FACTORS INFLUENCING AVIAN COMMUNITIES IN HIGH-ELEVATION SOUTHERN ALLEGHENY MOUNTAIN FORESTS

Harry A. Kahler and James T. Anderson[1]

Abstract.—Myriad factors may influence bird community characteristics among subalpine, central, and northern hardwood forest cover types of the southern Allegheny Mountains. Differences in forest cover types may result from natural characteristics, such as tree species composition, topography, or elevation, as well as from past influences, such as poor logging practices. Our objectives were to: 1) compare breeding bird diversity, richness, and density among 90+ year-old central hardwood (white oak-black oak-Northern red oak) (*Quercus alba-Q. velutina-Q. rubra*), northern hardwood (black cherry-maple) (*Prunus serotina-Acer* spp.), and subalpine (red spruce-yellow birch) (*Picea rubens-Betula alleghaniensis*) stands; and 2) analyze avian community compositions among the three forest categories (n = 30 plots per cover type). We conducted our study on the Monongahela National Forest in Pendleton, Pocahontas, and Randolph Counties, WV. Overall, 57 species of birds were tallied. The most numerous species were red-eyed vireos (*Vireo olivaceus*) and black-throated green warblers (*Dendroica virens*). We found no differences in avian species' diversity, richness, or overall density among a central hardwood, northern hardwood, and subalpine forest type ($P > 0.05$). However, avian community composition varied among the three forest types. Of 27 species analyzed, only 6 had similar densities among cover types. Increased basal area of yellow birch and sugar maple (*Acer saccharum*) together increased the likelihood of occurrence of the Blackburnian warbler (*Dendroica fusca*), black-throated blue warbler (*Dendroica caerulescens*), and winter wren (*Troglodytes troglodytes*). Basal area was a consistent covariate among analyses of diversity richness, and density. The ability to support avian communities is relatively equal among mature forest stands (i.e., >90 yrs) of the three main forest classes within southern Allegheny Mountain forests, yet the likelihood of occurrence of individual species varies with individual stand characteristics. Our results will be useful in formulating management strategies for avian conservation in high-elevation forests.

INTRODUCTION

Habitat fragmentation is a major factor in the loss of forest biodiversity (Hagan et al. 1996, Villard et al. 1999). Wildlife population declines have been attributed not only to direct losses of suitable habitat, but also to isolation effects (i.e., habitat configuration). Increased amounts of habitat edges also have negatively affected wildlife population levels (Hagan et al. 1996, Villard et al. 1999). Poor timber-harvesting practices of the past, such as those throughout the late 1800s in the southern Allegheny Mountains of West Virginia (Clarkson 1993), are often cited as causes of forest fragmentation. Incipient harvesting and fragmentation affect wildlife population levels quite differently from residual and historical causes (Hagan et al. 1996).

A topic less discussed by conservationists is that forest fragmentation can coalesce from natural processes and anthropomorphic disturbances and natural processes. The Allegheny Mountains are within the central hardwoods region, yet northern hardwood and boreal forest types also can be found within the immediate area (Eyre 1980, Hicks 1998). The physiographic Allegheny Mountain section of the Appalachian Plateau runs southwesterly from central Pennsylvania to the highest peaks of West Virginia

[1] (HAK), U.S. Fish and Wildlife Service, 2800 Cottage Way, Sacramento, CA 95825; Professor (JTA), Division of Forestry and Natural Resources, West Virginia University, Box 6125, Morgantown, WV 26506. JTA is corresponding author: to contact, call (304) 293-3825 or email at jim.anderson@mail.wvu.edu.

(Fenneman 1938). At the highest elevations of the Allegheny Mountains in West Virginia, generally above 1,000 m, relict patches of boreal forests remain from cooler, periglacial times (Lesser 1993). Moving down in elevation, forests become a mosaic between higher, north-facing northern hardwood types and lower, south-facing central hardwood stands (Hicks 1998).

Furthermore, since the 1960s, evidence shows that boreal forests of North America are shrinking in area, mainly due to increasing mortality rates of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* L.) at higher elevations (Stephenson and Adams 1993). Coupled with these natural processes, Allegheny Mountain forests in West Virginia were cleared to establish farmsteads, red spruce tracts at higher elevations were girdled and burned to produce cattle pastures, and subsequent timber logging altered forest composition (Clarkson 1993, Stephenson and Adams 1993). Removal of the timber has left mostly a mosaic of second- and third-growth forests (Stephenson 1993). Preferential harvesting and introduced diseases and pests also have changed stand composition over time (Carvell 1986, Acciavatti et al. 1993). In view of these processes, our objectives were to compare avian community composition, diversity, and density among central hardwood, northern hardwood, and boreal forest cover types of the southern Allegheny Mountains region and relate bird occurrence to plot characteristics.

