

THE SIGNIFICANCE OF HEMLOCK FOR BREEDING BIRDS IN THE WESTERN GREAT LAKES REGION

Robert W. Howe¹ and Michael Mossman²

¹Department of Natural and Applied Sciences, University of Wisconsin-Green Bay, Green Bay, WI 54311-7001 and ²Wisconsin Department of Natural Resources, Bureau of Research, 1350 Femrite Drive, Monona, WI 53716.

Abstract

Several species of songbirds (Black-throated Green Warbler, Blackburnian Warbler, Solitary Vireo, Winter Wren, and Red-breasted Nuthatch) show statistically significant associations with hemlock forests in Wisconsin and Upper Michigan. Comparisons of birds in managed forests with birds in the relatively pristine Sylvania Wilderness of Upper Michigan suggest that significant changes in bird species assemblages have resulted from the selective removal of hemlock from today's landscapes. Stands which retain at least some hemlocks and an uneven-aged forest structure support high bird densities compared with even-aged managed hardwood forests. Bird assemblages in isolated, hemlock-dominated natural areas of northern Wisconsin support unusually high bird densities and species richness. Bird assemblages in hemlock stands tend to show more local variability in bird density and, in the Nicolet National Forest, less numerical dominance by abundant species. Managed hemlocks are inhabited by characteristic hemlock bird species, but in many cases their densities are lower than in old growth sites. Many bird species characteristic of hardwood forests also occur in managed hemlocks, however, giving managed hemlocks high species richness and high conservation value.

Introduction

Hemlock provides physically unique microhabitats for breeding birds due to its shade tolerant lower branches and its dense, evergreen leaves (Benzinger 1994). Unlike white pine, hemlock typically retains foliage on its lower branches, providing important foraging and nesting substrates for mid-canopy specialists like Black-throated Green Warbler (Morse 1989, Collins 1983, Holmes 1986, Benzing 1994). The furrowed and irregular bark, particularly on older trees, provides hiding places for insects, which in turn provide favorable foraging opportunities for birds like Brown Creeper and Red-breasted Nuthatch. Finally, the dense shade under hemlock trees creates a cool, moist microenvironment that is favorable to birds like Winter Wren, especially when coarse woody debris accumulates on the forest floor (Holmes and Robinson 1988, Wolf and Howe 1991). Mixed stands of hardwoods and hemlock are characterized by high degrees of vertical and horizontal heterogeneity, qualities that are known to promote bird species diversity (MacArthur et al. 1962, Karr and Roth 1971, Freemark and Merriam 1986, Martin 1988).

Given these characteristics, forests containing hemlocks can be expected to support a high diversity of breeding birds, a prediction that will be addressed by this paper. Benzinger (1994) provides an excellent review of hemlock breeding bird assemblages in North America, but his analysis reveals remarkably few quantitative studies of birds in hemlock dominated forests (Kendeigh 1946, Beals 1960, Speiser 1982, Temple et al. 1979), perhaps reflecting the paucity of hemlock forests in today's human-dominated landscape (Frelich 1995). Here we describe the composition and abundances of breeding birds in hemlock forests of northern Wisconsin and the Upper Peninsula of Michigan. We hope to illustrate the importance of hemlock to breeding birds of this region, and we offer recommendations for forest management in light of our findings.

Specifically, we will attempt to answer four questions regarding bird assemblages in hemlock-dominated forests of Wisconsin and Upper Michigan: 1) Does the bird species richness in hemlock forests differ from that in ecologically similar forests where hemlock is absent? 2) Does the density of breeding birds in hemlock dominated forests differ from that in ecologically similar forests? 3) Do hemlock dominated forests support a *unique* assemblage of breeding bird species? and 4) Do hemlock dominated forests support a *distinct* assemblage of breeding bird species when compared to ecologically similar forests? Answers to these questions will help guide forest managers in assessing the impacts of forest management plans on the abundance and composition of regional bird communities.

Methods

Our analysis is based on two major studies of breeding birds in northern Wisconsin and Upper Michigan. The Nicolet National Forest Bird Survey is a long term monitoring program established by the Northeastern Wisconsin Audubon Society and the U.S. Forest Service (Howe et al. 1995). Since 1987, volunteer observers have conducted semi-annual point counts at 516 permanent stations distributed in representative habitats (n=316) and at randomly selected roadside points (n=200) in the Nicolet National Forest. (Sites in the northern half of the forest and southern half of the forest are visited during alternate years; beginning in 1995, roadside points in both halves of the forest are visited annually.)

The second study is part of an interdisciplinary investigation of old growth and managed forests funded by the Wisconsin Department of Natural Resources, U.S. Forest Service, U.S. Fish and Wildlife Service, and private sources. In collaboration with managers and other researchers, we selected 46 sites on moderately rich soils with similar geological history and topography (Figure 1). Ten of these sites were located in the 6000+ ha Sylvania Wilderness Area of the Ottawa National Forest, one of the largest remaining stands of old growth forest in the western Lake States (Frelich 1995). Four additional sites (all dominated by hemlock) were located in Wisconsin State Natural Areas, each < 100 ha in extent. The remaining sites were located in nearby multiple use forests managed by the U.S. Forest Service, Wisconsin Department of Natural Resources, or private timber companies. These sites were sampled more intensively than the Nicolet National Forest Bird Survey point counts. Within each study site a 250 m x 250 m plot was marked at 50 m intervals around the perimeter and at the center. Teams of 2 observers visited the plot 3 times between 1 June and 5 August 1993 and again 3 times during 1994. Each visit consisted of a 3 hour search, during which the observers

