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Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA

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Abstract

Bird species distribution and predation rates on natural and artificial nests were compared among unmanaged mature, shelterwood, and clearcut northern hardwoods forest to evaluate the effect of these practices on bird populations. Twenty-three of the 48 bird species detected during the study differed significantly in abundance among unmanaged mature forest, shelterwoods, and clearcuts. Results of multiple regressions of bird abundance and habitat variables suggest that differences in bird species distribution among treatments were the result of differences in habitat structure among treatments. Bird species diversity and species richness were significantly higher in shelterwoods than either mature forest or clearcuts, although there were bird species that occurred exclusively, or nearly so, in each of the three treatments. Predation rates on artificial nests were lowest in mature forest, and predation rates on natural nests was highest in mature forest, although neither of these differences was statistically significant. We conclude that use of partial cutting exclusively would result in the decline of several species of mature forest and clearcut specialists, and, consequently, a decrease in species diversity at the landscape scale. The use of a variety of silvicultural techniques is recommended to maintain bird species diversity in forested landscapes.

Keywords: Bird habitat; Bird species diversity; Forest birds; Forest management; Ice damage; Nest predation; Silviculture

1. Introduction

Silvicultural activities affect bird communities through their effect on vegetation structure (Maurer et al., 1981; Thompson et al., 1995; DeGraaf et al., 1991). The effect of management activities varies in proportion to the magnitude of the alteration of the vegetation — intermediate levels of disturbance result in intermediate levels of alteration of the bird community (Tobalske et al., 1991; Annand and Thompson, 1997; Norton and Hannon, 1997), whereas clearcutting results in nearly complete replacement of the mature forest bird community with early-successional bird species (Conner and Adkisson, 1977; Titterington et al., 1979; Costello, 1995; DeGraaf, 1991).

Forest management activities have come under increasing public scrutiny in recent years. As a result, forest management activities are evaluated increas-

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ingly on the basis of their effect on non-timber values of managed forests, including the provision of habitat for forest birds. Clearcutting is a widely used silvicultural technique that has received particular public criticism, which has led managers to emphasize alternative forms of silviculture. Partial cutting, such as single tree selection or the initial stage of a shelterwood cut, appear to have great potential for managing forest birds because it alters the vegetation structure in a stand enough to permit the establishment of at least some early-successional birds without eliminating all of the mature forest bird community (Webb et al., 1977; Annand and Thompson, 1997).

Our goal in the present study was to evaluate the effect of partial cutting on bird communities by comparing bird species distributions among mature forest, shelterwoods and clearcut habitats. In addition, we tested whether differences in bird communities among treatments were associated with differences in vegetation variables using multiple regression analysis. Furthermore, although there have been many studies of partial-cut logging on bird communities (Franzreb, 1977; Franzreb and Ohmart, 1978; Crawford et al., 1981; Freedman et al., 1981; DeGraaf et al., 1991; Tobalske et al., 1991; Hagan et al., 1997; Norton and Hannon, 1997), these studies did not include information on factors affecting bird productivity (although see Annand and Thompson, 1997). Thus, we also include a comparison of nest predation rates on natural and artificial nests in the present study. Lastly, Askins, (1993) stated that early-successional bird species may be declining more rapidly than mature forest bird species because they are more habitat-specific. Therefore, we compared niche breadth of birds among mature forest, partial cut and clearcut habitats.

2. Methods

The study was conducted May–July, 1998 on the Androscoggin Ranger District of the White Mountain National Forest. Abundance of breeding bird and nest predator abundance was compared among mature forest, partial cut, and clearcut stands using 10 min 50 m radius point counts. Mature forest stands had closed canopy and no recent evidence of management activity. The partial cut stands in this study were the result of the initial stages of a shelterwood cut, and ranged from 12.4 to 41.6 m^2/ha basal area. Shelterwood and clearcut stands had been harvested 3–5 years prior to the initiation of the study. Forty point count stations were established, 10 in mature forest stands, 20 in shelterwood stands, and 10 in clearcut stands (a larger sample of shelterwood stands was included to ensure that as wide a range as possible of stand conditions was represented). Point count stations were located $\geq$200 m apart. Each point was visited three times between 05: 00 and 11: 00 hours during the month of June, 1998. The highest of the three counts for each species at a given point was used in the analyses.