STUDY AREA

The study was conducted on the Potomac and Greenbrier Ranger Districts of the Monongahela National Forest in Pendleton, Pocahontas, and Randolph Counties, WV during 2000 and 2001. In reaction to past over-harvesting and subsequent fire damage, the Monongahela National Forest was formed in 1920 to protect the forest resources in the southern Allegheny Mountains (Clarkson 1993).

All study plots were within 27 km of a geographic center near Lost Run in Highland County, VA, which is about 11.8 km east of the Greenbrier District Ranger Station in Bartow, WV. Elevation ranges from 540 m to 1,481 m, with some slopes near 70 percent grade. In general, elevations above 1,000 m contain boreal forests that are relicts from periglacial periods (Hall 1983). Below the boreal cover, forests are typically a mosaic of higher, north-facing northern hardwood types and lower, south-facing central hardwood stands (Hicks 1998). Site indices typically range from 35 to 80, indicating the expected height of trees after 50 years growth (Pyle et al. 1982, Estepp 1992, Flegel 1999). Stands averaged 103 years old and had an average basal area of 26-27 m^2/ha.

METHODS

Plot Establishment

Ninety 50-m radius study plots were divided evenly among white oak (*Quercus alba* L.)-black oak (*Q. velutina* Lam.)-northern red oak (*Q. rubra* L.) (WO-BO-NRO), which includes the sub-type scarlet oak (*Q. coccinea* Munchh.)-chestnut oak (*Q. Montana* Willd.); black cherry (*Prunus serotina* Ehrh.)-maple (*Acer* spp.) (BC-M); and red spruce-yellow birch (*Betula alleghaniensis* Britton) (RS-YB) cover types (Eyre 1980). These types represent central hardwood, northern hardwood, and boreal forests, respectively.

We randomly selected appropriate forest stands from a Monongahela National Forest database of stands >90 years to establish study plots (Kahler and Anderson 2006). We avoided areas with recent or intense management activity. Each plot was within one mapped stand, and plots were at least 250 m apart for independent sampling (Ralph et al. 1995).

Plot Inventory

In summer months we estimated percentage overstory cover (codominant and dominant canopy), understory cover (2 m tall to overtopped canopy), and shrub cover (<2 m tall) at center points and estimates at three random equidistant points about 25 m from the plot center, for average plot values (Kahler and Anderson 2006). Center locations were marked with a geographic positioning system unit, and point slope and prevailing aspect also were recorded (Marcot 1983, Marzluff and Lyon 1983). Plot elevations were determined from digital elevation grids (with cell sizes of 90 m) using ArcView GIS software (ESRI, Redlands, CA).

We sampled center points with a basal-area factor-10 prism to determine basal area and tallied all trees >10 cm diameter at breast height (d.b.h.) within plots (DeGraaf and Shigo 1985, Kahler and Anderson 2006). For each tallied tree the species, d.b.h., and height (determined with a clinometer) were recorded. Plot composition, basal area, and number of standing trees were estimated from prism-tally information (Avery and Burkhart 1997).

Breeding Bird Counts

We estimated relative bird abundance using a 50-m fixed radius point count method on all plots (Ralph et al. 1995). Thirty original plots (10 per forest type) were established and visited twice between 27 May and 2 July 2000. All 90 plots were surveyed twice between 26 May and 4 July 2001. Counts were 10 minutes in duration, and all sky and wind conditions were acceptable as per Ralph et al. (1995). Plot information was pooled between visits but separated by year. For comparisons among forest types, all maximum yearly plot tallies were used in statistical analyses.