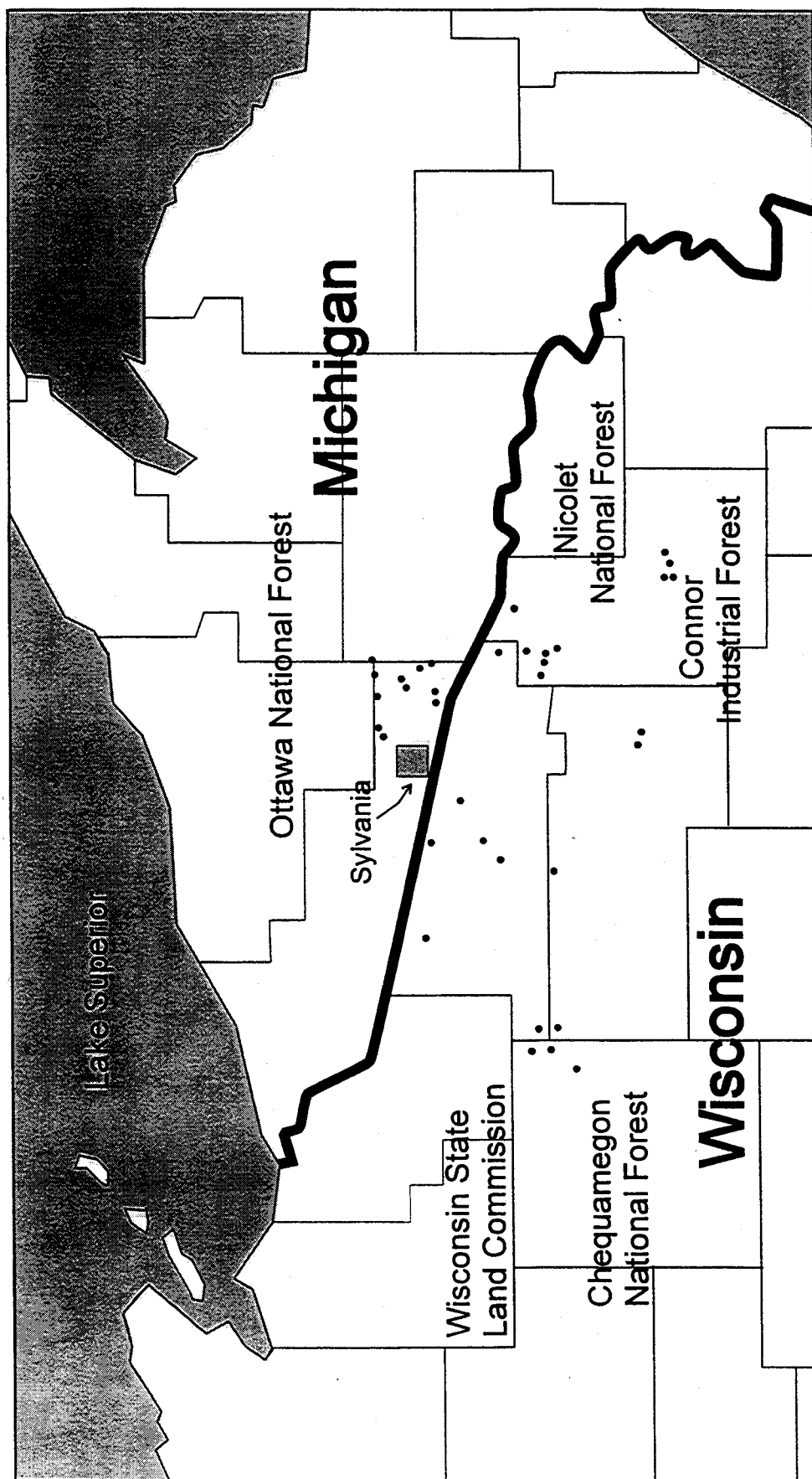


Figure 1. Location of sites for interdisciplinary study of old growth and managed forests.

Table 1. Comparison of species frequencies (% occurrence) in point counts of the Nicolet National Forest Bird Survey, 1987-1995. Numbers indicate the percent of counts during which the species was observed. Bird species which show a statistically significant association with hemlock are shown in bold

Species	Hemlock (n=55)	Hardwoods (n=281)
Ovenbird (<i>Seiurus aurocapillus</i>)	81.8 %	94.0 %
Black-throated Green Warbler (<i>Dendroica virens</i>)	78.2	67.3
Red-eyed Vireo (<i>Vireo olivaceus</i>)	78.2	91.1
Blackburnian Warbler (<i>Dendroica fusca</i>)	49.1	13.5
Winter Wren (<i>Troglodytes troglodytes</i>)	43.6	15.7
American Robin (<i>Turdus migratorius</i>)	36.4	28.8
Hermit Thrush (<i>Catharus guttatus</i>)	34.6	30.6
Blue Jay (<i>Cyanocitta cristata</i>)	30.9	22.4
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	30.9	11.0
Black-capped Chickadee (<i>Parus atricapillus</i>)	29.1	18.2
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	29.1	52.0
Scarlet Tanager (<i>Piranga olivacea</i>)	29.1	24.6
Nashville Warbler (<i>Vermivora ruficapilla</i>)	27.3	7.8
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	25.5	6.8
Northern Parula (<i>Parula americana</i>)	21.8	10.0
Solitary Vireo (<i>Vireo solitarius</i>)	21.8	3.9
Least Flycatcher (<i>Empidonax minimus</i>)	20.0	45.6
American Crow (<i>Corvus brachyrhynchos</i>)	18.2	21.0
Brown Creeper (<i>Certhia familiaris</i>)	18.2	14.6
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	18.2	13.5
Song Sparrow (<i>Melospiza melodia</i>)	16.4	4.6
Northern Raven (<i>Corvus corax</i>)	14.6	17.4
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	14.6	5.0
Woodpecker sp. (unidentified)	14.6	16.0
Black-and-white Warbler (<i>Mniotilta varia</i>)	12.7	8.2
Common Yellowthroat (<i>Geothlypis trichas</i>)	12.7	3.2
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	12.7	9.6
Veery (<i>Catharus fuscescens</i>)	12.7	19.9
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	12.7	23.8
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	10.9	6.4
Eastern Wood Pewee (<i>Contopus virens</i>)	10.9	38.4
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	10.9	4.3
Cape May Warbler (<i>Dendroica tigrina</i>)	9.1	0.7
Hairy Woodpecker (<i>Picoides villosus</i>)	9.1	9.6
Mourning Warbler (<i>Oporornis philadelphia</i>)	9.1	20.3
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	9.1	10.3
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	0.0	16.4
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	7.3	15.3
Wood Thrush (<i>Hylocichla mustelina</i>)	1.8	10.0

mapped locations of all birds encountered in the 6.25 ha area. Standardized codes were used to identify evidence of breeding (adults carrying food, nest locations, presence of juveniles, etc.). Six categories of sites were chosen, representing: old growth hardwoods in the Sylvania Wilderness (n=6), uneven-aged managed hardwoods (n=12), even-aged managed hardwoods (n=12), old growth hemlock in the Sylvania Wilderness (n=4), old growth hemlock in Wisconsin Research Natural Areas (n=4), and managed hemlock (n=8).