Indices of nest-predation rates in mature forest, uneven-aged forest, and clearcuts were determined using artificial wicker nests, each baited with a House Sparrow (*Passer domesticus*) egg and placed in a shrub within a meter of the ground in the manner of a shrub-nesting warbler. Ten nests were placed systematically 70 m apart on square grids in four stands each of mature forest, shelterwoods, and clearcuts. Nests were deployed using latex gloves and rubber boots to minimize the deposition of human scent. Nests were exposed to predation for a 2 week period during the month beginning 12 June. Nests were checked 14 days after deployment, and classified as either depredated or non-depredated. In addition, all actual bird nests located during the study were checked every 3–5 days, and the contents recorded.

At each bird survey point, vegetation measurements were made at four points 25 m from the bird survey points in the four cardinal directions. Basal area of all woody stems $\geq$2.5 cm dbh was measured using a 10 factor prism. Basal area of deciduous, coniferous and dead stems were recorded separately. The study area had been extensively damaged as the result of a major ice storm the previous winter (Irland, 1998), therefore, basal area of trees missing $\geq$50% of their canopy was also measured. Percent canopy coverage was measured using a spherical densiometer. The vertical structure of the understory vegetation was measured by counting the number of contacts of vegetation in three 1 m height classes with a metal pole. All four measurements of each variable were averaged for each survey point.

Bird species diversity was calculated separately for each survey point using the Shannon and Weaver (1949) index. Habitat niche breath was calculated for each species using the Shannon and Weaver (1949) index (Morrison et al., 1992).

Bird abundance, bird species diversity, nest predator abundance, vegetation variables and predation rates on artificial nests were compared among mature forest, shelterwood and clearcut forest using one-way ANOVA and Tukey's post-hoc multiple comparisons. Similarly, niche breadth was compared among species reaching their highest abundance in mature forest, shelterwood and clearcuts, using one-way ANOVA and Tukey's post-hoc multiple comparisons.

Predation rates on natural nests were calculated using the Mayfield (1975) estimator, and compared among mature forest, shelterwoods and clearcuts following Sauer and Williams (1989). Statistical differences were considered significant at $P \leq 0.05$.

3. Results

Not surprisingly, there were significant differences in vegetation structure among mature forest, shelterwood and clearcut forest. Basal area of deciduous trees, as well as canopy coverage, was highest in mature forest stands, significantly lower in shelterwood stands, and lowest in clearcut stands (Table 1). In contrast, basal area of dead trees was lowest in clearcuts and did not differ between mature forest and shelterwoods (Table 1). Vegetation structure between 0 and 1 m and 1–2 m above ground was highest in clearcuts, significantly lower in shelterwood stands, and lowest in mature forest (Table 1).

The abundance of 23 of 48 bird species detected at point count survey stations differed significantly among mature forest, shelterwoods and clearcuts (Table 2). Scarlet Tanagers (scientific names are given in Table 2) were more abundant in mature forest than either shelterwoods or clearcuts. Black-throated Green Warblers, Blackburnian Warblers, and Brown Creepers were more abundant in mature forest, significantly less abundant in shelterwoods, and significantly least abundant in clearcuts. Red-eyed Vireos, Ovenbirds, Winter Wrens and Hermit Thrushes were equally abundant in mature forest and shelterwoods, and were significantly more abundant in these stands than in clearcuts. Black-throated Blue Warblers were most abundant in shelterwoods, significantly less abundant in mature forest, and significantly least abundant in clearcuts. Rose-breasted Grosbeaks, Least Flycatchers, Blue-headed Vireos, and Hairy Woodpeckers were significantly more abundant in shelterwoods than either mature forest of clearcuts. Mourning Warblers and Canada Warblers were equally abundant in clearcuts and shelterwoods, and were significantly more abundant in these stands than in mature forest. Common Yellowthroats, White-throated Sparrows, Alder Flycatchers, Northern Flickers, Indigo Buntings and Tree Swallows were equally abundant in mature forest and shelterwoods, and were significantly less abundant in these stands than in clearcuts. Black-and White Warblers and Chestnut-sided Warblers were most abundant in clearcuts, significantly less abundant in shelterwoods, and significantly least abundant in mature forest.

