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Songbird response to group selection harvests and clearcuts in a New Hampshire northern hardwood forest

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Abstract

Clearcutting creates habitat for many species of early successional songbirds; however, little information is available on bird use of small forest openings created by group selection harvests. Group selection harvests are increasing on the White Mountain National Forest due to negative public response to clearcutting. The objective of this study was to determine if avian species richness and composition differ between clearcut and group selection openings, and between mature stands and the uncut portions of group selection stands. Point count surveys were conducted during the 1992 and 1993 breeding seasons within six study blocks in the White Mountain National Forest, NH. Each block consisted of a clearcut stand, a group selection stand and a mature stand. Species richness per stand was significantly higher in clearcut openings ($p = 0.010$) than in group selection openings. Forested areas surrounding group selection openings were similar to mature stands in species richness ($p = 0.848$) and composition. Our data suggest that, relative to avian use, the group selection system does not provide habitat similar to that created by clearcutting in extensive northern hardwood stands. The group selection system appears to retain much of the mature forest bird community while providing for a limited number of early successional bird species. Gradual replacement of clearcutting with group selection harvests could result in reduced avian diversity across large forested tracts.

Keywords: Forest birds; Clearcut; Group selection; Northern hardwood forest; Early successional

1. Introduction

Public concerns have pressured the National Forest System to eliminate or reduce even-aged forest management as a silvicultural practice and increase uneven-aged forest management. Clearcutting is the most common method of even-aged management practiced on the White Mountain National Forest, and although it is an efficient method for regenerating many tree species (Leak et al., 1987), and is an effective means of providing wildlife habitat (Hunter, 1990; DeGraaf et al., 1992), the use of clearcutting has been reduced significantly on public lands. Reasons for this reduction are mainly due to public sensitivity

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to the visual impact of clearcuts and perceived detrimental effects to wildlife habitat and forest health. This criticism has led to increased utilization of uneven-aged silvicultural practices, such as group selection on the White Mountain National Forest. Under this system, groups of two or more adjacent trees are removed from the forest overstory at intervals ranging from 10 to 20 years. The size of these openings ranges from 0.05 to 0.80 ha depending on management objectives. If group selection openings are large enough, tree regeneration is similar to that produced by clearcutting (Leak et al., 1987).

Neotropical birds are of current interest in light of research which suggests that their populations are declining (Robbins et al., 1989; Askins et al., 1990; Hagan and Johnston, 1992). Many of these species require early successional stages of forest habitat for breeding (Witham and Hunter, 1992; Hagan, 1993). For example, data from U.S. Fish and Wildlife Service Breeding Bird Surveys of the northeast region indicate that the majority of declining neotropical migrant species (22 species, 75.9%) inhabit early successional or disturbed habitat types (Smith et al., 1993). In New England, this type of habitat has become less abundant over the last century as former agricultural land reverted to forest. New England is currently at least 75% forested and, northern New England is >90% forested (Brooks and Birch, 1988).

Much research has focused on avian responses to clearcutting (e.g. Webb et al., 1977; Titterington et al., 1979; DeGraaf, 1987; Thompson III et al., 1992). These studies indicate that clearcutting creates early successional habitat that provides important breeding grounds for neotropical and short-distant migrants, and resident avian species. Comparatively little information exists on avian responses to group selection openings.

If group selection replaces clearcutting as the predominant silvicultural technique, managed forest openings on the White Mountain National Forest will be limited to 0.80 ha in size. Previous studies have focused on the minimum size of forest fragments required to support songbirds that breed in mature stands (Galli et al., 1976; Ambuel and Temple, 1983; Robbins et al., 1989); however, information is lacking on the area sensitivity of species requiring early successional habitat. The size of a forest opening may be an important feature with respect to breeding bird composition and evidence to support this has been described by Rudnicky and Hunter (1993) who found an increase in species richness with an increase in clearcut size up to 20 ha. Information is also sparse on the communities that utilize the uncut forested portions of a group selection stand. The objectives of this study were:

1. to compare avian species richness, abundance, and composition within clearcut, group selection, and mature stands;
2. to compare avian species richness and composition within clearcut and group selection openings;
3. to compare avian species richness, abundance, and composition within mature forest stands and the uncut portions of a group selection stand; and
4. to assess the potential effects of replacing even-aged management with uneven-aged management on songbird populations in the White Mountain National Forest.

2. Methods

This study was conducted on the Saco and Ammonoosuc Ranger Districts of the White Mountain National Forest in north-central New Hampshire (44° N, 71° W). The forest covers 304 050 ha of which ≈97% are forested. Much of the forest was logged during the late 1800s and early 1900s (Belcher, 1980), and subsequently followed by extensive fires, resulting in an ≈90–110-year-old even-aged forest today. Current Forest Service regulations on the White Mountain National Forest limit timber management practices to small-scale disturbances with maximum clearcut sizes of 10–12 ha (USDA Dept. of Agriculture and Forest Service, 1986).

Six study blocks were established within northern hardwood forests, dominated by American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*), with smaller amounts of red maple (*Acer rubrum*) and eastern hemlock (*Tsuga canadensis*). Each block consisted of three stands; clearcut, group selection, and mature. Stands within blocks were as similar as possible with respect to initial cover type and years since harvest. Clearcuts and group selection openings were between 0 and 5 years post-harvest at the onset of the study and ranged approximately in size from 8–12 ha to 0.13–0.65 ha, respectively. Because the use of the group selection silvicultural system is relatively new in the study area, all group selection stands used in this study were only subjected to the first in a series of harvests required under this uneven-aged system. Stands were classified as mature if ≈50% of their basal area consisted of sawtimber-sized trees (>28.9 cm). All mature stands were second growth and had no recent harvest activity, with one exception. The mature stand in one block was harvested between the 1992 and 1993 field seasons, and subsequently replaced with a nearby stand that was managed with single-tree selection in 1954.