Statistical Analyses

Maximum species abundance values between the two yearly point counts were used to determine yearly richness and density (number of birds counted divided by area of the plot) for each plot (Nur et al. 1999) and we used Shannon's Index to quantify yearly plot diversities (Nur et al. 1999). Because of unequal plot sample sizes between years, data were analyzed by two principle methods to include information from all points in both years. We tested the equality of occurrence for species among the three forest types in 3x2 χ^2 contingency tests using maximum count data by point from 2000-2001 (Dowdy and Wearden 1991, Zar 1999). Only species with expected frequencies (i.e., total number of observed frequencies/3 for each forest type) of >5 individuals/forest type were tested (Dowdy and Wearden 1991, Zar 1999). We used logistic regression models to determine whether individual species' presence on plots was related to the following plot characteristics: basal area, stem density, overstory cover, understory cover, shrub cover, elevation, and basal areas and stem densities of the eight most common tree species (Nur et al. 1999). Hosmer and Lemeshow goodness-of-fit tests were used to measure model significance (Cody and Smith 1997). Between-year data were tested using a nested analysis of variance (ANOVA) design; forest types were treatment groups, with 10 plots per treatment, and two replications per plot (Dowdy and Wearden 1991). Diversity, richness, and total species abundance were tested using the nested design.

RESULTS

Fifty-seven bird species were tallied among the three forest cover types. Thirty-eight species were found in RS-YB plots, 42 were counted in BC-M, and 39 were in WO-BO-NRO plots. The 2001 maximum tally of all species on all plots totaled 1,020 birds; 412 were counted in RS-YB stands, 313 individuals in BC-M stands, and 295 individuals in WO-BO-NRO stands. Using the maximum species abundance values between years for each plot (birds/ha/year), the maximum densities were 10.6 in RS-YB plots, 8.9 in BC-M stands, and 7.7 in WO-BO-NRO plots.

We recorded 27 species at least 15 times using maximum tallies at each plot for each species (Table 1). Only 6 of the 27 species showed equal occurrences among all forest cover types. The most numerous species among all plots per breeding season were red-eyed vireos (See Table 1 for scientific names of most bird species) and black-throated green warblers, each recorded 60 times in 2001. Only dark-eyed juncos were found on all RS-YB plots. Red-eyed vireos were most widespread among BC-M and WO-BO-NRO plots, occupying 28 and 24 of 30 plots, respectively. In contrast, red-eyed vireos occupied only 10 RS-YB plots.

Logistic regression models explained the likelihood of occurrence of 13 bird species (Table 2).The presence of three species varied positively with both elevation and shrub cover (percent). The presence of two species varied negatively with those variables. Among tree species, increased basal area per plot of yellow birch and sugar maple (*Acer saccharum* Marsh.) together increased the likelihood of occurrence of Blackburnian warblers, black-throated blue warblers, and winter wrens. Separately, the likelihood of four species increased with greater yellow birch stem densities while the presence of three species increased with higher sugar maple stem densities.

Species diversity between years was similar among RS-YB ($\overline{X}$ = 0.94, SE = 0.024), BC-M ($\overline{X}$ = 0.85, SE = 0.040), and WO – BO – NRO ($\overline{X}$ = 0.84, SE = 0.039) forest types ($F_{2,27}$ = 1.95, P = 0.162). Likewise, overall species richness was similar among RS-YB ($\overline{X}$ = 9.4, SE = 0.48), BC-M ($\overline{X}$ = 8.1, SE = 0.71), and WO-BO-NRO ($\overline{X}$ = 7.95, SE = 0.64) cover types when considering both years' data ($F_{2,27}$ = 1.70, P = 0.202). Furthermore, total species densities among RS-YB ($\overline{X}$ = 15.5, SE = 0.93), BC-M ($\overline{X}$ = 12.7, SE = 1.15), and WO-BO-NRO (= 12.8, SE = 0.98) were not significantly different ($F_{2,27}$ = 2.53, P = 0.099).

DISCUSSION

Forests of the southern Allegheny Mountains are a mosaic of hardwood, northern hardwood, and boreal forest cover types (Hicks 1998). Because of the differences in silvicultural composition, we hypothesized that wildlife species diversity, richness, and densities would differ among these forest classes as well. Using RS-YB, BC-M, and WO-BO-NRO forest cover types to represent the three forest classes, we found no evidence to support the hypotheses that bird species diversity, richness, and density differ among the forest cover types. Thus, it appears that the ability to support avian communities is relatively equal among mature forest stands (i.e., >90 yrs) of the three main forest classes within southern Allegheny Mountain forests, yet the likelihood of occurrence of individual species varies with individual stand characteristics.