Bird species diversity and bird species richness was significantly highest in shelterwood stands, and did not differ between mature forest and clearcut stands

Table 1
Vegetation characteristics compared among 10 mature forest, 20 shelterwood, and 10 clearcut stands in northern New Hampshire. Values with the same superscript do not differ significantly from each other[a]

Parameter	Mature	Shelter	Clearcut	*P*
Basal area deciduous trees [a]	21.2 (1.03) [a]	14.5 (1.14) [b]	0.95 (0.38) [c]	<0.001
Basal area coniferous trees [a]	2.61 (1.22) [a]	1.61 (0.39) [a]	0.00 (0.00) [a]	0.086
Basal area damaged trees [a]	2.28 (1.38) [a]	5.06 (1.34) [a]	0.00 (0.00) [a]	0.068
Basal area dead trees [a]	1.27 (0.47) [a]	1.69 (0.27) [a]	0.95 (0.42) [b]	0.014
Percent canopy coverage	85.3 (2.15) [a]	55.9 (3.33) [b]	0.67 (0.67) [c]	<0.001
Vegetation structure 0–1 m	1.00 (0.14) [a]	3.40 (0.32) [b]	5.58 (0.78) [c]	<0.001
Vegetation structure 1–2 m	0.28 (0.10) [a]	1.12 (0.21) [b]	1.86 (0.45) [c]	0.004
Vegetation structure 2–3 m	0.28 (0.09) [a]	0.79 (0.24) [a]	0.50 (0.31) [a]	0.333

[a] m^2/ha.

Table 2
Bird abundance compared among 10 mature forest, 20 shelterwood, and 10 clearcut stands in northern New Hampshire[a]

Species	Mature	Shelter	Clearcut	*N*	*P*	Niche breadth
Black-throated Blue Warbler (*Dendroica caerulescens*)	1.20 (0.20)[a]	2.30 (0.16)[b]	0.00 (0.00)[c]	58	<0.001	0.280
Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.00 (0.00)[a]	1.25 (0.30)[b]	3.20 (0.25)[c]	57	<0.001	0.259
Red-eyed Vireo (*Vireo olivaceus*)	1.40 (0.37)[a]	1.65 (0.20)[a]	0.50 (0.17)[b]	52	0.007	0.434
Ovenbird (*Seiurus aurocapillus*)	2.00 (0.39)[a]	1.25 (0.24)[a]	0.00 (0.00)[b]	45	<0.001	0.290
American Redstart (*Setophaga ruticilla*)	0.50 (0.22)[a]	1.30 (0.26)[a]	1.30 (0.30)[a]	44	0.116	0.444
Black-throated Green Warbler (*Dendroica virens*)	1.80 (0.36)[a]	0.50 (0.12)[b]	0.10 (0.10)[c]	29	<0.001	0.293
White-throated Sparrow (*Zonotrichia albicollis*)	0.20 (0.13)[a]	0.50 (0.14)[a]	1.50 (0.17)[b]	27	<0.001	0.354
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	0.10 (0.10)[a]	0.95 (0.11)[b]	0.10 (0.10)[a]	21	<0.001	0.253
Least Flycatcher (*Empidonax minimus*)	0.00 (0.00)[a]	1.00 (0.25)[b]	0.00 (0.00)[a]	20	0.002	0.007
Winter Wren (*Troglodytes troglodytes*)	0.40 (0.22)[a]	0.80 (0.16)[a]	0.00 (0.00)[b]	20	0.006	0.279
Veery (*Catharus fuscescens*)	0.30 (0.15)[a]	0.60 (0.13)[b]	0.50 (0.24)[c]	20	0.445	0.461
Mourning Warbler (*Oporornis philadelphia*)	0.00 (0.00)[a]	0.65 (0.18)[b]	0.70 (0.21)[b]	20	0.034	0.303
Hermit Thrush (*Catharus guttatus*)	0.80 (0.13)[a]	0.50 (0.14)[a]	0.00 (0.00)[b]	18	0.002	0.292
Common Yellowthroat (*Geothlypis trichas*)	0.00 (0.00)[a]	0.20 (0.09)[a]	1.40 (0.27)[b]	18	<0.001	0.166
Canada Warbler (*Wilsonia canadensis*)	0.00 (0.00)[a]	0.60 (0.17)[b]	0.50 (0.17)[b]	17	0.043	0.302
Magnolia Warbler (*Dendroica magnolia*)	0.10 (0.10)[a]	0.50 (0.14)[a]	0.40 (0.16)[a]	15	0.165	0.410
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.50 (0.17)[a]	0.45 (0.11)[a]	0.10 (0.10)[a]	15	0.117	0.408
Cedar Waxwing (*Bombycilla cedrorum*)	0.10 (0.10)[a]	0.40 (0.11)[a]	0.60 (0.16)[a]	15	0.067	0.398
Black-and-white Warbler (*Mniotilta varia*)	0.00 (0.00)[a]	0.30 (0.11)[b]	0.60 (0.17)[c]	12	0.012	0.280
Swainson's Thrush (*Catharus ustulatus*)	0.20 (0.13)[a]	0.30 (0.11)[a]	0.30 (0.15)[a]	11	0.840	0.470
Scarlet Tanager (*Piranga olivacea*)	0.60 (0.16)[a]	0.15 (0.08)[b]	0.10 (0.10)[b]	10	0.010	0.349
Alder Flycatcher (*Empidonax alnorum*)	0.00 (0.00)[a]	0.00 (0.00)[a]	0.90 (0.23)[b]	9	<0.001	0.008
Yellow-rumped Warbler (*Dendroica coronata*)	0.30 (0.15)[a]	0.20 (0.09)[a]	0.10 (0.10)[a]	8	0.556	0.439
Blackburnian Warbler (*Dendroica fusca*)	0.50 (0.17)[a]	0.15 (0.08)[b]	0.00 (0.00)[c]	8	0.012	0.239
Blue-headed Vireo (*Vireo solitarius*)	0.00 (0.00)[a]	0.35 (0.13)[b]	0.00 (0.00)[a]	7	0.042	0.017
Evening Grosbeak (*Coccothraustes vespertinus*)	0.20 (0.13)[a]	0.10 (0.07)[a]	0.20 (0.20)[a]	6	0.769	0.458
Eastern Wood-Pewee	0.00 (0.00)[a]	0.30 (0.13)[a]	0.00 (0.00)[a]	6	0.081	0.019