2.1. Bird surveys

Breeding bird surveys were conducted between 24 May and 1 July, in 1992 and 1993, using the point count method (Ralph et al., 1995). Surveys were started by 0500 h and were completed by 0930 h. All stands within a block were surveyed on the same day, and each block was surveyed four times/season. Two observers participated in the study; each observer surveyed each of the six blocks twice per year; and all six blocks were surveyed before the next survey cycle began. The order in which stands were re-surveyed was reversed to compensate for time of day bias associated with singing behavior. Surveys were not conducted in rainy or windy weather.

Six survey points were established within each stand (18 points per block). In the mature stands, survey points were located 100 m apart along a systematic transect. All points within these stands were >100 m from any edge. Within clearcut stands, three points were established 10–20 m from clearcut edges (edge points), and three points were located >50 m from the edge (interior points). Survey points within group selection stands consisted of three points inside the group openings (open points) and three points in the forested areas between openings (group forested points). All survey points were at least 100 m apart. All birds seen or heard within 50 m of survey points were recorded during a 7-min period. In the case of edge points in a clearcut stand, the 50 m radius would include both, forested and open areas. Interior points included only open area. Because group selection openings were <0.80 ha, the 50 m radius included both, forested and open area, although the proportions varied. Plot boundaries were marked with flagging in at least one direction to facilitate estimation of a 50 m radius while surveying. Birds heard within the openings (open species) and forested areas (forest species) of clearcut and group selection stands were distinguished in the recorded data. The terms 'open species' and 'forest species' were used to distinguish where birds were observed, not to categorize a bird by habitat use.

We intentionally placed 50% of our survey points within the openings of group selection stands because one of our primary objectives was to investigate species composition within group selection openings. If survey points were placed randomly throughout the stand the number of survey points that would fall within openings would be insufficient to address this question (i.e. ≈10% of group selection stands consisted of openings). Additionally, stands in this study will be re-entered at 10–20-year intervals with the entire rotation cycle taking ≈100 years to complete at which time new group selection openings will be surrounded by several age/size classes. Therefore, the placement of more survey points within group selection openings than would typically be represented after an initial harvest was also done in an attempt to gain insight into the long-term effects of this treatment in a realistic time frame.

2.2. Vegetative sampling

One vegetation plot was established at each survey point ($n = 108$) during the summer of 1992. Species, diameter at breast height (DBH), and condition (live vs. dead) of overstory trees >8.9 cm DBH were recorded on a variable radius plot using a 10 basal area factor prism. Live understory vegetation was measured at four circular 0.0016 ha subplots (plot radius = 2.27 m) placed 10 m in the four cardinal directions from a survey point. Stems taller than 1.4 m were tallied by species into four DBH classes: 0.25–1.20, 1.3–3.7, 3.8–6.3, and 6.4–8.6 cm DBH. Woody stems ≥0.5 and <1.4 m tall (seedlings) were also tallied by species on each of the four circular subplots. Woody and herbaceous vegetation <0.5 m tall (ground cover) was measured by the point intercept method along four 10-m transects leading to the circular subplots. Vegetation in this category covering the markings was recorded by presence/absence. This same method was used to obtain estimates of slash cover (woody debris left by harvesting operations). During summer 1993, vegetation plots were remeasured on all of the survey points within clearcut and group selection openings to account for the rapid turnover in density of stems and percent ground cover.

2.3. Data analysis

Data were collected from 108 survey points in 1992 and 1993. Bird species richness was defined as the total number of species observed and abundance was defined as the total number of observations per species. Birds flying above the canopy were recorded but not included in analysis. Additionally, species that were observed <2 times per treatment group were excluded from analysis. Observations were classified as open species (species observed within openings), or forest species (species observed within forest).

Analyses were performed as a Randomized Complete Block design with six blocks. Some of the hypotheses being tested were based on three treatment groups; clearcut, group selection and mature. For these analyses, the experimental unit was the stand, representing one of the three treatment groups within a block. Each experimental unit consisted of six survey points which were surveyed four times per year; all observations at these points were pooled to produce a single value of mean species abundance per survey point per year for each experimental unit. The value for mean total species abundance was obtained by dividing the total number of observations by six survey points. However, the value for mean open species abundance in group selection stands was obtained by dividing the total number of observations by three survey points, because only three open points existed. This same procedure was followed for mean forest species abundance in any clearcut stand, where only three edge points existed to record observations in the forest.

Since different sections of stand types may differ in species composition and richness (i.e. clearcut edges and clearcut interiors), a second series of analyses was performed as a Randomized Complete Block. However, in this case the survey points were segregated into five treatment groups; clearcut edges, clearcut interiors, group selection openings, group selection forest, and mature forest. Within a stand, all survey points belonging to a particular treatment group were combined and treated as a single experimental unit, and the four repeated observations per year were pooled. Values of abundance were obtained as described above. Differences in open species abundance were not tested in this part of the analysis due to unequal area of open habitat sampled between clearcut interiors, clearcut edges, and group selection openings. Differences in forest species abundance were tested between the group selection forest and mature forest treatment groups because equal areas of forested habitat were sampled here.