Of habitat structure, the basal area of standing wood was the only consistent covariate in wildlife guild diversity, richness, and density models. In central Allegheny Mountain hardwood forests bird species richness and abundance sharply increased in stands with basal areas below 18 m^2/ha (but not for interior forest species), and decreased sharply in stands with basal areas exceeding 26 m^2/ha (due to diminishing edge species) (Ross et al. 2001). The mean basal area of our study plots was 26-27 m^2/ha (Kahler 2002). Higher basal areas are generally associated with lower shrub and understory density. In turn, greater vertical diversity (i.e., higher shrub and understory densities) may accommodate greater avian diversity and abundances (Rodewald and Smith 1998, Hobson and Bayne 2000). Thus, management strategies involving timber harvesting at 90- to 100-yr rotations should mimic small gap disturbances within forest patches to optimize bird diversity and richness among forest edge and interior species.

Forest Cover Types

Point count surveys did not detect differences in bird species diversity or richness among forest cover types, yet avian community structure within southern Allegheny Mountain forests varies along an elevational gradient. Some species were recorded only in RS-YB stands, such as Swainson's thrush and the red crossbill. Other species, such as winter wren and hermit thrush, were counted only within the northern forest types. Three species were found only in BC-M stands, yet only alder flycatchers (*Empidonax alnorum* Brewster) were recorded more than once. At lower elevations, white-breasted nuthatch, tufted titmouse, and wood thrush appeared only in hardwood stands, while eastern wood-pewee and black-and-white warbler (*Mniotilta varia* L.) were observed only in WO-BO-NRO plots.

Differences in forest structure, such as basal area, understory cover, and shrub cover, among stands of the same forest type may shape differences in breeding bird community structure. Chances of black-throated green warbler presence seemed to increase with increased stand basal area and decreased stem densities and the Blackburnian warbler also was associated with larger-diameter trees. Likewise, Hobson and Bayne (2000) found these species more abundant on contiguous forest tracts than on fragmented areas. Openings in understory and shrub cover negatively impact black-throated blue warbler forest movements (Belisle et al. 2001, Harris and Reed 2001). Thus we found black-throated blue warbler presence associated with denser shrub layers. Moreover, we found Canada warbler only in RS-YB and BC-M plots with shrub cover >75 percent, with rhododendron (*Rhododendron maximum*) the major shrub component. Hobson and Schiek (1999) found significantly more Canada warblers in 28-year-old post-harvest stands than on uncut stands, possibly due to the denser shrub layer on post-harvest stands.

Table 1.—Most common bird species recorded in 50-meter point count plots in Monongahela National Forest, 2000-2001. Numbers reflect maximum tally for each plot (n = 30 for each forest type).

Species	Forest Type[a] S	N	C	χ^2	P
Acadian flycatcher (*Empidonax virescens*)	1ad	2ad	13bd	16.625	<0.001
American robin (*Turdus migratorius*)	10a	8a	6a	1.000	0.607
Blackburnian warbler (*Dendroica fusca*)	38a	17b	15b	13.914	0.001
Black-capped chickadee[b] (*Poecile atricapilla*)	36a	14b	9b	20.983	<0.001
Black-throated blue warbler (*Dendroica caerulescens*)	33a	8b	8b	25.510	<0.001
Black-throated green warbler (*Dendroica virens*)	25a	30a	20a	2.000	0.368
Blue jay (*Cyanocitta cristata*)	8a	9a	8a	0.080	0.961
Blue-headed vireo (*Vireo solitarius*)	12a	17a	13a	1.000	0.607
Brown creeper (*Certhia americana*)	15a	7a	0b	15.364	<0.001
Cedar waxwing (*Bombycilla cedrorum*)	7a	10a	1b	7.000	0.030
Dark-eyed junco (*Junco hyemalis*)	48a	24b	4c	38.316	<0.001
Downy woodpecker[b] (*Picoides pubescens*)	2a	9b	12b	6.870	0.032
Golden-crowned kinglet *(Regulus satrapa*)	33a	6b	0c	47.538	<0.001
Eastern wood-pewee (*Contopus virens*)	0a	0a	15b	30.000	<0.001
Hermit thrush (*Catharus guttatus*)	12a	17a	0b	15.793	<0.001
Magnolia warbler (*Dendroica magnolia*)	39a	20b	3c	31.387	<0.001
Ovenbird (*Seirus aurocapillus*)	0a	11b	12b	11.565	0.003
Red-breasted nuthatch[b] (*Sitta canadensis*)	25a	3b	1b	36.690	<0.001
Red-eyed vireo (*Vireo olivaceus*)	10a	37b	36b	16.940	<0.001
Acadian flycatcher (*Empidonax virescens*)	1ad	2ad	13bd	16.625	<0.001
Scarlet tanager (*Piranga olivacea*)	6a	11a	14a	3.161	0.206
Swainson's thrush (*Catharus ustulatus*)	20a	0b	0b	40.000	<0.001
Tufted titmouse[b] (*Baeolophus bicolor*)	0a	5a	14a	15.895	<0.001
Veery (*Catharus fuscescens*)	16a	22a	18a	1.000	0.607
White-breasted nuthatch[b] (*Sitta carolinensis*)	0a	15b	27b	26.143	<0.001
Wood thrush (*Hylocichla mustelina*)	0a	9b	12b	11.143	0.004
Yellow-bellied sapsucker[b] (*Sphyrapicus varius*)	1a	2a	14b	18.471	<0.001