Results

Thirteen of the 316 habitat-based sites in the Nicolet National Forest Bird Survey are dominated by hemlocks, in nearly every case by predominantly mature trees >70 years in age. Neither species richness (=numbers of species) nor numbers of individuals in these sites differ significantly from the corresponding numbers in hardwood dominated sites ($p > .15$, t -test). The types of bird species, on the other hand, show both similarities and differences when compared with counts at hardwood-dominated sites (Table 1). The most abundant species at both groups of sites is the Ovenbird, clearly the most ubiquitous species in forested landscapes of the western Lake States (Howe et al. 1996). The next two most abundant species are the same for both groups, but Black-throated Green Warbler is second most abundant in hemlock, while Red-eyed Vireo is second most abundant in hardwoods.

Five bird species (Table 1) show statistically significant affinities for hemlock in the Nicolet National Forest (Howe et al. 1996). Several other species (White-throated Sparrow, Nashville Warbler, Northern Parula, Song Sparrow, Yellow-rumped Warbler, Common Yellowthroat, and Cape May Warbler) also occur more frequently in hemlock sites than in hardwood sites, perhaps reflecting the tendency of hemlock sites to occur near lowland conifers or other moist habitats favored by these species. Nine species (Rose-breasted Grosbeak, Least Flycatcher, Veery, Yellow-bellied Sapsucker, Eastern Wood Pewee, Mourning Warbler, Black-throated Blue Warbler, Chestnut-sided Warbler, and Wood Thrush) occur at least twice as frequently in hardwood sites than in hemlock sites.

Note that the most abundant species in the hardwood sites occur at higher frequencies than the most abundant species in hemlock sites. This reflects a general difference in the equitability or evenness component of species diversity ($E_{\text{hemlock}} = .27$, $E_{\text{hardwoods}} = .13$, where $E = D/D_{\text{max}}$, $D = 1/\sum p_i^2$, p_i = the proportion of all individuals in species i , and $D_{\text{max}} = S$, the total number of species observed between 1987 and 1995). In other words, fewer species comprise a higher proportion of individuals in hardwood forests of the Nicolet National Forest. The two most abundant species at hardwood sites (Ovenbird and Red-eyed Vireo) account for 33% of all individuals observed, whereas the two most abundant species at hemlock sites (Ovenbird and Black-throated Green Warbler) account for only 25% of all individuals; the 20th most abundant species in hardwoods (Winter Wren) contributes 1.1% of all individuals, whereas the 20th most abundant species in hemlocks (Northern Parula) contributes 1.4% of all individuals.

Results from the more intensive study of old growth and managed forests are consistent with the Nicolet National Forest Bird Survey data, but they provided clearer answers to questions about the effects of forest management on species richness and bird density. Highest bird densities and species richness were recorded at the hemlock-dominated Research Natural Areas (RNA's) in Wisconsin (Table 2). Managed hemlocks also yielded high densities, on average not significantly different from those in old growth hemlock. Old growth hardwoods, old growth hemlocks in Sylvania, and uneven-aged managed hardwoods showed somewhat lower bird densities than those in the RNA's and managed hemlocks, but only the RNA hemlocks were richer in bird species. The most striking result of this investigation was the significantly lower densities and diversities found in even-aged managed hardwoods. Values for all of the relevant variables (Table 2) were significantly lower than those for the other site categories.

Another finding of interest was consistently higher variation in the density of birds at hemlock dominated sites (Table 2). This result was due to extremely high densities at several of the hemlock sites; the fact that high variation occurred in all three categories of hemlock sites suggests that our results reflect biologically meaningful differences between bird assemblages in hemlock and hardwood forests.

No bird species is found exclusively in hemlock forests. Blackburnian Warbler, for example, shows a strong affinity for hemlock forests in the Nicolet National Forest but it also occurs in a variety of other forest types (Figure 2). All of the birds which are characteristic of hemlock forests in this region are found commonly in at least one other forest type; Black-throated Green Warbler, the most abundant species in both old growth and managed hemlocks, is one of the three most common bird species in northern hardwoods of the Nicolet National Forest (Table 1).

Table 2. Summary of bird surveys at 6.25 ha forest plots in northern Wisconsin and Upper Michigan during 1993-94. Each site was visited 6 times by teams of two observers. Values in parentheses = standard deviations.

Category	# sites	Avg. number of pairs/visit	Avg. number of species/visit	Avg. species richness (6 visits)	Total # species confirmed breeding
Hemlock old growth (Sylvania)	4	25.5 (10.8)	11.5 (1.9)	23.3 (0.5)	8.3 (2.8)
Hemlock old growth (RNA)	4	32.3 (18.0)	13.7 (4.0)	25.5 (3.7)	6.3 (2.4)
Hemlock managed	8	28.4 (17.8)	11.7 (2.8)	24.8 (6.1)	8.8 (3.0)
Hardwoods old growth (Sylvania)	6	25.5 (5.7)	11.8 (2.1)	24.3 (3.6)	9.2 (3.7)
Hardwoods managed (uneven-aged)	12	25.7 (4.6)	11.7 (1.9)	24.7 (3.8)	8.7 (2.6)
Hardwoods managed (even-aged)	12	17.7 (3.7)	8.1 (2.1)	17.7 (4.0)	5.7 (2.3)

While not unique, bird assemblages in hemlock forests are nevertheless *distinct* from those in other major forest types. We compared species assemblages in the old growth/managed forest study using Principal Components Analysis (PCA). PCA is one of many ordination techniques which reduces multi-species similarities and differences into visually interpretable maps, usually in 2 or 3 dimensions (Gauch 1982). Results using the log-transformed mean number of pairs for each species at each site (Figure 3) show that hemlock forest bird assemblages are consistently different from bird assemblages in hardwood dominated forests. Birds of even-aged hardwoods are most different from the birds of hemlock sites, while birds of old growth hardwoods in Sylvania are most similar. Species responsible for these differences are consistent with those identified in our analysis of the Nicolet National Forest Bird Survey data (Table 1). Northern Parula, Blackburnian Warbler, Red-breasted Nuthatch, Black-capped Chickadee, Golden-crowned Kinglet, Blue Jay, Hermit Thrush, Solitary Vireo, Yellow-rumped Warbler, and Black-throated Green Warbler (in that order) are correlated positively (i.e., showed high component loadings) with PCA Axis 1; Rose-breasted Grosbeak, Downy Woodpecker, Black-throated Blue Warbler, Veery, and Chestnut-sided Warbler (in that order) are correlated negatively. As expected, hemlock-dominated sites tend to appear on the positive side of this axis. (In fact, only one hemlock site - a managed stand - showed a negative score on Axis 1). PCA Axes 2 and 3 are more difficult to interpret, because they emphasize birds that occur in both hardwood and hemlock sites. Least Flycatcher, Veery, Chestnut-