The GLM (general linear model) analysis of variance module of Systat for Windows (Wilkinson et al., 1992) was used to test for differences in total, open, and forest species richness and abundance. In situations where a significant interaction by year was detected, each year was analyzed separately. Tukey's multiple comparison tests were used to test for pairwise differences between treatment group means. Because the data for abundance and richness counts had non-normal distributions, the data were transformed using a square root and rank transformation. Similar conclusions were obtained with the transformed and untransformed data, therefore reported results are based on the untransformed data (Conover and Iman, 1981).

Nonparametric Mann–Whitney tests were performed on vegetative descriptors and slash. Understory stems >1.4 m tall were tested as one variable rather than divided into four DBH classes because stem numbers were low in all DBH classes except for the smallest (0.25–1.00 cm).

3. Results

3.1. Stand type

A total of 50 bird species and 3208 observations were included in the analysis (Table 1); 46 species (1000 observations) were observed in clearcut stands, 33 (1181 observations) in group selection stands, and

Table 1
Number of observations and relative abundance of songbirds detected in clearcuts, group selection and mature stands during the 1992 and 1993 breeding seasons in the White Mountain National Forest, New Hampshire

Species	Scientific names	Clearcut				Group selection				Mature		Total	
		Forest	Open	Total	Relative abundance[a]	Forest	Open	Total	Relative abundance	Forest	Relative abundance	Total	Relative abundance
Neotropical migrants[b]													
alder flycatcher	*Empidonax alnorum*	0	12	12	0.012	0	0	0	0.000	0	0.000	12	0.004
American redstart	*Setophaga ruticilla*	24	3	27	0.027	96	0	96	0.081	119	0.116	242	0.075
black-and-white warbler	*Mniotilta varia*	3	10	13	0.013	0	0	0	0.000	2	0.002	15	0.005
blackburnian warbler	*Dendroica fusca*	16	0	16	0.016	32	0	32	0.027	18	0.018	66	0.021
black-thr blue warbler	*Dendroica caerulescens*	30	0	30	0.030	146	0	146	0.124	91	0.089	267	0.083
black-thr green warbler	*Dendroica virens*	21	0	21	0.021	125	0	125	0.106	80	0.078	226	0.070
Canada warbler	*Wilsonia canadensis*	2	4	6	0.006	0	0	0	0.000	0	0.000	6	0.002
common yellowthroat	*Geothlypis trichas*	0	89	89	0.089	0	24	24	0.020	0	0.000	113	0.035
chestnut-sided warbler	*Dendroica pensylvanica*	0	220	220	0.220	2	73	75	0.064	0	0.000	295	0.092
eastern wood pewee	*Contopus virens*	7	3	10	0.010	3	0	3	0.003	17	0.017	30	0.009
indigo bunting	*Passerina cyanea*	0	41	41	0.042	0	0	0	0.000	0	0.000	41	0.013
least flycatcher	*Empidonax minimus*	6	0	6	0.006	5	0	5	0.004	86	0.084	97	0.030
magnolia warbler	*Dendroica magnolia*	2	0	2	0.002	3	0	3	0.003	0	0.000	5	0.002
mourning warbler	*Oporornis philadelphia*	0	44	44	0.044	0	22	22	0.019	0	0.000	66	0.021
northern parula	*Parula americana*	0	0	0	0.000	0	0	0	0.000	2	0.002	2	0.000
olive-sided flycatcher	*Contopus borealis*	0	3	3	0.003	0	0	0	0.000	0	0.000	3	0.000
ovenbird	*Seiurus aurocapillus*	41	0	41	0.041	154	0	154	0.130	120	0.117	315	0.098
red-eyed vireo	*Vireo olivaceus*	49	0	49	0.050	179	0	179	0.152	257	0.250	485	0.151
rose-breasted grosbeak	*Pheucticus ludovicianus*	7	5	12	0.012	19	0	19	0.016	11	0.011	42	0.013
scarlet tanager	*Piranga olivacea*	12	0	12	0.012	39	0	39	0.033	34	0.033	85	0.027
solitary vireo	*Vireo solitarius*	18	0	18	0.018	45	0	45	0.038	27	0.026	90	0.028
Swainson's thrush	*Catharus ustulatus*	5	2	7	0.007	17	0	17	0.014	21	0.020	45	0.014
veery	*Catharus fuscescens*	7	2	9	0.009	12	0	12	0.010	15	0.015	36	0.011
wood thrush	*Hylocichla mustelina*	0	0	0	0.000	13	0	13	0.011	11	0.011	24	0.007
Short-distant migrants													
American robin	*Turdus migratorius*	2	7	9	0.009	0	0	0	0.000	0	0.000	9	0.003
brown creeper	*Certhia americana*	0	0	0	0.000	0	0	0	0.000	2	0.002	2	0.000
cedar waxwing	*Bombycilla cedrorum*	0	8	8	0.008	6	0	6	0.005	2	0.002	16	0.005
dark-eyed junco	*Junco hyemalis*	3	51	54	0.054	0	6	6	0.005	0	0.000	60	0.019
eastern bluebird	*Sialia sialis*	0	4	4	0.004	0	0	0	0.000	0	0.000	4	0.001
eastern phoebe	*Sayornis phoebe*	2	0	2	0.002	0	0	0	0.000	0	0.000	2	0.000
hermit thrush	*Catharus guttatus*	17	5	22	0.022	44	0	44	0.037	27	0.026	93	0.029
northern flicker	*Colaptes auratus*	0	3	3	0.003	0	0	0	0.000	0	0.000	3	0.000
purple finch	*Carpodacus purpureus*	0	3	3	0.003	3	0	3	0.003	0	0.000	6	0.002
rufous-sided towhee	*Pipilo erythrophthalmus*	0	7	7	0.007	0	0	0	0.000	0	0.000	7	0.002