[a] Forest types are as follows: S-subalpine (red spruce-yellow birch) forest cover type; N-northern hardwood (black cherry-maple) forest cover type; and C -central hardwood (white oak-black oak-Northern red oak) forest cover type.

[b] Species demonstrates at least facultative use of tree cavities.

[c] 3x2 χ^2 test ($\chi^2_{0.05,2} = 5.991$).

[d] Same letters indicate no likelihood separation, 2x2 χ^2 test ($\chi^2_{0.05,1} = 3.841$).

Blue-headed vireo presence was associated with understory cover, in concurrence with results from a Canadian boreal forest (Drolet et al. 1999). In contrast, Drolet and others (1999) found American robin in association with poorly forested landscapes. Similarly, American robin was associated with increased stems counts of black cherry, an early successional species (Marquis 1990), and red maple (*Acer rubrum* L.), which is common on poor growing sites (Walters and Yawney 1990).

Furthermore, wood thrush, Swainson's thrush, hermit thrush, and veery are all considered ground-foraging species, yet foraging heights of the thrush species were stratified among species present from 0-8 m above ground level (Holmes and Robinson 1988). Wood thrushes spend >98 percent of foraging time <2 m from the ground (Holmes and Robinson 1988). Similarly, we found the likelihood of wood thrush presence increased significantly with increased overstory cover, which suggests less understory and shrub cover presence. Furthermore, Swainson's thrushes will use a

Table 2.—Logistic regression models based on presence of bird species on 90 plots, Monongahela National Forest, 2000-2001.

Species	Parameter[a]	Estimate	χ^2	*P*
Acadian flycatcher	overstory cover (%)	7.432	4.172	0.041
Empidonax virescens	elevation (m)	-0.021	15.664	<0.001
(*n* = 15)	n. red oak basal area (m^2/ha)	1.360	5.000	0.025
	Hosmer-Lemeshow goodness-of-fit[b]		4.714	0.788
American robin	overstory cover (%)	7.432	4.172	0.041
Turdus migratorius	elevation (m)	-0.009	7.158	0.008
(*n* = 21)	black cherry density (stems/ha)	0.961	8.281	0.004
	red maple density (stems/ha)	0.585	4.000	0.046
	red spruce density (stems/ha)	0.666	4.584	0.032
	yellow birch density (stems/ha)	0.685	5.867	0.015
	Hosmer-Lemeshow goodness-of-fit[b]		4.890	0.769
Blackburnian warbler	sugar maple basal area (m^2/ha)	0.787	8.643	0.003
Dendroica fusca	yellow birch basal area (m^2/ha)	0.749	15.531	<0.001
(*n* = 50)	white oak density (stems/ha)	0.747	5.892	0.015
	Hosmer-Lemeshow goodness-of-fit[b]		3.900	0.866
Black-throated blue warbler	shrub cover (<2 m) (%)	3.589	10.524	0.001
	elevation (m)	0.011	10.313	0.001
Dendroica caerulescens	sugar maple basal area (m^2/ha)	0.744	7.348	0.007
(*n* = 40)	yellow birch basal area (m^2/ha)	0.470	6.058	0.014
	Hosmer-Lemeshow goodness-of-fit[b]		7.897	0.444
Black-throated green warbler	basal area (m^2/ha)	4.944	3.568	0.059
	inventory density (stems/ha)	-4.732	6.929	0.009
Dendroica virens	elevation (m)	0.011	14.291	<0.001
(*n* = 62)	red spruce density (stems/ha)	-1.038	5.199	0.023
	Hosmer-Lemeshow goodness-of-fit[b]		9.010	0.341
Blue-headed vireo	understory cover (>2m) (%)	1.834	2.952	0.086
Vireo solitarius	Hosmer-Lemeshow goodness-of-fit[b]		9.010	0.341
(*n* = 39)				
Canada warbler	understory cover (>2m) (%)	-4.056	3.338	0.068
Wilsonia canadensis	shrub cover (<2 m) (%)	5.309	9.112	0.003
(*n* = 10)	Hosmer-Lemeshow goodness-of-fit[b]		4.486	0.811
Scarlet tanager	basal area (m^2/ha)	4.919	4.359	0.037
Piranga olivacea	sugar maple density (stems/ha)	1.444	9.941	0.002
(*n* = 31)	white oak density (stems/ha)	1.077	12.613	<0.001
	Hosmer-Lemeshow goodness-of-fit[b]		7.910	0.442
Swainson's thrush	shrub cover (<2m) (%)	3.517	7.827	0.005
Catharus ustulatus	yellow birch density (stems/ha)	0.525	6.484	0.011
(*n* = 17)	Hosmer-Lemeshow goodness-of-fit[b]		4.456	0.726
Veery	inventory stems	-2.252	4.379	0.036
Catharus fuscescens	understory cover (> 2m)	2.854	5.519	0.019
(*n* = 43)	elevation	0.004	3.706	0.054
	sugar maple stems	0.457	2.915	0.088
	Hosmer-Lemeshow goodness-of-fit[b]		6.920	0.545

