Bird responses to the first cut of the uniform shelterwood silvicultural system in white pine forest

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Abstract

The response of birds to the first cut of the white pine uniform shelterwood sylvicultural system was examined in Algonquin Provincial Park, Ontario, in 1995 and 1996. Bird abundances and vegetation cover were compared between stands logged 2 to 18 years previously and mature stands with no recorded logging history. Of 61 bird species recorded, six varied significantly in relative abundance among treatments. Ruffed Grouse, White-throated Sparrows, Chestnut-sided Warblers, and Mourning Warblers were most abundant in recently cut stands, whereas Black-capped Chickadees were most abundant in stands with no recorded logging history. Ovenbirds were least common in stands cut 10 to18 years previously and more common in both recently cut stands and those with no recorded logging history. Bird species richness was greatest in unlogged stands and in stands logged 10 to18 years previously. Closed canopy and cavity-nesting species had the highest relative abundance in stands with no recorded logging history, whereas open-nesting species had the highest relative abundance in the recently cut stands. Bird communities in stands with similar logging history were similar, although there were some recently cut stands with similar communities to old cut stands. Percent cover of deciduous canopy and sub-canopy trees, and density of understory vegetation, explained significant variation in relative abundance of open shrub-nesting species. A longer rotation period would ensure higher numbers of canopy species and greater species richness in the landscape, although this method of timber harvesting is relatively benign in its impact on avian communities.

Résumé

Nous avons étudié la réponse des oiseaux à la première récolte du système sylvicole de coupe progressive d'ensemencement uniforme en forêt de pins blancs dans le parc provincial Algonquin, Ontario en 1995 et 1996. L'abondance des oiseaux et le couvert végétatif furent comparés entre des parcelles coupées il y a 2 à 18 ans et des parcelles de forêt mature sans histoire de coupe. L'abondance de seulement 6 des 61 espèces observées variait de façon significative entre les traitements. La Gélinotte huppée, le Bruant à Gorge blanche, la Paruline à flancs marrons et la Paruline triste étaient plus abondants dans les peuplements coupés récemment alors que la Mésange à tête noire était plus abondante dans les peuplements matures sans histoire de coupe. La richesse en espèces était plus élevée dans les peuplements intacts de même que dans ceux exploités il y a 10 à 18 ans auparavant. Les espèces de canopée fermée et les espèces nichant dans les cavités d'arbres étaient les plus abondantes dans les peuplements intacts alors que les espèces de milieux ouverts étaient plus abondantes dans les peuplements récemment coupés. Les variations dans l'abondance des espèces de milieux ouverts associées aux buissons étaient expliquées en grande partie par le pourcentage de couvert de la canopée décidue et des arbres de la sous canopée. Quoique cette pratique sylvicole ait relativement peu d'effets sur les communautés aviennes, une période de rotation plus longue assurerait la persistance d'un plus grand nombre d'espèces associées à la canopée de même qu'une plus grande richesse d'espèce dans le paysage.

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Introduction

White pine *(Pinus strobus)* is an economically and ecologically important species in Canada's mixed and southern boreal forests, especially in the Great Lakes-St.Lawrence Forest Region (Lowe 1994; Naylor et al. 1994). The management of these forests has recently been the focus of debate, as it is estimated that 80% of Central Ontario's forest-inhabiting wildlife use forests that contain red (*Pinus rugosa*) or white pine (Naylor et al. 1994).

Recent declines in neotropical migrant bird populations have been a cause for concern in both their breeding and wintering grounds, and habitat change is implicated as one possible explanation for the decline (Robbins et al. 1989; Thompson et al. 1995). Changes in breeding and wintering habitats may be due to logging and silvicultural practices, and may significantly affect avian populations at both the landscape and stand level (Franzreb and Ohmart 1978; Thompson et al. 1995). Information on how birds respond to clearcut logging is plentiful (Steffen 1985;Thompson et al. 1992; Welsh and Healy 1993; King et al. 1996; Norton and Hannon 1997), but there is less information on the effects of other silvicultural systems on bird communities (Franzreb and Ohmart 1978; Freedman et al. 1981; Thompson and Capen 1988; Thompson 1993; Thompson et al. 1995; Annand and Thompson 1997).

