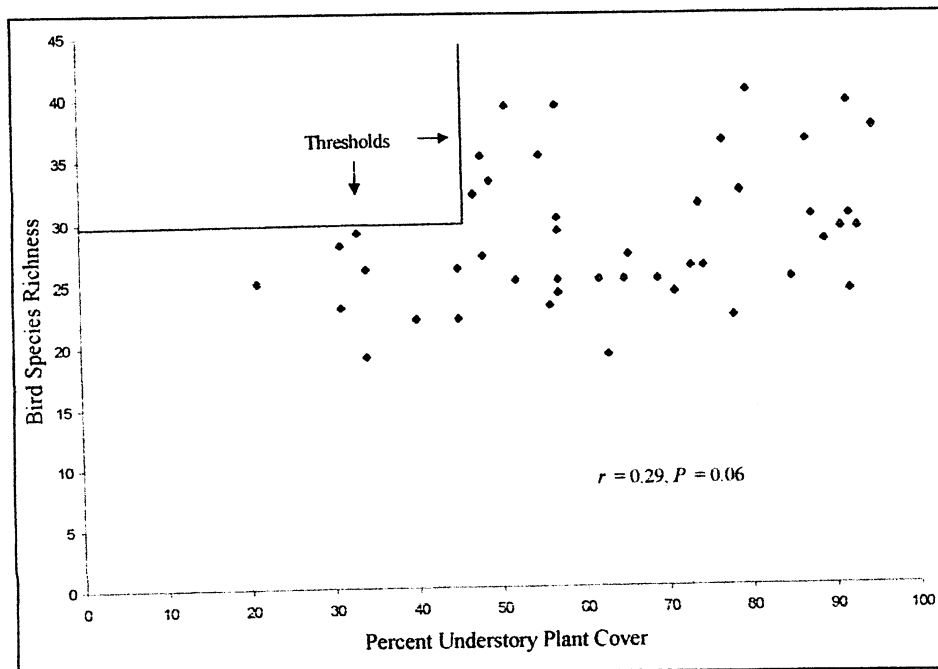


FIGURE 2. Relationship between bird species richness and understory plant cover for 47 forest sites in northeastern Pennsylvania during 1996-98.