Table 1 (*Continued*)

Species	Scientific names	Clearcut				Group selection				Mature		Total	
		Forest	Open	Total	Relative abundance[a]	Forest	Open	Total	Relative abundance	Forest	Relative abundance	Total	Relative abundance
song sparrow	*Melospiza melodia*	0	2	2	0.002	0	0	0	0.000	0	0.000	2	0.000
winter wren	*Troglodytes troglodytes*	2	3	5	0.005	2	0	2	0.002	0	0.000	7	0.002
white-throated sparrow	*Zonotrichia albicollis*	3	76	79	0.079	0	4	4	0.003	0	0.000	83	0.026
yellow-rumped warbler	*Dendroica coronata*	2	2	4	0.004	11	0	11	0.009	7	0.007	22	0.007
yellow-bellied sapsucker	*Sphyrapicus varius*	5	6	11	0.011	18	0	18	0.015	9	0.009	38	0.012
tree swallow	*Tachycineta bicolor*	0	59	59	0.059	0	0	0	0.000	0	0.000	59	0.018
Residents													
American goldfinch	*Carduelis tristis*	0	2	2	0.002	2	0	2	0.002	3	0.003	7	0.002
black-capped chickadee	*Parus atricapillus*	10	7	17	0.017	32	0	34	0.029	16	0.016	67	0.021
blue jay	*Cyanocitta cristata*	3	2	5	0.005	14	0	14	0.012	2	0.002	21	0.007
downy woodpecker	*Picoides pubescens*	0	2	2	0.002	3	0	3	0.003	5	0.005	10	0.003
evening grosbeak	*Coccothraustes vespertinus*	0	2	2	0.002	2	0	0	0.000	14	0.014	16	0.005
golden-crowned kinglet	*Regulus satrapa*	2	0	2	0.002	0	0	0	0.000	0	0.000	2	0.000
hairy woodpecker	*Picoides villosus*	2	0	2	0.002	12	0	12	0.010	11	0.011	25	0.008
pileated woodpecker	*Dryocopus pileatus*	3	0	3	0.003	0	0	0	0.000	4	0.004	7	0.002
red-breasted nuthatch	*Sitta canadensis*	0	0	0	0.000	7	0	7	0.006	2	0.002	9	0.003
white-breasted nuthatch	*Sitta carolinensis*	5	0	5	0.005	6	0	6	0.005	12	0.012	23	0.007
Total number of observations		311	689	1000		1054	127	1181		1027		3208	
Total number of species		30	32	46		29	5	33		30		50	

[a] Relative abundance calculated by dividing the total number of observations recorded for an individual species by the total number of observations in a stand type.
[b] Migratory status designations based on National Fish and Wildlfie Foundation, Partners in Flight Newsletter, 1992, vol. 2, no. 1, p. 30.

30 (1027 observations) in mature stands. Eleven species were observed exclusively within clearcut stands, although only the tree swallow (*Tachycineta bicolor*), indigo bunting (*Passerina cyanea*), and alder flycatcher (*Empidonax alnorum*) were observed >10 times. The northern parula (*Parula americana*) and brown creeper (*Certhia americana*) were observed only within mature stands; no species was exclusive to group selection stands.

The most abundant species (≥5% relative abundance) in clearcut stands, accounting for 50% of total observations, were the chestnut-sided warbler (*Dendroica pensylvanica*), common yellowthroat (*Geothlypis trichas*), white-throated sparrow (*Zonotrichia albicollis*), dark-eyed junco (*Junco hyemalis*), and tree swallow (Table 1). The red-eyed vireo (*Vireo olivaceus*), ovenbird (*Seiurus aurocapillus*), black-throated blue warbler (*Dendroica caerulescens*), black-throated green warbler (*Dendroica virens*), and American redstart (*Setophaga ruticilla*) were the most abundant (≥5% relative abundance) species observed in group selection stands (Table 1), and collectively accounted for 58% of the total observations. These species, and the least flycatcher (*Empidonax minimus*), were also the most abundant in mature stands (Table 1).

Total species richness was higher in clearcut stands ($F = 1.93$, df = 10, $p = 0.038$) than mature stands (Fig. 1(a)). Open species richness was significantly higher in clearcut stands than group selection stands ($F = 14.50$, df = 5, $p = 0.010$). Mature stands and group selection stands were similar in forest species richness ($F = 0.877$, df = 10, $p = 0.848$); clearcut stands were lower in forest species richness than group selection stands ($F = 6.70$, df = 10, $p = 0.025$).