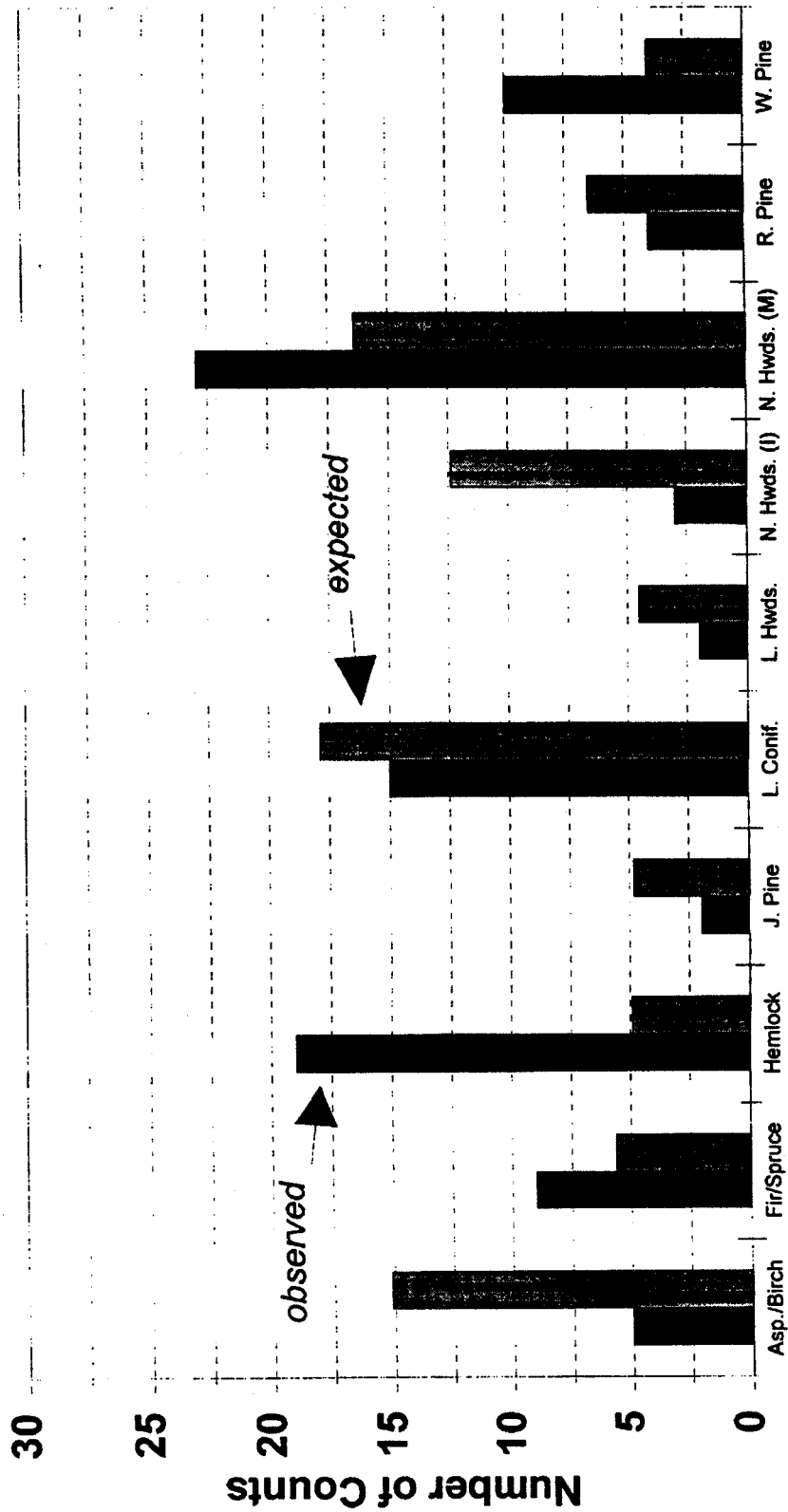
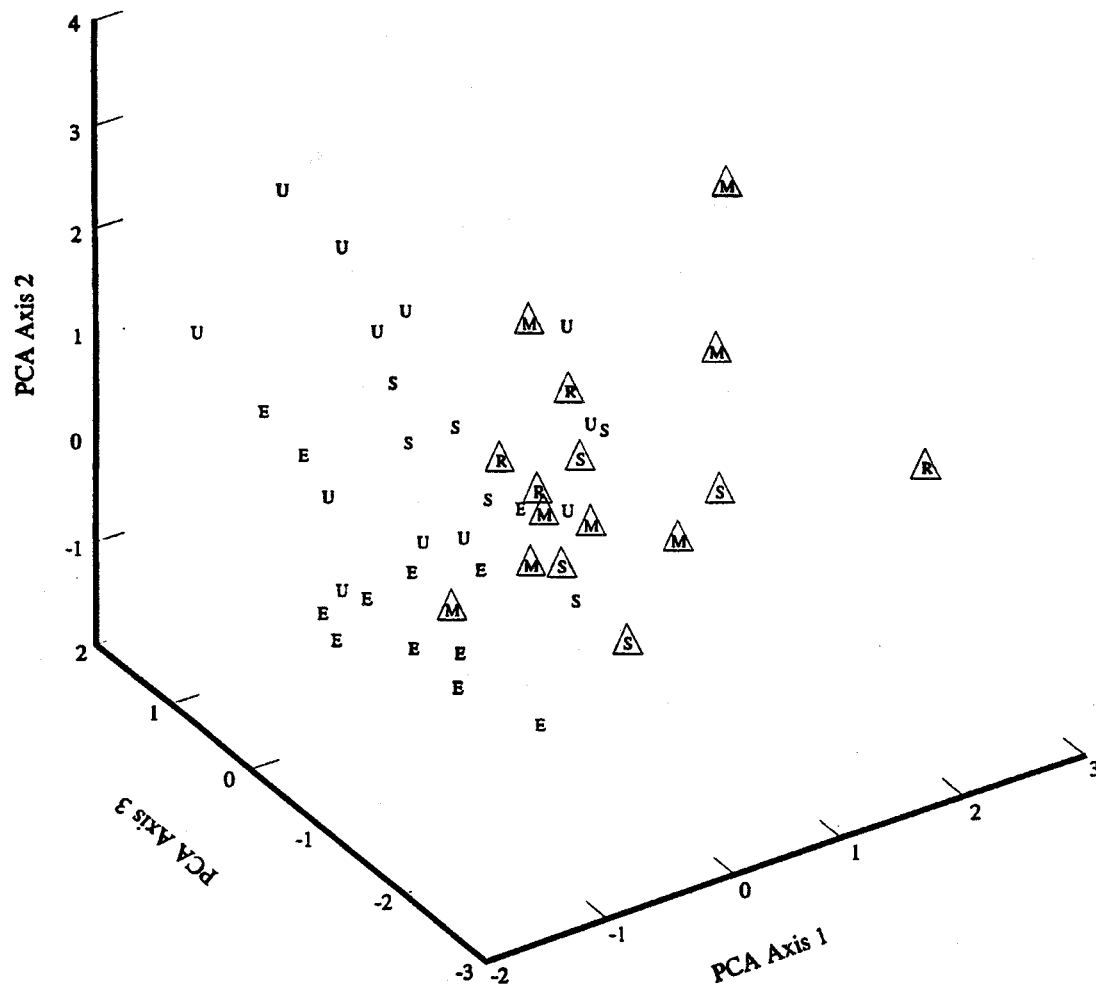