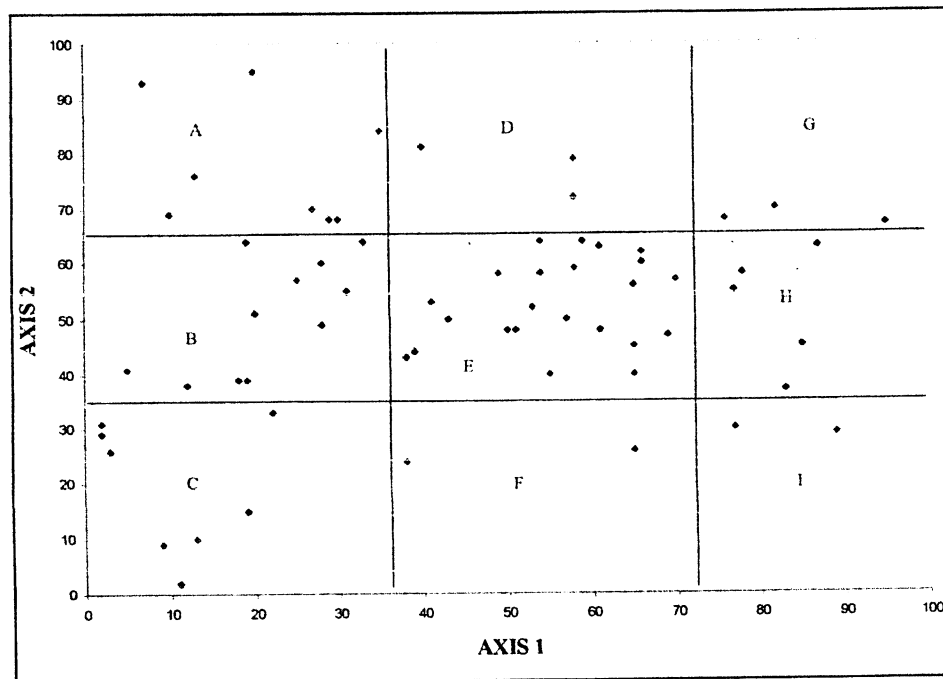


FIGURE 3. Distribution of bird species in relation to detrended correspondence analysis axes 1 and 2 for 47 forest sites in northeastern Pennsylvania during 1996-98. Increasing values for axis 1 correspond to increasing shrub, understory plant, and slash cover and volume of downed woody material and decreasing conifer, snag, and live tree basal area and overstory, midstory, and litter cover. Increasing values for axis 2 correspond to a shift from northern hardwood to oak-hickory sites, decreasing fern, blackberry, and conifer cover, and increasing blueberry

a broad scattering of species across the first two DCA Axes. Visual interpretation of the plot led to the identification of 9 species groups (Figure 3 and Table 2). Groups A (8 species), B (11 species), and C (8 species) occupied the left portion of the plot, and contained mature forest species. Group B is composed of mature forest species that can be found in either northern hardwood or oak-hickory forest types. Group B separates the species above (group A) that were associated with mature oak-hickory stands containing blueberry cover, from those below (group C) that occupied closed-canopy northern hardwood stands containing water, conifers, blackberry, and fern cover. Groups D (3 species), E (23 species), and F (2 species) were composed of species found on stands exposed to various intensities of timber harvesting. These groups contain a range of species from those associated with light selection harvests (e.g., Hairy Woodpecker, Veery, Yellow-bellied Sapsucker, and Yellow throated Vireo) to species associated with stands characterized by open canopies and low amounts of residual tree basal area (i.e. Chestnut-sided Warbler, Common Yellowthroat, and Eastern Towhee) (scientific names are found in Table 2). American Robin, Least Flycatcher, and Yellow-throated Vireo comprised Group D and were associated with oak hickory stands exposed to various intensities of logging, whereas Group F contained Indigo Bunting and Yellow-bellied Sapsucker

that were associated with northern hardwood stands of varying harvest intensities. Birds that were located within Group E contained 23 generalist species and separated oak-hickory birds from northern hardwood associates. Although some of these species (i.e., Baltimore Oriole, Black-and-white Warbler, and Rose-breasted Grosbeak) were more abundant within

Table 4. Significant ($P < 0.01$) Pearson's correlation coefficients between forest site characteristics and the first three axes from detrended correspondence analysis of 47 forested stands in northeastern Pennsylvania.

Variable	Axis 1	Axis 2	Axis 3
Forest Type		0.65	-0.55
Tree Basal Area	-0.80		0.39
Conifer Basal Area	-0.47	-0.41	
Snag Basal Area	-0.38		
Overstory Cover	-0.76		
Midstory Cover	-0.75		
Number of Cavities			0.40
Shrub Cover	0.45		-0.47
Understory Plant Cover	0.76		
Fern Cover		-0.47	
Blackberry Cover	0.52		
Blueberry Cover		0.41	-0.44
Slash Cover	0.40		
Litter Cover	0.53		
Temporary Water			0.45
Permanent Water			0.38

one of the forest types, these 23 species were found within both forest types (Table 2). Blue-winged Warbler, Golden-winged Warbler, and Yellow-breasted Chat comprised group G and occupied oak-hickory forest stands with large canopy openings between trees and an abundance of shrub and blueberry cover. Field Sparrow and Mourning Dove comprised group I and were associated with heavily harvested northern hardwood stands characterized by an abundance of blackberry and fern cover. The remaining 5 species were classified within group H and occupied stands with large canopy openings between trees within both forest types. House Wren and Song Sparrow were more abundant on northern hardwood stands and eastern towhee were more abundant on oak hickory stands, but these species existed in both forest types (Table 2).