A significant interaction by survey year existed with respect to total species abundance ($F = 4.32$, df = 2, $p = 0.033$); therefore, each year's data were analyzed

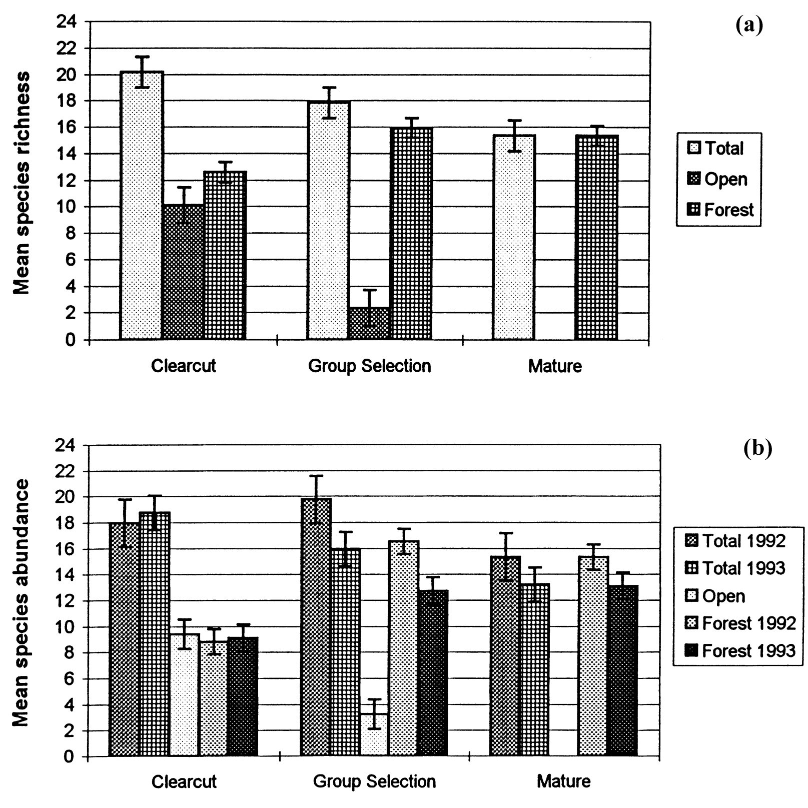


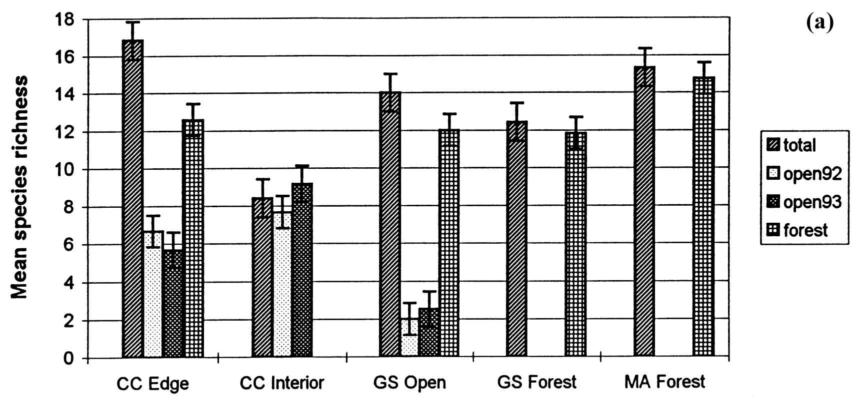
Fig. 1. (a) Least squares means and standard errors of total, open, and forest species richness in clearcut, group selection, and mature stands. (b) Least squares means and standard errors of total, open, and forest species abundance for clearcut, group selection, and mature stands.

separately. No differences ($F = 1.48$, df $= 2$, $p = 0.273$) were detected between treatments in 1992, however, in 1993 abundance was higher ($F = 4.41$, df $= 2$, $p = 0.042$) in clearcut stands than in mature stands (Fig. 1(b)). Open species abundance was significantly higher in clearcut stands than group selection stands ($F = 10.48$, df $= 5, p = 0.012$) (Fig. 1(b)). The abundance of forest species differed between years ($F = 6.16$, df $= 2$, $p = 0.011$), and was determined to be similar between mature stands and group selection stands in both, 1992 and 1993. In 1992, mature stands and group selection stands were higher in forest species abundance than clearcut stands ($F = 18.40$, df $= 2$, $p = 0.002$, 0.001, respectively); however in 1993, significant differences were only found between mature stands and clearcut stands ($F = 4.65$, df $= 2$, $p = 0.047$) (Fig. 1(b)).

3.2. Openings

By definition, observations of open species could occur at three treatment groups; clearcut interior, clearcut edge, and group selection open. Thirty-two species were observed within clearcut openings and five species were observed within group selection openings (Table 1). The chestnut-sided warbler, common yellowthroat, and mourning warbler (*Oporornis philadelphia*) accounted collectively for ≈94% of the observations within group selection openings.

All five of the species observed within group selection openings were also observed within clearcut openings. Of the twenty-seven open species exclusive to clearcuts openings, only the tree swallow, indigo bunting, black and white warbler, and alder flycatcher were observed >10 times. Tree swallows and black



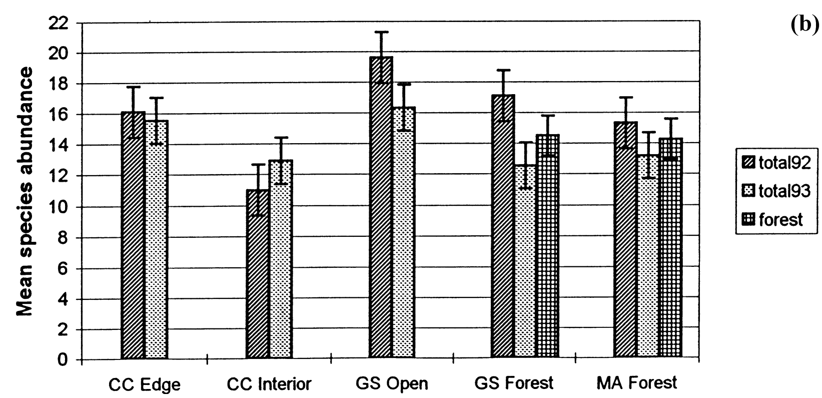


Fig. 2. (a) Least squares means and standard errors of total, open, and forest species richness at five types of survey points. CC, clearcut; GS, group selcetion; and MA, mature. (b) Least squares means and standard errors of total, open, and forest species abundance at five types of survey points. CC, cleacut; GS, group selection; and MA, mature.

and white warblers were observed in five out of six and four out of six clearcuts, respectively. Indigo buntings were observed both years in the same two clearcuts which were two and three years post-harvest. Alder flycatchers were restricted to the oldest clearcut (five and six years post-harvest).