Table 2 (*Continued*)

Species	Mature	Shelter	Clearcut	*N*	*P*	Niche breadth
(*Contopus virens*)						
Ruby-throated Hummingbird (*Archilochus colubris*)	0.00 (0.00) [a]	0.20 (0.09) [a]	0.20 (0.13) [a]	6	0.326	0.308
American Robin (*Turdus migratorius*)	0.10 (0.10) [a]	0.15 (0.08) [a]	0.20 (0.13) [a]	6	0.833	0.461
Hairy Woodpecker (*Picoides villosus*)	0.00 (0.00) [a]	0.25 (0.10) [b]	0.00 (0.00) [a]	5	0.058	0.022
Northern Flicker (*Colaptes auratus*)	0.00 (0.00) [a]	0.05 (0.05) [a]	0.40 (0.16) [b]	5	0.007	0.158
Brown Creeper (*Certhia americana*)	0.40 (0.17) [a]	0.05 (0.05) [b]	0.00 (0.00) [c]	5	0.007	0.158
Black-capped Chickadee (*Parus atricapillus*)	0.20 (0.13) [a]	0.20 (0.09) [a]	0.10 (0.10) [a]	5	0.785	0.458
Purple Finch (*Carpodacus purpureus*)	0.10 (0.10) [a]	0.20 (0.09) [a]	0.00 (0.00) [a]	5	0.301	0.285
White-breasted Nuthatch (*Sitta carolinensis*)	0.20 (0.13) [a]	0.05 (0.05) [a]	0.00 (0.00) [a]	3	0.209	0.228
Wood Thrush (*Hylocichla mustelina*)	0.00 (0.00) [a]	0.15 (0.08) [a]	0.00 (0.00) [a]	3	0.210	0.034
Nashville Warbler (*Vermivora ruficapilla*)	0.00 (0.00) [a]	0.10 (0.07) [a]	0.10 (0.10) [a]	3	0.602	0.313
Downy Woodpecker (*Picoides pubescens*)	0.00 (0.00) [a]	0.10 (0.07) [a]	0.00 (0.00) [a]	2	0.368	0.048
Indigo Bunting (*Passerina cyanea*)	0.00 (0.00) [a]	0.00 (0.00) [a]	0.20 (0.13) [b]	2	0.042	0.027
Tree Swallow (*Tachycineta bicolor*)	0.00 (0.00) [a]	0.00 (0.00) [a]	0.20 (0.13) [b]	2	0.042	0.027
Red Breasted Nuthatch (*Sitta canadensis*)	0.00 (0.00) [a]	0.05 (0.05) [a]	0.00 (0.00) [a]	1	0.618	0.082
Ruffed Grouse (*Bonasa umbellus*)	0.00 (0.00) [a]	0.05 (0.05) [a]	0.00 (0.00) [a]	1	0.618	0.082
Dark-eyed Junco (*Junco hyemalis*)	0.00 (0.00) [a]	0.05 (0.05) [a]	0.00 (0.00) [a]	1	0.618	0.082
Olive-sided Flycatcher (*Contopus borealis*)	0.00 (0.00) [a]	0.05 (0.05) [a]	0.00 (0.00) [a]	1	0.618	0.082
Northern Waterthrush (*Seiurus noveboracensis*)	0.00 (0.00) [a]	0.05 (0.05) [a]	0.00 (0.00) [a]	1	0.618	0.082
Gray Catbird (*Dumetella carolinensis*)	0.00 (0.00) [a]	0.00 (0.00) [a]	0.05 (0.05) [a]	1	0.618	0.048
Eastern Bluebird (*Siala sialis*)	0.00 (0.00) [a]	0.00 (0.00) [a]	0.05 (0.05) [a]	1	0.618	0.048
Bird Species Diversity	0.93 (0.04) [a]	1.11 (0.03) [b]	0.94 (0.04) [a]	40	<0.001	N/A
Bird Species Richness	12.4 (0.92) [a]	19.3 (0.84) [b]	14.1 (1.59) [a]	40	<0.001	N/A