Figure 2. Frequency of Blackburnian Warblers in point counts in the Nicolet National Forest Bird Survey between 1989-1994 (n=736). Expected frequencies were generated on the assumption that birds occurred in direct proportion to the number of sample points in each habitat category.



- △ Old Growth Hemlocks (Sylvania Wilderness)
- △ Old Growth Hemlocks (Research Natural Area)
- △ Managed Hemlocks
- s Old Growth Hardwoods (Sylvania)
- u Managed Hardwoods (Uneven-aged)
- E Managed Hardwoods (Even-aged)

Figure 3. Principal Components Analysis of bird assemblages in old growth and managed forests of northern Wisconsin and Upper Michigan. Variable used to generate the ordination was the average number of pairs for each species at each site. Points represent sites; the closer two sites are to one another, the more similar they were in bird species composition.

sided Warbler, and Rose-breasted Grosbeak (which showed negative correlations with Axis 1) are positively associated with Axis 2, along with Mourning Warbler, Eastern Wood Pewee, White-throated Sparrow, Yellow-bellied Sapsucker, Red-eyed Vireo, American Robin, Ovenbird, and White-breasted Nuthatch; Hermit Thrush, Yellow-rumped Warbler, and Black-throated Green Warbler are negatively associated with Axis 2. A combined category of "other raptors" including Northern Goshawk (*Accipiter gentilis*), Bald Eagle (*Haliaeetus leucocephalus*), Red-shouldered Hawk (*Buteo lineatus*), and Sharp-shinned Hawk (*Accipiter striatus*) is most highly correlated with PCA Axis 3, along with Winter Wren, Pileated Woodpecker, Black-throated Blue Warbler, Eastern Wood Pewee, Least Flycatcher, Brown Creeper, and White-breasted Nuthatch; high negative correlations on Axis 3 are shown by Black-throated Green Warbler, Ovenbird, "finches" (including American Goldfinch, *Carduelis tristis*; Pine Siskin, *Carduelis pinus*; and Purple Finch, *Carpodacus mexicanus*), Red-eyed Vireo, Black-and-white Warbler, and Cedar Waxwing.

A Principal Components Analysis of the hemlock dominated sites only (Figure 4) shows that birds of managed hemlocks are most different from the birds in Sylvania old growth (with one exception), while bird assemblages in Wisconsin RNA's are intermediate. Species that tend to be unique to hemlocks in Sylvania include Swainson's Thrush, Yellow-rumped Warbler, Downy Woodpecker, Brown Creeper, Hairy Woodpecker, and Black-throated Blue Warbler (negatively associated with Axis 1) and Hermit Thrush, Blackburnian Warbler, Winter Wren, American Robin, Blue Jay, and Northern Parula (negatively associated with Axis 2). Swainson's Thrush and Black-throated Blue Warbler are more common toward the north in this region (Davis 1996) and might reflect a geographic difference in the location of our study sites. All of the Sylvania sites are in the northern part of our study area. Species more characteristic of managed forests (positively associated with Axes 1 and 2) include Least Flycatcher, Veery, Chestnut-sided Warbler, Nashville Warbler, White-throated Sparrow, Rose-breasted Grosbeak, and American Crow.

An alternative way of looking at the results from our old growth/managed forest study is simply to compare species abundances in the 3 major categories of sites (Table 3). The most striking message from this analysis is the dramatic reduction of hemlock-associated species in even-aged managed forests, and the conspicuous absence or near-absence of Least Flycatcher, Rose-breasted Grosbeak, Veery, Chestnut-sided Warbler, and Mourning Warbler from Sylvania hemlock sites. The last three of these also are absent or are nearly-absent from Sylvania hardwoods. Unlike the Principal Components Analysis, this approach does not illustrate the variation among sites in species composition; some sites in each category support bird assemblages that are more typical of other categories. Recognition of this variation is important for more detailed investigations of bird-habitat associations.

Discussion

Two independent investigations, the Nicolet National Forest Bird Survey and our study of birds in old growth and managed forests, show consistent patterns in the bird assemblages of hemlock forests. As a result of this research, we can answer the questions posed in the introduction to this paper.

Hemlock-dominated forests generally support high species richness and bird densities when compared with even-aged managed hardwood forests, but these values are not significantly different than the species richness and bird densities in uneven-aged or old growth hardwoods. Birds in the hemlock dominated Research Natural Areas in Wisconsin, on the other hand, show exceptionally high bird densities and species richness; particularly high densities were observed for Blackburnian Warbler and Black-throated Green Warbler, two of the most widely recognized hemlock associated bird species. An explanation for the rich bird assemblages in the RNA's will await more detailed analysis, but relatively high densities of hardwood associated bird species like Least Flycatcher, Scarlet Tanager, White-breasted Nuthatch, Veery, and Eastern Wood Pewee are clearly at least partly responsible. Low levels of species richness and bird density in even-aged hardwoods are consistent with the idea that vertical structure is an important element of bird habitat; even-aged stands possess simple vertical structure comprised of relatively few tree species.

Table 3. Average number of pairs of common bird species observed at 6.25 ha study plots (1993-94).