Composition of open species was similar between clearcut edges and clearcut interiors, as no species was unique to either. An interaction by survey year ($F = 3.85$, df $= 2$, $p = 0.045$) existed with respect to open species richness. Richness of open species was higher in clearcut interiors than in group selection openings during both survey years; 1992: ($F = 13.0$, df $= 2$, $p = 0.002$) and 1993: ($F = 12.70$, df $= 2$, $p = 0.001$) (Fig. 2(a)). Clearcut edges were higher in open species richness than group selection openings in 1992 ($F = 13.0$, df $= 2$, $p = 0.007$), no significant difference occurred in 1993 ($p = 0.088$). No difference in the richness of open species existed between clearcut interiors and edges during 1992 ($F = 13.0$, df $= 2$, $p = 0.686$) or 1993 ($F = 12.70$, df $= 2$, $p = 0.059$) (Fig. 2(a)).

The chestnut-sided warbler was the only open species abundant enough to be tested for individual differences due to stand type and was found to be more abundant in clearcut stands than in group selection stands ($F = 8.88$, df $= 5$, $p = 0.035$).

3.3. Forested areas

Observations of forest species could occur at four treatment groups; clearcut edge, group selection open, group selection forest, and mature. Most birds observed at group selection openings were in the surrounding forest (83%), not within the openings. Approximately 56% of the observed birds at edges of clearcuts were in the adjacent forest. The combined forested areas contained a total of 37 species (Table 1). The red-eyed vireo, ovenbird, black-throated blue warbler, American redstart, and black-throated green warbler were among the most abundant species observed within these four treatment groups.

No differences in forest species richness were found among these treatment groups ($F = 0.90$, df $= 15$, $p = 0.575$) (Fig. 2(a)). Forest species abundance did not differ between the group selection forest and mature forest treatments ($F = 5.91$, df $= 5$, $p = 0.903$) (Fig. 2(b)).

Five species were abundant enough to be tested for individual differences between group selection and mature stands (Table 2). The red-eyed vireo was the only forest species that was more abundant in mature stands than in group selection stands. This difference in abundance was found when tests were done comparing the whole group selection stand (both forested and open points) to mature stands ($F = 0.86$, df $= 5$, $p = 0.014$) and also when comparing only the forested points in group selection stands to mature stands ($F = 0.54$, df $= 5$, $p = 0.005$). The abundance of the ovenbird, black-throated blue warbler, black-throated green warbler and the American redstart was similar in these two areas ($p > 0.05$).

3.4. Vegetation

Mature stands and the forest surrounding group selection openings were structurally similar ($p > 0.05$) (Table 3). Overstory vegetation within these

Table 2
Tukey pairwise comparisons of least square mean (LSM) differences of abundance for five forest species in group selection and mature stands on the White Mountain National Forest

Species	Group selection (total)[a]		Group selection (forest)[b]		Mature		p Value	
	LSM	SE	LSM	SE	LSM	SE		
American redstart	1.33	0.393	1.31	0.330	1.65	0.330	$p = 0.319$	$p = 0.491$
Black-throated blue warbler	2.03	0.305	1.86	0.436	1.26	0.436	$p = 0.137$	$p = 0.378$
Black-throated green warbler	1.74	0.394	1.58	0.393	1.11	0.393	$p = 0.313$	$p = 0.435$
Ovenbird	2.14	0.597	2.08	0.554	1.67	0.554	$p = 0.601$	$p = 0.618$
Red-eyed vireo	2.49	0.208	2.38	0.176	3.57	0.176	$p = 0.014$	$p = 0.005$

[a] Whole stand (group selection forest and open points) included in analysis.
[b] Only group selection forest points included in analysis.

Table 3
Structural characteristics in clearcut, group selection, and mature stands on the White Mountain National Forest, New Hampshire