DISCUSSION

At the forest stand level, vertical and horizontal structure and complexity of vegetation are important factors affecting the species richness, composition, distribution, and abundance of birds (Maurer et al. 1981, Niemi and Hanowski 1984, Yahner 1986, DeGraaf et al. 1998). Logging introduces heterogeneity within homogeneous forest, changes the structure and complexity of vegetation, and tends to increase bird abundance and richness (Blake et al. 1994, Gates and Gysel 1978, Whitcomb et al. 1981, Yahner 1993). In our study, the variables most significantly related to the species richness and abundance of birds were tree basal area, overstory cover, and understory plant cover. As tree basal area and overstory cover were decreased by logging, understory plant cover increased, changing the structure and increasing the horizontal and vertical complexity of vegetation, except for clearcuts. Bird species richness and abundance concomitantly increased with the removal of tree basal area and subsequent increase in understory plant cover. However, these stand characteristics used to exemplify changes in bird species richness and abundance were not strong, suggesting the a suite of factors including conifer, shrub, litter, and slash cover and the presence of water sources influence the richness and abundance of birds.

Multivariate examination (DCA) of bird-habitat relationships further revealed a broad overlap in habitat preferences among species. Similar to the work of DeGraaf et al. (1998), we found that variables associated with forest stand structure (e.g., tree basal area, understory plant cover, etc.) explained the most amount of variation in bird communities, but that cover-type was also significant variable for identifying clusters of bird species. Clusters of species could be qualitatively identified that reflect the changes in bird composition associated with forest cover composition associated with forest cover-type and changes in forest stand characteristics

following timber harvesting. Furthermore, several species occurred in outlying positions within the ordination, indicating their association with a specific forest type and/or level of tolerance to timber harvesting. For example, species from group G such as Golden-winged Warbler were separated from other species and occupied heavily-harvested oak-hickory stands. On the other extreme, species from group C such as Winter Wren and Magnolia Warbler were separated from all other species and occupied heavily-forested northern hardwood stands.

Five bird species including Black-throated Blue Warbler, Canada Warbler, Cerulean Warbler, Golden-winged Warbler, and Wood Thrush have been identified as species of management concern in north-eastern Pennsylvania according to the National Audubon Society Watchlist for Pennsylvania (Muehther 1998). Additionally, three of the five species, Canada Warbler, Wood Thrush, and Golden-winged Warbler have shown significant ($P \leq 0.03$) population declines over the past 35 years according to the North America Breeding Bird Survey (Sauer et al. 1997). Four of these species, Black-throated Blue Warbler, Canada Warbler, Cerulean Warbler, and Wood Thrush are mature forest associates, and Golden-winged Warbler is an early successional species. Although harvesting is beneficial to some birds, forest fragmentation and decreasing amounts of contiguous forest have been shown to adversely affect bird populations associated with mature forest including Black-throated Blue Warbler and Wood Thrush (Holmes et al. 1992, Hoover et al. 1995). Black-throated Blue Warbler and Wood Thrush are partial to large contiguous tracts of deciduous or mixed conifer forests with abundant understory vegetation (Holmes et al. 1992, Hoover et al. 1995). Black-throated Blue Warbler and Wood Thrush are partial to large contiguous tracts of deciduous or mixed conifer forests with abundant understory vegetation (Holmes et al. 1992, Hoover et al. 1995, Brauning 1992, Ehrlich et al. 1988). Black-throated Blue Warblers favor rhododendron, laurel, and young conifers in the understory and Wood Thrush favor hardwood saplings and young conifers (Brauning 1992, Ehrlich et al. 1988). Black-throated Blue Warblers are also known to inhabit partially harvested areas with considerable shrub growth located within an extensive forested landscape (Brauning 1992, Ehrlich et al. 1988). Our research supports past work identifying these two species as deciduous or mixed forest associates in northeastern Pennsylvania, as both Black-throated Blue Warbler and Wood Thrush were grouped in section B of the DCA analysis. Although our regression analyses failed to show any additional associations between Black-throated Blue Warbler and the vegetative characteristics of the stands, we found Wood Thrush to be positively associated with increasing mid-story and conifer cover. Similar to Black-throated Blue Warbler and Wood Thrush, Canada Warbler prefer damp,

mixed forests with extensive understory thickets comprised of hemlock, rhododendron, and laurels (Brauning 1992, Ehrlich et al. 1988). Our findings support this habitat classification for Canada Warbler within northeastern Pennsylvania, as Canada Warbler was grouped with the mature northern hardwood forest birds and was positively associated with stands containing an abundance of midstory and coniferous cover.