Species	Hemlock			Hardwoods		
	Sylvania	RNA's	Managed	Sylvania	Managed (Uneven-aged)	Managed (Even-aged)
Black-throated Green Warbler	5.00	5.13	4.83	2.91	3.65	3.47
Red-eyed Vireo	3.79	3.29	4.79	4.17	4.31	3.81
Ovenbird	2.79	3.29	3.60	3.29	3.42	3.29
Blackburnian Warbler	2.54	5.08	1.56	1.03	0.31	0.03
Brown Creeper	1.46	1.00	0.56	0.94	0.72	0.63
Winter Wren	1.38	1.42	0.73	1.43	0.60	0.18
Black-capped Chickadee	1.21	1.17	1.27	0.86	0.78	0.35
Northern Parula	1.17	0.83	0.50	0.37	0.17	0.00
Hermit Thrush	1.00	1.17	0.75	0.97	0.39	0.61
Yellow-rumped Warbler	0.63	0.63	0.13	0.31	0.24	0.04
Blue Jay	0.50	0.42	0.33	0.23	0.18	0.17
Hairy Woodpecker	0.50	0.21	0.19	0.37	0.18	0.26
Solitary Vireo	0.50	0.58	0.25	0.11	0.08	0.01
Scarlet Tanager	0.29	0.42	0.35	0.34	0.29	0.33
Swainson's Thrush	0.29	0.00	0.00	0.09	0.28	0.00
White-breasted Nuthatch	0.29	0.58	0.56	0.80	0.58	0.31
American Robin	0.25	0.58	0.21	0.37	0.46	0.29
Red-breasted Nuthatch	0.25	0.42	0.31	0.23	0.08	0.03
Yellow-bellied Sapsucker	0.25	0.54	0.33	0.40	0.57	0.50
Black-throated Blue Warbler	0.21	0.17	0.08	0.63	1.86	0.69
Downy Woodpecker	0.13	0.00	0.08	0.37	0.24	0.19
Golden-crowned Kinglet	0.13	0.67	0.23	0.00	0.06	0.00
Least Flycatcher	0.00	1.83	2.88	2.46	2.10	0.75
Eastern Wood Pewee	0.04	0.38	0.33	1.09	0.68	0.29
Rose-breasted Grosbeak	0.04	0.29	0.38	0.43	0.82	0.49
Veery	0.00	0.25	0.60	0.03	0.76	0.28
Chestnut-sided Warbler	0.00	0.00	0.54	0.00	0.50	0.04
Black-and-white Warbler	0.04	0.25	0.04	0.03	0.10	0.01
Mourning Warbler	0.00	0.00	0.35	0.00	0.18	0.00
Nashville Warbler	0.00	0.00	0.21	0.14	0.06	0.03

The Nicolet National Forest Bird Survey is based only on occurrence of species at different sites, but our more intensive study of old growth and managed forests was aimed at resident pairs and evidence of breeding. Except for the lower productivity of birds in even-aged hardwood forests, we found little difference in breeding success among forest habitat categories. In general, birds that were observed most commonly as pairs also were the species showing highest evidence of breeding and breeding success.

Birds of hemlock forests in the Nicolet National Forest are not as strongly dominated by abundant species as are hardwood forests, perhaps due to the small extent and rather isolated character of hemlock stands in this region. Birds of surrounding habitats are present (and in some cases abundant) in remnant hemlocks, creating mixed species assemblages with a more even distribution of individuals among species. As described earlier for Research Natural Areas, the same effect might help explain the high species richness of managed hemlocks; species characteristic of both hardwoods and hemlocks are present in these relatively isolated stands. Bird assemblages in the more extensive hardwood forests of the Nicolet National Forest, on the other hand, are strongly dominated by Ovenbird and Red-eyed Vireo, which are ubiquitous in today's landscape. In the Sylvania Wilderness, where hemlocks are a more important element of the landscape, the situation is actually reversed: hardwood dominated stands show a more even distribution of individuals among species. The two most abundant species in hemlocks (Black-throated Green Warbler and Red-eyed Vireo) account for approximately 35.5% of all individuals, while the two most abundant species in hardwoods (Red-eyed Vireo and Ovenbird) account for 30.6%.

The higher variability of hemlock forest bird assemblages observed in our study is more difficult to explain and deserves further investigation. While it is possible that hemlock forests are more prone to local "hot spots" of bird abundance, the possibility cannot be dismissed that our result merely reflects a sampling artifact. Point counts at hemlock dominated stands in the Nicolet National Forest do not show significant difference in variability compared with counts at hardwood dominated stands.

Results from both studies identify a suite of hemlock associated bird species which is distinct from bird species assemblages in other forest habitats of this region. Although none of these species is restricted to hemlock, Blackburnian Warbler, Black-throated Green Warbler, Winter Wren, Brown Creeper, Hermit Thrush, Northern Parula, Yellow-rumped Warbler, Solitary Vireo, and Red-breasted Nuthatch are characteristic hemlock birds in Wisconsin and Upper Michigan. This assemblage is similar to those described by Benzinger (1994) in New Jersey. He considered Black-throated Green Warbler, Solitary Vireo, and Northern Goshawk, to be "hemlock obligates," while Hermit Thrush, Barred Owl (*Strix varia*), Acadian Flycatcher (*Empidonax virescens*), Winter Wren, Red-shouldered Hawk, Brown Creeper, Blackburnian Warbler, Cooper's Hawk (*Accipiter cooperii*), Purple Finch, Yellow-rumped Warbler, Magnolia Warbler (*Dendroica magnolia*), and Red-breasted Nuthatch also show affinities for hemlock. Many of these species (e.g., Blackburnian Warbler, Hermit Thrush, Yellow-rumped Warbler, Red-breasted Nuthatch) also occur in pine forests, a result that is consistent with observations in the Nicolet National Forest (Howe et al. 1996). Perhaps the most interesting contrast between birds of New Jersey hemlocks and those in the northern Wisconsin and Upper Michigan is the absence of Acadian Flycatcher. In Wisconsin, this species occurs in southern forests, where Mossman and Lange (1982) note that it is sometimes associated with hemlock. In