continued

Table 2.— Continued.

Species	Parameter[a]	Estimate	χ^2	*P*
White-breasted nuthatch	basal area	4.180	3.209	0.073
Sitta carolinensis	shrub cover (< 2m)	-1.861	3.565	0.059
(*n* = 30)	yellow birch stems	-0.915	11.054	0.001
	Hosmer-Lemeshow goodness-of-fit[b]		5.568	0.696
Wood thrush	overstory cover	4.284	3.730	0.054
Hylocichla mustelina	shrub cover (< 2m)	-3.027	6.530	0.011
(*n* = 20)	yellow birch stems	-0.527	3.423	0.064
	Hosmer-Lemeshow goodness-of-fit[b]		4.442	0.815
Winter wren	understory cover (> 2m)	-3.949	4.025	0.045
Troglodytes troglodytes	sugar maple basal area	2.911	4.822	0.028
(*n* = 12)	yellow birch basal area	0.857	7.326	0.007
	sugar maple stems	-2.788	2.926	0.087
	Hosmer-Lemeshow goodness-of-fit[b]		4.442	0.815

[a] All independent variables with P<0.10 are left in the model.

[b] All P>0.05 show significant model fit.

slightly higher foraging substrate (Holmes and Robinson 1988). Likewise, the likelihood of Swainson's thrush presence increased significantly with increased shrub cover. Thus, the presence or absence of a particular bird species may not wholly depend on forest cover type; the amount and quality of sub-canopy vegetation also may influence avian community structure.

The occurrences of 9 of 13 species were directly related to amounts of sugar maple and yellow birch present in stands. These tree species occur together in greatest proportion in an elevational gradient between the pure red spruce stands and northern hardwood forest types such as BC-M, maple-beech (*Fagus grandifolia* Ehrh.)-birch, and beech-sugar maple (Eyre 1980). Thus, edge effects (i.e., increased species occurrences) may happen between forest cover types of similar ages.

As with foraging substrate resources, we found evidence that cavity tree resources may influence dependent, secondary cavity-nesting bird densities. Conifers usually will not hold durable and usable cavities for secondary species (Van Balen et al. 1982). Indeed, we observed the tufted titmouse and white-breasted nuthatch only among hardwood stands. Moreover, cavity tree abundances were highest within the WO-BO-NRO forest cover type, along with 75 percent and 66 percent of all tufted titmouse and white-breasted nuthatch observations, respectively. Tree hardness influences nest-site choices of excavating birds (Schepps et al. 1999). We observed weak-excavating species (i.e., red-breasted nuthatch, black-capped chickadee) mostly in the RS-YB forest cover type (85 percent and 63 percent of all observations, respectively), where the softer, decayed wood of red spruce and yellow birch may provide a substrate easier to excavate than other hardwood species. Furthermore, territoriality has been shown to influence differential habitat use among sympatric chickadees (Hill and Lein 1989). The larger tufted titmouse and white-breasted nuthatch may out-compete the smaller red-breasted nuthatch and black-capped chickadee for territories, relegating weak-excavators to that part of their niche where there is no sympatric overlap.