[a] Values with the same superscript do not differ significantly from each other.

(Table 2). Habitat niche breadth did not differ significantly between bird species that were most abundant in mature forest (0.27), shelterwood (0.20) and clearcut (0.17) stands ($F_{2,46} = 0.96$, $P = 0.39$).

Four species commonly regarded as nest predators (DeGraaf and Rudis, 1986) were detected during this study, eastern chipmunk, red squirrel, Blue Jay, and Common Grackle. Average number of detections of eastern chipmunks, and of all predator species combined, did not differ between mature forest and shelterwoods, and were significantly more abundant in these habitats than in clearcuts (Table 3).

Table 3
Predator abundance compared among 10 mature forest, 20 shelterwood, and 10 clearcut stands in northern New hampshire. Values with the same superscript do not differ significantly from each other

Species	Mature	Shelter	Clearcut	*N*	*P*
Chipmunk (*Eutamias striatus*)	0.75 (0.37) [a]	0.70 (0.16) [a]	0.00 (0.00) [b]	21	0.034
Red Squirrel (*Tamiasciurus hudsonicus*)	0.25 (0.25) [a]	0.20 (0.12) [a]	0.10 (0.10) [a]	9	0.500
Blue Jay (*Cyanocitta cristata*)	0.20 (0.13) [a]	0.25 (0.10) [a]	0.00 (0.00) [a]	7	0.243
Common Grackle (*Quiscalus quiscula*)	0.00 (0.00) [a]	0.05 (0.05) [a]	0.00 (0.00) [a]	1	0.618
Total	1.30 (0.37) [a]	1.20 (0.23) [a]	0.10 (0.10) [b]	38	0.008

Table 4
Predation rates (SE) of artificial and natural nests compared among mature forest, shelterwood, and clearcut stands in northern New Hampshire

	Mature forest	Shelterwood	Clearcut	*N*	*P*
Artificial nests[a]	45.0 (13.2)	61.8 (9.90)	65.0 (13.2)	120	0.44
Natural nests[b]	0.043 (0.006)	0.012 (0.002)	0.012 (0.002)	23	0.62

[a] Percentage of nests depredated.
[b] Daily mortality rate.