	Clearcut		Group selection		Group selection		Group selection		Mature	
			Open		Forest		Total			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Overstory: *>8.9 cm DBH*										
Density poles										
Live trees/ha	0.00	0.00	0.00	0.00	516.03	59.06	258.02	29.53	413.31	41.69
Dead trees/ha	0.00	0.00	0.00	0.00	49.82	28.50	24.91	14.25	12.13	6.22
Density sawtimber										
Live trees/ha	0.00	0.00	0.00	0.00	131.70	13.78	65.85	6.89	122.41	6.79
Dead trees/ha	0.00	0.00	0.00	0.00	14.92	4.94	7.46	2.47	14.33	3.01
Basal area live poles (m^2/ha)	0.00	0.00	0.00	0.00	14.08	0.90	7.04	0.45	10.43	1.03
Basal area live sawtimber (m^2/ha)	0.00	0.00	0.00	0.00	13.96	1.18	6.98	0.59	14.93	0.89
Total basal area	0.00	0.00	0.00	0.00	28.04	0.98	14.02	0.49	25.36	1.24
Understory: *<8.9 cm DBH*										
Density (stems/ha): >1.4 m tall										
0.25–1.20 cm DBH	3553.00	584.48	10 261.76	3380.27	1518.01	390.33	5889.89	1761.43	1337.92	153.02
1.30–3.70 cm Dbh	461.69	96.55	274.44	104.04	797.61	168.03	536.01	83.73	737.57	66.57
3.80–6.30 cm DBH	6.42	3.66	17.14	17.14	274.44	53.75	145.80	25.52	295.88	35.00
6.40–8.60 cm DBH	0.00	0.00	0.00	0.00	77.19	28.58	38.61	10.89	99.59	21.32
Total	4021.11	628.86	10 553.35	3428.88	2667.35	495.31	6610.31	1773.78	2470.78	171.25
Density (stems/ha): <1.4 m tall										
seedlings and shrubs	37 335.85	3195.34	41 652.35	5547.62	7650.58	1651.27	24 651.46	3461.68	5278.88	615.85
% Ground cover										
<0.5 m	56.21	3.01	46.94	3.52	23.19	4.18	35.07	2.67	17.97	1.83
% Slash cover										
<0.5 m	18.06	1.58	14.17	2.25						
>0.5 m	0.50	0.26	0.97	0.38						

two areas was dominated by American beech, sugar maple, and yellow birch. American beech was the predominant woody species in the understory of mature stands. Understory vegetation in the forest around group selection openings was more evenly distributed between beech, striped maple (*Acer pensylvanicum*), and sugar maple.

Pin cherry (*Prunus pensylvanica*), *Rubus* spp., and yellow birch were the predominant understory species >1.4 m tall within clearcut openings. Group selection openings were dominated by *Rubus* spp., beech, and striped maple. Density of understory stems >1.4 m tall was more than 2.5 times greater in group selection openings than in clearcut openings, however, differences were not significant ($p = 0.490$). The major shrub and seedling component within both types of openings consisted of *Rubus* spp., pin cherry, and beech. Average total density of seedlings and shrubs, and percent ground cover were similar between the two types of openings ($p = 0.757$, 0.057, respectively). Percent slash cover was higher in clearcuts ($p = 0.019$), and was the only structural descriptor that differed between the two types of openings.

4. Discussion

Our data indicated that clearcutting provides habitat for a more diverse group of early successional bird species than group selection. This observation suggests that there may be minimum opening size requirements for some species associated with early successional habitat. The chestnut-sided warbler, common yellowthroat, and mourning warbler were the most abundant species observed in group selection openings, and were observed in group openings of all sizes. However, other species common in clearcuts, were absent or rarely observed in group selection openings.

Home range requirements, habitat heterogeneity, and edge effects, factors often considered to influence the relationship between species richness and forest patch size (Galli et al., 1976; Ambuel and Temple, 1983; Robbins et al., 1989), may also influence such relationships in forest openings (Rudnicky and Hunter, 1993). Most of the songbirds observed in this study have small home ranges and defend small territories (DeGraaf and Rudis, 1986), although some exceptions did exist. Species with territory sizes that exceeded the size of the largest group selection opening (0.65 ha) were the eastern bluebird (*Sialia sialis*), indigo bunting, alder flycatcher, and olive-sided flycatcher (*Contopus borealis*). Bluebirds were absent from group selection openings, and although uncommon in this study, are known to breed in clearcut openings (Conner and Adkisson, 1975; Crawford et al., 1981). Alder flycatchers and olive-sided flycatchers were observed exclusively in clearcuts, although low numbers of observations prohibited any definitive conclusion of size requirements. However, Hagan et al. (1997) found that large expanses of early successional habitat and recent clearcuts in northern Maine were more likely to contain alder flycatchers and olive-sided flycatchers, respectively. Indigo buntings were also observed exclusively in clearcuts in this study; however, Kerpez (1994) and King et al. (in review) observed this species in group selection openings in Virginia and New Hampshire hardwood forests, respectively.

A difference in habitat heterogeneity also may have contributed to differences in species richness between the two types of openings. Vegetation, soil, and topography is likely to be more heterogeneous as the size of a forest patch or forest opening increases, and thereby provide a more diverse range of microhabitats (Wilcove et al., 1986; Rudnicky and Hunter, 1993) and influence the presence of bird species within an opening. For example, rufous-sided towhees (*Pipilo erythrophthalmus*) were observed in two out of six clearcut openings and absent from group selection openings. Low density of regenerating vegetation may have precluded their presence in the two youngest clearcuts and group selection openings; however, the factors that contributed to their absence in the other openings are not as obvious. In central hardwood habitats, rufous-sided towhees are common inhabitants of clearcuts, but only an occasional inhabitant of group selection openings (Annand and Thompson III, 1997). Perhaps some birds select particular plant species for their nest sites and foraging areas. For example, 10 foliage gleaning bird species showed preferences for yellow birch, and near uniform avoidance of beech in mature northern hardwood stands in New Hampshire (Holmes and Robinson, 1981). Although both types of openings were selected to be as homogeneous as possible, clearcuts were more likely to contain a greater variety of plant species than group selection openings. Differences in microclimate are likely to be greater between the edges and interiors of clearcuts than between the edges and interiors of group selection openings. This would contribute to a more heterogeneous vegetative community within clearcut openings.

The presence of slash may be significant to avian habitat selection as it can provide added protective cover to ground nesters, and elevated singing and hunting perches during the early stages of regeneration when woody and herbaceous cover is minimal. The clearcuts in this study contained a higher percentage of slash than group selection openings, and although this is not a designed consequence of clearcutting, it may have contributed to higher species richness there.