All three cover types are important for maintaining overall avian diversity in the Southern Allegheny Mountains. Species composition varied among cover types and hence species-specific management may be best suited to a particular cover type. Based on trends in cover type abundance, we recommend a focus on restoration of subalpine cover types to ensure long-term maintenance of avian diversity.

ACKNOWLEDGMENTS

We thank the following agencies for supporting this project: U.S. Fish and Wildlife Service; U.S. Department of Agriculture, Forest Service; and the McIntire-Stennis Program. We also thank the personnel at the Greenbrier Ranger District of the U.S. Forest Service for cooperation, help, and advice, as well as R.R. Hicks and J.S. Rentch for reviewing earlier drafts of this manuscript. This manuscript is Scientific Article number 3042 of the West Virginia University Agriculture and Forestry Experiment Station.

LITERATURE CITED

Acciavatti, R.E.; Allen, T.J.; Miller, A.R.; Pechuman, L.L.; Kondratieff, B.C.; Kirchner, R.F.; Wheeler, A.G., Jr.; Clark S.M.; van den Berghe E.; Arnold, W.J. 1993. **Insects and spiders of the upland forests.** In: Stephenson, S.L., ed. **Upland forests of West Virginia.** Parsons, WV: McClain Printing Co.: 143-178.

Avery, T.E.; Burkhart, H.E. 1997. **Forest measurements.** Fourth Edition. Boston, MA: McGraw Hill Co. xx p.

Belisle, M.; Desrochers, A.; Fortin, M.J. 2001. **Influence of forest cover on the movements of forest birds: A homing experiment.** Ecology. 82: 1893-1904.

Carvell, K.L. 1986. **Effect of past history on present stand composition and condition.** In: Smith, H.C.; Eye, M.C., eds. Guidelines for managing immature Appalachian hardwood stands. Morgantown, WV: West Virginia University Books: 1-7.

Clarkson, R.B. 1993. **Destruction of the upland forests by lumbering and fire.** In: Stephenson, S.L., ed. Upland forests of West Virginia. Parsons, WV: McClain Printing Co.: 35-65.

Cody, R.P.; Smith, J.K. 1997. **Applied statistics and the SAS programming language.** New York, NY: Simon and Schuster Inc. 445 p.

DeGraaf, R.M.; Shigo, A.L. 1985. **Managing cavity trees for wildlife in the Northeast.** Gen. Tech. Rep. NE-101. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 23 p.

Dowdy, S.M.; Wearden, S. 1991. **Statistics for research.** Second Edition. New York, NY: John Wiley and Sons. 629 p.

Drolet, B.; Desrochers, A.; Fortin, M.J. 1999. **Effects of landscape structure on nesting songbird distribution in a harvested boreal forest.** Condor. 101: 699-704.

Estepp, R. 1992. **Soil survey of Pendleton County, West Virginia.** Washington, D.C.: U.S. Department of Agriculture, Soil Conservation Service. 274 p.

Eyre, F.H. 1980. **Forest cover types of the United States and Canada.** Bethesda, MD: Society of American Foresters. 148 p.

Fenneman, N.M. 1938. **Physiography of eastern United States.** New York, NY: McGraw-Hill Book Co. 714 p.

Flegel, D.G. 1999. **Soil survey of Pocahontas County, West Virginia.** Washington, D.C.: U.S. Department of Agriculture, Natural Resources Conservation Service. 301 p.

Hagan, J.M., III; Vander Haegen, W.M.; McKinley, P.S. 1996. **The early development of forest fragmentation in birds.** Conservation Biology. 10(1): 188-202.

Hall, G.A. 1983. **West Virginia birds: distribution and ecology.** Special Publication No. 7. Pittsburgh, PA: Carnegie Museum of Natural History.180 p.

Harris, R.J.; Reed, M.J. 2001.**Territorial movements of black-throated blue warblers in a landscape fragmented by forestry.** Auk. 118: 544-549.

Hicks, R.R., Jr. 1998. **Ecology and management of central hardwood forests.** New York: John Wiley and Sons. 412 p.

Hill, B.G.; Lein, M.R. 1989. **Territory overlap and habitat use of sympatric chickadees.** Auk. 106: 259-268.

Hobson, K.A.; Bayne, E. 2000. **The effects of stand age on avian communities in aspen-dominated forests of central Saskatchewan, Canada.** Forest Ecology and Management. 136:121-134.

Hobson, K.A.; Schiek, J. 1999. **Changes in bird communities in a boreal mixed wood forest: Harvest and wildfire effects over 30 years.** Ecological Applications. 9: 849-863.