Table 5
Regression coefficients, r^2 and *P* values for stepwise regressions of bird abundance and vegetation characteristics measured at 40 bird survey points in northern New Hampshire. Only bird species for which regressions were significant and which differed significantly among treatments were included in the analyses. Scientific names given in Table 2[a]

Species	DC	CN	DM	DD	CAN	LOW	MED	HI	r^2	*P*
Black-throated Blue Warbler	0.190	–	0.248	0.634	–	0.201	–	–	0.51	<0.001
Chestnut-sided Warbler	–	–	–	0.850	−0.036	–	–	–	0.78	<0.001
Red-eyed Vireo	0.178	−0.316	–	–	–	–	–	–	0.37	0.001
Ovenbird	–	–	–	–	0.019	−0.178	–	–	0.51	<0.001
American Redstart	–	−0.233	0.106	–	−0.015	–	–	–	0.48	<0.001
Black-throated Green Warbler	0.244	–	−0.256	–	–	–	–	–	0.65	<0.001
White-throated Sparrow	−0.152	–	–	–	–	–	–	–	0.50	<0.001
Mourning Warbler	–	–	0.129	–	−0.013	–	–	−0.271	0.50	0.001
Hermit Thrush	–	–	–	–	0.010	–	–	–	0.30	0.001
Common Yellowthroat	−0.179	–	–	−0.352	–	–	–	−0.193	0.72	<0.001
Canada Warbler	−0.091	–	–	0.608	–	–	–	–	0.29	0.004
Black-and-white Warbler	−0.190	−0.169			0.016	−0.085	0.318		0.62	<0.001
Scarlet Tanager	–	–	−0.056	–	–	−0.103	–	–	0.22	0.013
Alder Flycatcher	–	–	–	–	−0.013	–	–	–	0.49	<0.001
Hairy Woodpecker	–	–	–	0.335	–	–	–	–	0.19	0.009
Blackburnian Warbler	–	0.244	–	–	–	–	–	−0.158	0.33	0.002
Blue-headed Vireo	–	–	–	0.395	–	–	0.182	–	0.16	0.035
Northern Flicker	−0.065	–	–	–	–	–	–	–	0.37	<0.001
Brown Creeper	–	–	−0.060	−0.295	0.008	–	–	–	0.29	0.007

[a] DC: Basal area of deciduous trees; CN: Basal area of coniferous trees; DM: Basal area of ice-damaged trees; DD: Basal area of dead trees; CAN: Percent canopy cover; LOW: Number of contacts with vegetation 0–1 m above ground; MED: Number of contacts with vegetation 0–1 m above ground; HI: Number of contacts with vegetation 0–1 m above ground.

Twenty-three natural nests of eight different passerine bird species were located during the course of the study. Predation rates on artificial and natural nests did not differ among mature forest, shelterwoods, and clearcuts (Table 4).

Regressions between habitat variables and abundance of 26 of the 48 bird species were statistically significant, and explained between 13 and 78% of the variability in abundance of bird species among survey points (Table 5).

4. Discussion

The patterns of bird species distribution among mature forest, shelterwoods and clearcuts that we observed are generally consistent with the results of other studies comparing the effects of partial cutting versus clearcutting on bird communities (Kilgore, 1971; Franzreb, 1977; Webb et al., 1977; Franzreb and Ohmart, 1978; Freedman et al., 1981; Maurer et al., 1981; Tobalske et al., 1991; Hansen et al., 1995; Annand and Thompson, 1997; Hagan et al., 1997). Results of multiple regression analyses suggest that changes in vegetation structure resulting from silvicultural activities is probably responsible for observed differences in bird species distributions among mature forest, shelterwoods and clearcuts. Of nine bird species that were most abundant in mature forest or shelterwoods, and for which regressions were significant, the abundance of seven of these species were positively correlated with basal area of deciduous or coniferous trees and percent canopy coverage, habitat characteristics that had significantly highest values in mature forest or shelterwoods (although the difference in conifer basal area among treatments was not statistically significant). Conversely, of nine bird species that were most abundant in clearcuts or shelterwoods, and for which regressions were significant, eight were negatively correlated with the basal area of deciduous trees and/or percent canopy coverage, variables that had significantly lowest values in clearcuts. Greater bird species diversity and species richness in shelterwood stands resulted from the overlap of bird species characteristic of mature forest, such as Scarlet Tanagers and Black-throated Green Warblers, and early-successional habitats, such as Chestnut-sided Warblers and Common Yellow throats.