Studies of avian habitat use have generally stressed the importance of vertical diversity or foliage height diversity (MacArthur and MacArthur, 1961; Capen, 1985). An increase in the number of layers of foliage increases the number of potential niches, providing a theoretical increase in bird species diversity. Species diversity has also been related to habitat patchiness or horizontal diversity (Roth, 1976). The effects of habitat patchiness on avian community structure can be interpreted much like the effects of foliage height diversity; individual species are added to the community by adding pieces of adequate habitat (Rice et al., 1984). The importance of horizontal diversity has been demonstrated for certain avian species. For example, Whitmore (1981) found that grasshopper sparrows (*Ammodramus savannarum*) not only require open grasslands to fulfill nesting and foraging requirements, but grasslands that are mixed with areas of bare ground. The golden-winged warbler (*Vermivora chrysoptera*), a shrubland bird, appears to require open habitat with patches of herbs, shrubs, and trees rather than areas of dense vegetation (Confer and Knapp, 1981). These differences in microhabitat are more difficult to distinguish, but smaller forest openings are less likely to have the habitat diversity to satisfy a species with a broad range of microhabitat requirements.

Lastly, proximity to a forest edge may also influence avian selection of early successional habitat. Evidence to support this theory has been reported by King et al. (in review) who found fewer chestnut-sided warbler nests in cut edges than in cut interiors of clearcut and group selection openings in northern hardwood stands on the White Mountain National Forest. Additionally, Kerpez (1994) found greater numbers of indigo buntings and rufous-sided towhees in the interior of clearcuts than in group selection openings, or near the edges of clearcut openings in Virginia hardwoods.

Forested areas surrounding group selection openings were similar to mature stands in vegetative structure as well as breeding bird composition, richness and abundance. Further, when group selection stands were examined as a whole, rather than as separate sections of openings and forest, they were more similar to mature stands than to clearcut stands with respect to breeding bird composition. Although this data suggests that group selection openings do not have a negative impact on the abundance of forest interior birds, a study in Vermont found somewhat different results. Germaine et al. (1997) examined the effects of 0.40 ha group selection cuts on the forest interior bird community and found an increase in abundance of these birds with increasing distance from group selection openings. However, the ratio of openings to forest in his group selection stands (20–36%) was greater than in the present study (10–20%).

The red-eyed vireo was the only species statistically more abundant in mature stands than in group selection stands. This bird nests in various stages of forest regeneration, from sapling to sawtimber stands. However, Lawrence (1953) suggested that a continuous canopy may be a major habitat requirement, indicating that the broken canopy in group selection stands may have some negative effect on this species. Although the red-eyed vireo was lower in abundance in group selection stands, it was still the most abundant species observed in these areas

The results of this study indicate that the group selection system does not provide habitat similar to that created by clearcutting in northern hardwood stands. Clearcut openings contained diverse early successional bird communities. Group selection stands appeared to retain much of the mature forest bird community, and provide habitat for a few early successional bird species. Size of opening and related habitat diversity at the macro- and microhabitat scale probably influenced species differences. Conclusions based on these data suggest that the elimination of even-aged management on the White Mountain National Forest will result in less diverse early successional songbird communities.

As with any study, it is important to recognize certain limitations of the data. This study measured species richness and abundance, not productivity. Measurement of productivity is preferable to presence of singing males because reproduction is only inferred from the latter (Van Horne, 1983; Vickery et al., 1992). In addition, this study examined only the effects of the initial series of harvests under the group selection system. These conclusions are based on a region that is >90% forested, and are not necessarily applicable to less forested areas.

5. Management implications

There is no single management system that will provide habitat for all species of forest breeding birds. Even-aged management and uneven-aged management are suited for sustaining different components of a forest ecosystem and choosing the appropriate system will depend on specific goals. The group selection system appears to be an appropriate silvicultural technique if the goal is to maintain a mature forest bird component within a stand, or increase overall community diversity within an uncut forest. This system is also flexible from a timber management perspective in that it has potential for regenerating a variety of tree species depending on the size of the opening created. However, if the goal is to provide early successional habitat for a diversity of shrubland nesting species, or to maximize avian diversity, clearcutting is a more effective silvicultural technique. In the present study, almost half of the birds observed within clearcut openings prefer early successional habitat (DeGraaf and Rudis, 1986), and many species were unique to these areas. In contrast, early successional bird species in group selection stands were only a small component of the total bird community. This suggests that the group selection system will not provide the habitat required to sustain current songbird populations that require this habitat.

This study was not designed to determine if edge effects exist around openings within forested landscapes; however, another study on the White Mountain National Forest noted higher ovenbird nest predation rates in a 200-m zone adjacent to small clearcuts (2.1–5 ha) than in forest interiors (King et al., 1996). If edge effects do exist, the impact on the forest interior bird community is presumably greater in stands with numerous and widespread openings managed by group selection than in stands managed by clearcutting (Thompson III et al., 1996).

Determining when, and where, different management practices are suitable will depend on the present conditions of the stand and the surrounding landscape. For example, the increase and protection of forest interior habitat may be of immediate concern in the midwest and southeastern United States where agriculture and development have fragmented the forest landscape (Ambuel and Temple, 1983; Blake and Karr, 1984). Conversely, the significance of the decline of early successional habitat and wildlife diversity in New England also needs to be recognized (Witham and Hunter, 1992; Askins, 1993; Litvaitis, 1993).

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