Holmes, R.T.; Robinson. S.K. 1988. **Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwood forest.** Wilson Bulletin. 100: 377-394.

Kahler, H.A. 2002. **Nest-site resources for cavity-nesting birds in the Southern Allegheny Mountain forests of West Virginia.** Morgantown, WV: West Virginia University. 127 p. M.S. thesis.

Kahler, H.A.; Anderson, J.T. 2006. **Tree cavity resources for dependent cavity-using wildlife in the southern Allegheny Mountains.** Northern Journal of Applied Forestry. 23: 114-121.

Lawler, J.J.; Edwards, T.C., Jr. 2002. **Composition of cavity-nesting bird communities in montane aspen woodland fragments: The roles of landscape context and forest structure.** Condor. 104: 890-896.

Lesser, W.H. 1993. **Prehistoric human settlement in the upland forest region.** In: Stephenson, S.L., ed. Upland forests of West Virginia. Parsons, WV: McClain Printing Co.: 231-260.

Marcot, B.G. 1983. **Snag use by birds in Douglas-fir clearcuts.** In: Davis, J.W.; Goodwin, G.A.; Ockenfels, R.A., tech. coord. Snag habitat management: Proceedings of the symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 134-139.

Marquis, D.A. 1990. ***Prunus serotina* Ehrh. black cherry.** In: Burns, R.M., Honkala, B.H., tech. coord. Silvics of North America. Volume 2. Hardwoods. Agric. Handbk. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 594-604.

Marzluff, J.M.; Lyon, L.J. 1983. **Snags as indicators of habitat suitability for open nesting birds.** In: Davis, J.W.; Goodwin, G.A.; Ockenfels, R.A., tech. coord. Snag habitat management: Proceedings of the symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 140-146.

Nur, N.; Jones, S.L.; Geupel, G.R. 1999. **Statistical guide to data analysis of avian monitoring programs.** Biological Tech. Public. BTR-R6001-1999. Washington, DC: U.S. Department of Interior, Fish and Wildlife Service.

Pyle, R.E.; Beverage, W.W.; Yoakum, T.; Amick, D.P.; Hatfield, W.F.; McKinney, D.E. 1982. **Soil survey of Randolph County area main part, West Virginia.** Washington, DC: U.S. Department of Agriculture, Soil Conservation Service. 181 p.

Ralph, C.J.; Sauer, J.R; Droege, S., eds. 1995. **Monitoring bird populations by point counts.** Gen. Tech. Rep. PSW-149. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 187 p.

Rodewald, P.G.; Smith, K.G. 1998. **Short-term effects of understory and overstory management on breeding birds in Arkansas.** Journal of Wildlife Management. 62: 1411-1417.

Ross, B.D.; Morrison, M.L.; Hoffman, W.; Fredericksen, T.S.; Sawicki, R.J.; Ross, E.; Lester, M.B.; Beyea, J.; Johnson, B.N. 2001. **Bird relationships to habitat characteristics created by timber harvesting in Pennsylvania.** Journal of the Pennsylvania Academy of Science. 74: 71-84.

Schepps, J.; Lohr, S; Martin T.E. 1999. **Does tree hardness influence nest-tree selection by primary cavity nesters?** Auk. 116: 658-665.

Stephenson, S.L. 1993. **Upland forest vegetation.** In: Stephenson, S.L., ed. Upland forests of West Virginia. Parsons, WV: McClain Printing Co.: 11-34.

Stephenson, S.L.; Adams, H.S. 1993. **Threats to the Upland Forests.** In: Stephenson, S.L., ed. Upland forests of West Virginia. Parsons, WV: McClain Printing Co.: 261-273.

Van Balen, J.H.; Booy, C.J.H.; Franeker, J.A.; Osieck, E.R. 1982. **Studies on hole-nesting birds in natural nest sites.** Availability and occupation of natural nest sites. Ardea. 70: 1-24.

Villard, M.A., Trzcinski, M.K.; Merriam, G. 1999. **Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy.** Conservation Biology. 13: 774-783.

Walters, R.S.; Yawney, H.W. 1990. ***Acer rubrum* L. red maple.** In: Burns, R.M.; Honkala, B.H., tech. coord. Silvics of North America. Volume 2. Hardwoods. Agricul. Handbk. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 60-69.

Zar, J.H. 1999. **Biostatistical analysis.** Fourth Edition. Upper Saddle River, NJ.: Prentice Hall. 663 p.