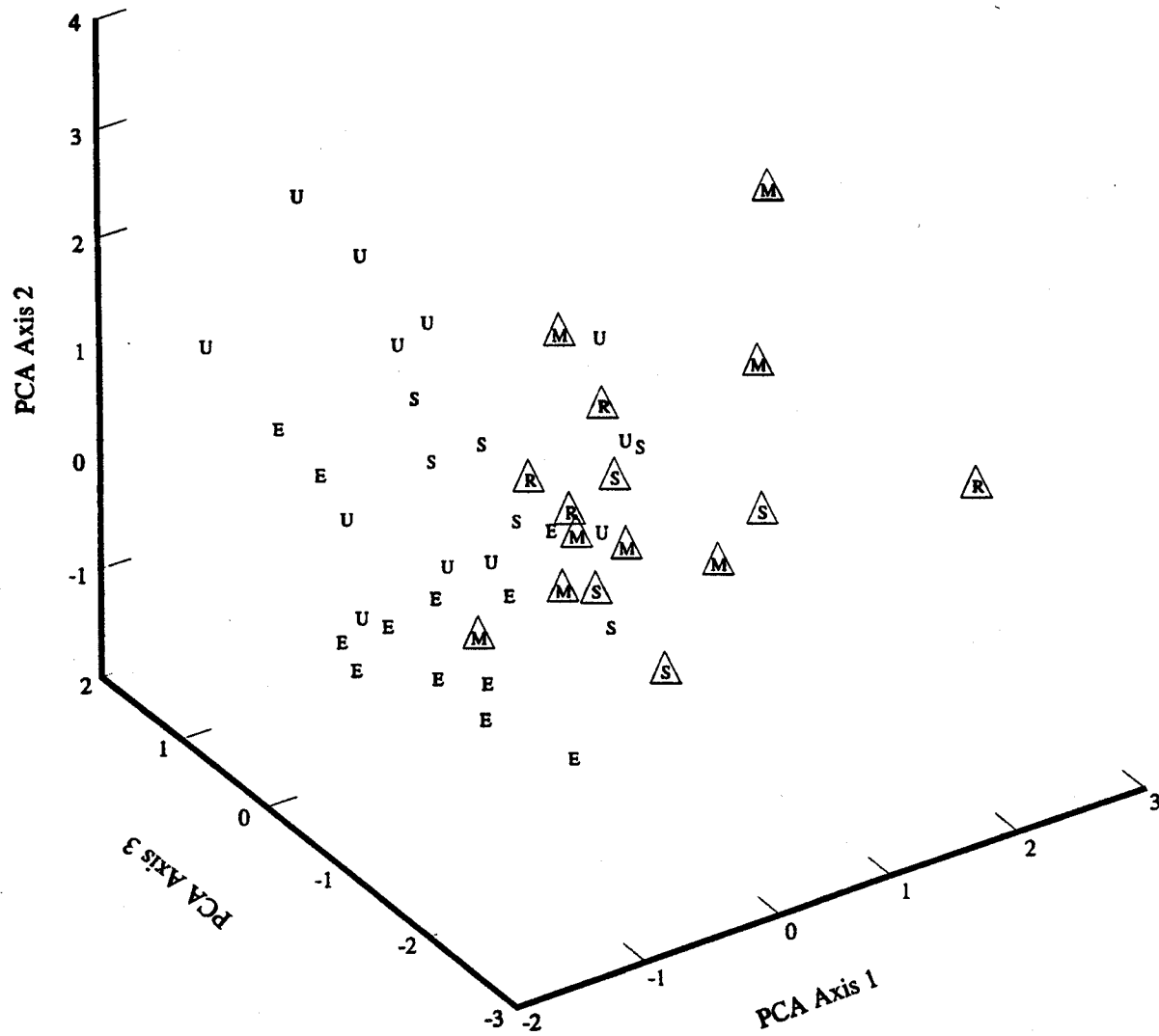
northern Wisconsin and Upper Michigan the Acadian Flycatcher is replaced by Least Flycatcher, although the absence of Least Flycatchers in hemlocks of the Sylvania Wilderness is striking.

Other studies support the findings presented here. Beals (1960) showed that bird assemblages of hemlocks in the Apostle Islands of Lake Superior were quite distinct from those of other forest types, although he emphasized the complex and individualistic response of birds to the forest environment. Ovenbird, Black-throated Green Warbler, Least Flycatcher, Red-eyed Vireo, and Eastern Wood Pewee were most abundant in hemlock-yellow birch stands. Also present were Blackburnian Warbler, Solitary Vireo, both species of nuthatches, Brown Creeper, Golden-crowned Kinglet, and Northern Parula. (Winter Wrens were absent from all of his study sites.) Kendeigh (1946) described bird assemblages in hemlock-beech-maple and hemlock-pine forests in New York and Vermont. Again, Ovenbird, Red-eyed Vireo, and Black-throated Green Warbler were common along with Blackburnian Warbler, Hermit Thrush, Black-throated Blue Warbler, and other species observed in Wisconsin and Michigan. Unlike our study areas, Magnolia Warbler and Canada Warbler were prominent in the forests described by Kendeigh. Northern Parula, Yellow-bellied Sapsucker, Red-breasted Nuthatch, Brown Creeper, Solitary Vireo, and Golden-crowned Kinglet were absent from the New York sites, although Kendeigh believed that they were present in primeval hemlock-hardwood forests of the region.

Management Implications

Conversion of mixed hardwood-hemlock forests to even-aged hardwoods leads to measurable reductions in bird species richness and bird density. The consequences of these changes on forest ecology are not known, but experimental studies (e.g., Holmes et al. 1979) suggest that birds play an important role in the control of forest insect populations, and of course bird populations themselves are valued by many people. Elimination of hemlock in northern forests leads to specific reductions in the local abundance of several bird species, notably Black-throated Green Warbler, Blackburnian Warbler, Solitary Vireo, Northern Parula and others. Because these species survive in other habitats, however, reductions in the extent of hemlock (as has occurred during the past century) are not likely to cause regional species extinctions over a period of decades; concern must be over the longer term, especially if combined with deterioration of habitat on these species' wintering grounds (Terborgh 1992) and the reduction of suitable alternative habitats.

With one exception, none of the major hemlock associated bird species has shown significant declines during the past 10 years according to the North American Breeding Bird Survey (Price et al. 1995). Northern Goshawk, a species found in several studies to be associated with hemlock-hardwood forests (Benzinger 1994), has declined significantly since 1984. Although this species was rare in our study area, we observed Goshawks in old growth and managed hemlocks and in uneven-aged managed hardwoods. Because this large, predatory species occurs in naturally low population densities, the effects of hemlock elimination are likely to be more acute for Northern Goshawks than for smaller birds. Special management efforts for Goshawks are therefore warranted in hemlock-hardwood forest landscapes.