Interestingly, of the four species that were significantly more abundant in mature forest than either shelterwoods or clearcuts (Scarlet Tanager, Black-throated Green Warbler, Blackburnian Warbler and Brown Creeper) three were significantly negatively related to the abundance of ice-damaged trees. Conversely, the only two species that were positively correlated with the abundance of ice-damage trees (Black-throated Blue Warbler and Mourning Warbler) were bird species that were significantly more abundant in shelterwoods and clearcuts than mature forest. These results suggest that the effect of shelterwood cutting on bird communities resembles the effect of natural reductions in canopy coverage that result from natural meteorological phenomena such as ice storms.

Changes in vegetative characteristics resulting from silvicultural activities may affect bird communities through their impact on the availability of foraging and nesting habitat. Canopy-dwelling species, such as the Scarlet Tanager, Black-throated Green Warbler, and Blackburnian Warbler may experience reduced foraging efficiency with the thinning of the canopy (Franzreb and Ohmart, 1978; Probst, 1979; Tobalske et al., 1991). Ground and shrub-dwelling species, such as the Hermit Thrush, Ovenbird, Black-throated Blue Warbler, and Chestnut-sided Warbler may be affected by increased understory density resulting from increased light penetration, which changes the availability of suitable foraging and nesting habitat for these species (Kilgore, 1971; Probst, 1979; Maurer et al., 1981; DeGraaf et al., 1991; Hansen et al., 1995; Annand and Thompson, 1997).

Although, the declines of mature forest dwelling birds has been a long-standing concern (Terborgh, 1989; Askins et al., 1990) recent studies indicate that bird species inhabiting early-successional habitats are undergoing even more severe population declines than their mature forest counterparts, particularly in the northeastern United States (Witham and Hunter, 1992; Askins, 1993; Hagan, 1993; Litvaitis, 1993). Greater habitat specialization of early-successional shrubland birds may make these species particularly vulnerable to changes in habitat abundance (Askins, 1993). We did not detect significant differences in habitat niche breadth among bird species that were most abundant in clearcuts, shelterwoods and mature-forest, although the value of niche breadth tended to be narrower for bird species that were most abundant in clearcuts relative to those species most abundant in mature forest, consistent with the view that early-successional bird species are more specialized in their habitat requirements than mature forest bird species (Askins, 1993).

We detected no significant differences among mature forest, shelterwood or clearcut stands in predation rates of either natural or artificial nests, although the predation rates on artificial nests appeared lower, and predation rates on natural nests appeared higher, in mature forest than in shelterwoods or clearcuts. We believe that the nonsignficant trend observed in natural nests likely reflects patterns of nest predation among mature forest, shelterwoods and clearcuts for the following reasons: (1) Understory density was lowest in mature forest and comparable in clearcuts and shelterwoods, and understory density is generally positively related to nest survival (Martin, 1992). (2) Predator abundance was significantly lower in clearcuts than in mature forest in this and other studies (King et al., 1998). (3) Survival rates of actual nests in clearcuts of similar age and vegetation structure were far higher (>80%, King et al., 1999a in Press) than in mature forests in this region (25–60%, King et al., 1996). And (4) although artificial nests may provide a reasonable index to predation rates within habitats (Wilson et al., 1998; King et al., 1999b in Press), there are reasons to believe that they do not provide an accurate indication of habitat specific predation rates, especially where predator communities differ among habitats (Martin, 1988; Haskell, 1995).

The results of this study are in agreement with the results of other studies indicating the intermediate levels of cutting, such as that created by the initial stages of shelterwood cutting, provides habitat simultaneously for mature forest and early-successional bird species (e.g. Webb et al., 1977; DeGraaf et al., 1991; Annand and Thompson, 1997). Furthermore, increased understory structure in shelterwood stands may decrease predation rates on forest birds relative to unmanaged forests. However, maximizing within-stand diversity by emphasizing shelterwood cutting may reduce diversity at the landscape scale because shelterwood cutting does not appear to accommodate either mature forest specialist bird species, such as the Brown Creeper, or early-successional specialist bird species, such as the Alder Flycatcher. Thus, exclusive reliance on shelterwood cutting would likely reduce bird diversity at the landscape scale as these specialized bird species decline in abundance.

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