A fourth mature forest associate of management concern, Cerulean Warbler, has shown a trend ($P = 0.15$) toward declining populations since 1966 (Sauer et al. 1997). Cerulean Warblers are partial to mature, upland oak woodlands containing water and are sensitive to forest fragmentation (Brauning 1992, Ehrlich et al. 1988, Robbins et al. 1989). The results of our research support past findings for Cerulean Warblers, as we identified them within only oak-hickory stands in close proximity (1km) to permanent water ($n = 7$). However, Cerulean Warblers were located on three harvested stands that contained between 12-15m²/ha residual tree basal area, and two pairs of birds successfully produced young within at least one of the harvested stands. Although Cerulean Warblers may be sensitive to permanent forms of forest fragmentation such as increased development, they may be tolerant of temporary, small scale habitat disturbances within extensive forested landscapes exemplified by 8-12ha selection harvests in the Pocono Plateau section of northeastern Pennsylvania.

Unlike these mature forest bird species, the Golden-winged Warbler is a species of management concern undergoing population declines that prefers early successional habitats (Sauer et al. 1997). Population declines are due primarily to the loss of habitat with natural forest succession or reverse forest fragmentation (Yahner 2000) and competition and hybridization with Blue-winged Warbler (Brauning 1992, Confer and Knapp 1981, Gill 1980). Golden-winged Warbler typically breed in recently abandoned old fields containing small oak saplings or in young oak regeneration on recently clearcut forest stands (Brauning 1992, Ehrlich et al. 1988). Similarly, we found positive associations between Golden-winged Warbler and decreasing overstory tree cover and tree basal area and increasing shrub cover. We recorded the highest densities of Golden winged Warbler on stands with 6-35% overstory tree cover, 3-14m²/ha tree basal area, and 15-50% shrub cover.

MANAGEMENT IMPLICATIONS

Forest harvesting influences the species richness, abundance, and species composition of birds in northern hardwood and oak-hickory forests by altering forest stand characteristics, especially tree basal area and understory plant cover. Identifying distinct thresholds between bird abundance or species richness and forest

characteristics combined with associating what bird species could be present with certain forest characteristics provides resource managers with specific guidelines for stand planning. If the goal is to maximize species richness and create habitat for early successional species of management concern including Eastern Towhee, Field Sparrow, and Golden-winged Warbler, then stands should retain less than 18.5 m²/ha tree basal area and have greater than 45% understory plant cover following logging. Likewise, bird abundance was maximized on stands with less than 18.5 m²/ha tree basal. However, if maintaining mature forest bird populations including Black-throated Blue Warbler, Blue-headed Vireo, Canada Warbler, Ovenbird, Scarlet Tanager, and Wood Thrush are a top priority, then the goal for a resource management professional should be to retain more than 26 m²/ha tree basal area on a stand after harvesting. Besides within stand characteristics, natural resource professionals need to consider land-use types surrounding the stand and the amount of contiguous forest within the landscape when managing for mature forest birds.

In addition to managing for certain sections of the bird community such as early successional or mature forest birds, individual bird species can also be incorporated into management plans. Combining the results of correlation and DCA analyses will aid with identifying habitat characteristics required by bird species, especially species of management concern. Natural resource professionals can improve vegetation characteristics that benefit species of management concern, such as retaining or helping to create shrub cover on oak-hickory stands for Golden-winged Warbler when harvesting timber. Resource managers can incorporate the habitat requirements of species with threshold information for tree basal area and understory plant cover to better address both species specific and community level relationships between birds and vegetative characteristics when harvesting timber in northeastern Pennsylvania.

It is important to note that this study only addresses temporary effects up to ten years following timber harvesting. Additional research is necessary to address how avian communities respond to timber management in other forest types and geographical regions over longer time periods than those examined in this study.

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