- △_S Old Growth Hemlocks (Sylvania Wilderness)
- △_R Old Growth Hemlocks (Research Natural Area)
- △_M Managed Hemlocks
- s Old Growth Hardwoods (Sylvania)
- u Managed Hardwoods (Uneven-aged)
- E Managed Hardwoods (Even-aged)

Figure 4. Principal Components Analysis of bird assemblages in old growth and managed hemlock forests of northern Wisconsin and Upper Michigan. Methods are identical to those used to generate Figure 3.

Several bird species of hardwood forests which also occur in hemlocks (Least Flycatcher, Eastern Wood Pewee, Veery, Canada Warbler, and Rose-breasted Grosbeak) are declining in North America (Peterjohn et al. 1995, Price et al. 1995). Managed hemlocks and uneven-aged hardwood forests appear to be productive habitats for these and other species (Table 4). In fact, careful forest management which retains a mix of conifer and hardwood tree species and uneven-aged forest structure might be an important element of conservation efforts for declining North American songbirds. The extensive forested landscapes of the western Lake States probably are important centers of production for many of these and other neotropical migratory bird species (Robinson et al. 1994, Howe et al. 1996), making management efforts in Michigan, Minnesota, and Wisconsin especially important.

Our analysis has focused on breeding birds, but the physical structure of hemlock and its production of seeds undoubtedly makes it important for birds during non-breeding periods and winter. Seed-eating birds, including Pine Siskin, Red Crossbill (*Loxia curvirostra*), White-winged Crossbill (*Loxia leucoptera*) and Evening Grosbeak (*Hesperiphona vespertina*), occur widely in the Lake States forests, and we observed all but Red Crossbill in our hemlock study sites. All of these species are rare and irregular in these forests during the breeding season, however. Benkman (1987) has argued that serious declines in crossbills, perhaps even extinction of subspecies or sibling species, have occurred in North America since European settlement. White-winged Crossbill, Pine Siskin, and Purple Finch have shown significant declines since 1984 according to the North American Breeding Bird Survey. The importance of hemlock to winter resident birds is a subject that deserves future study.

Finally, results from our investigation emphasize the significance of reserved old growth forests in the western Lake States. We have demonstrated that patterns of bird abundance and diversity are different in extensive old growth forests (Sylvania Wilderness) than in managed forests and even isolated Research Natural Areas. Besides serving as benchmarks for understanding the impacts of forest modification, old growth forests provide an environment where bird population dynamics are subject to natural disturbances and natural landscape configurations (Freemark et al. 1995). In other words, old growth forests provide insurance against unexpected consequences of forest management. Although some species appear to benefit from human caused landscape modifications, others are more likely to persist in an environment which retains the conditions under which they evolved. As we learn more about the ecology of forest birds, management efforts can be directed at certain species of concern; until we understand both the long term and large scale consequences of habitat changes, however, reserved forests will continue to play an important role in bird conservation.

References Cited

- Beals, E.W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. *Wilson Bulletin* 72:156-181.
- Benkman, C.W. 1987. Food profitability and the foraging ecology of crossbills. *Ecological Monographs* 57:251-267.
- Benzinger, J. 1994. Hemlock decline and breeding birds II. Effects of habitat change. *Records of New Jersey Birds* 20(2):34-51.
- Collins, S.L. 1983. Geographic variation in the habitat structure of the Black-throated Green Warbler (*Dendroica virens*). *Auk* 100:382-389.

- Davis, J.H. 1996. A spatial analysis of birds in the Nicolet National Forest. M.S. Thesis. University of Wisconsin-Green Bay, Green Bay, WI.
- Freemark, K.E. and H.G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biological Conservation* 36:115-141.
- Freemark, K.E., J.B. Dunning, S.J. Hejl, and J.R. Probst. 1995. A landscape ecology perspective for research, conservation, and management. pp. 381-427 in T.E. Martin and D.M. Finch (eds.), *Ecology and Management of Neotropical Migratory Birds: A synthesis and Review of Critical Ideas*. Oxford University Press, New York.
- Frelich, L.E. 1995. Old forest in the Lake States today and before European settlement. *Natural Areas Journal* 15(2):157-167.
- Gauch, H.G. Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, New York, NY.
- Holmes, R.T. 1986. Foraging patterns of forest birds: male-female differences. *Wilson Bulletin* 98:196-213.
- Holmes, R.T. and S.K. Robinson 1989. Tree species preferences of foraging insectivorous birds in a northern hardwood forest. *Oecologia* 48:31-35.
- Howe, R.W., A.T. Wolf, and T. Rinaldi. 1995. Monitoring birds in a regional landscape: lessons from the Nicolet National Bird Survey. pp. 83-92 in Ralph, C.J., J.R. Sauer, and S. Droege (eds.), *Monitoring Bird Populations by Point Counts*. USDA Forest Service Gen Techn. Rep. PSW-GTR-149. Albany, CA.
- Howe, R.W., G. Niemi, and J.R. Probst. 1996. Management of northern forest landscapes for the conservation of Neotropical migratory birds. in F.R. Thompson III (ed.). *Managing Midwestern Landscapes for Birds*. in prep.
- Karr, J.R. and R.R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. *American Naturalist* 105:423-435.
- Kendeigh, S.C. 1946. Breeding birds of the beech-maple-hemlock community. *Ecology* 27: 226-245.
- MacArthur, R.H., J.W. MacArthur, and J. Preer. 1962. On bird species diversity. Part 2, Predictions of bird census from habitat measurements. *American Naturalist* 96:167-174.
- Martin, T.E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology* 69:74-84.
- Morse, D.H. 1989. *American Warblers: An Ecological and Behavioral Perspective*. Harvard University Press. Cambridge, MA.
- Mossman, M.J. and K. I. Lange. 1982. *Breeding Birds of the Baraboo Hills, Wisconsin: Their History, Distribution, and Ecology*. Wisconsin Department of Natural Resources and Wisconsin Society for Ornithology, Madison, WI.
- Robinson, S.K., F.R. Thompson III, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987-1990.
- Speiser, R. 1982. *Breeding Birds of the Ramapo-Hudson Highlands, New Jersey and New York*. M.S. Thesis, Marshall University, Huntington, WV.
- Temple, S.A., M.J. Mossman, and B. Ambuel. 1979. The ecology and management of avian communities in mixed hardwood-conifer forests. pp. 132-153 in *Workshop Proceedings, Management of North Central and Northeastern Forests for Nongame Birds*. USDA Forest Service Gen. Tech. Rep. NC-51, St. Paul, MN.
- Wolf, A.T. and R.W. Howe. 1991. The winter wren in Wisconsin. *Passenger Pigeon* 52(2):103-112.

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