The uniform shelterwood silvicultural system results in gradual removal of the original forest rather than removing all or most trees in an initial cut, as is the case in a clearcut. A series of four cuts (preparation, regeneration, first removal, and final removal; Chapeskie et al. 1989), performed at twenty year intervals, removes the original stand while regeneration becomes established under the existing stand's canopy (Corbett 1994; Algonquin Forestry Authority (AFA) 1995; Thompson et al. 1995). The entire process is repeated after the passing of a further 40 years when the regeneration is 80 years old (AFA 1995). In Algonquin Park, Ontario, this silvicultural method has been used since the 1970's, at which time it was in an experimental stage. By the 1980's the system had been improved and deemed successful in promoting white pine regeneration (Chapeskie et al. 1989). Our purpose was to determine the effects of the first cutting of the uniform shelterwood silvicultural system on the abundance and richness of breeding birds, and on the vegetation structure of the white pine forests of Algonquin Provincial Park, Ontario. We predicted a loss of canopy species from the most recently cut stands, and a corresponding increase in shrub-nesting species, because the canopy is thinned to 50% canopy cover after the initial cut (Chapeskie et al. 1989). We also predicted that logging, in general, would increase the total number of bird species in the Algonquin landscape, through the creation of a diversity of forest age classes (Welsh and Healy 1993). We examine the relationship between vegetation features and birds to determine which vegetation characteristics best predicted relative abundance of forest birds. We also use similarity coefficients to determine the similarity of the bird communities in stands at different stages of regeneration after the initial cut.

Study sites and methods

The study was conducted on the east side of Algonquin Provincial Park, Ontario, Canada (44°10'N, 77°23'W). This area is dominated by white pine forests with trees that replaced the large white pine forests logged between 1850 and 1900 (Martin 1959). Existing white pine canopy trees were between 80 and 100 years in age and 25-30m in height (Naylor et al. 1994). The white pine forests in the study area are relatively continuous, separated only by logging roads and water bodies.

Forest stands with different logging histories were divided into three treatments: those logged between 1986 and 1994 (2-9 year cut), 1978 and 1986 (10-18 year cut); and stands without a written logging history (hereafter referred to as "old-cut"). Stands logged prior to 1978 were not included in this study because logging techniques other than the shelterwood system were used during those years, or the uniform shelterwood system was in an experimental stage (Kingsley 1998).

Stands were chosen using Forest Resource Inventory (FRI) maps, Ontario Ministry of Natural Resources (OMNR) and AFA logging history records. For a stand to be chosen it had to be accessible by road, have a minimum stand composition of 50% white pine, contain trees that were a minimum age of 70 years, fall into one of the three treatments, and be a minimum of 15 ha in size. Once stands were located, survey points for breeding birds were chosen within each stand (hereafter referred to as 'plot'). Points were placed at least 200 m from roads, water bodies or stand boundaries to minimize possible effects of edge habitat on bird and vegetation communities. The results from a total of 24 bird census plots from the spring of 1995 (old-cut [n=14]; 10-18 year cuts [n=10]); and 38 bird census plots from 1996 (old-cut [n=15]; 10-18 year cut [n=11]; 2-9 year cut [n=12]) are reported herein.

Most of the sites chosen in 1995 were recensused in 1996. Stands were never contiguous and were considered independent because they were separated by at least 500 m and usually over 1 km (up to 40 km).

Vegetation survey

A total of 28 plots (nearly all of the plots used for bird census points in 1996), ten in the 2-9 year cuts, and nine in each of old-cut and 10-18 year cuts, were surveyed once in 1996, after the completion of the bird surveys (July). To determine the cover characteristics of each site, a square 400 m^2 quadrat was established within each of the plots, centred at the point count station used during the bird surveys and with the sides parallel to the four cardinal compass directions. Diameter at breast height (DBH) measurements were taken for all trees and snags greater than 10cm DBH in the quadrat. Percent cover estimates were also taken for six vertical forest layers (ground, 0 to 0.33 m in height; <2m , 0.33 to 2 m in height; 2-5 m; 5-10 m; subcanopy; and canopy). To measure percent cover of the two lowest layers, 10 quadrats of 1 m^2 were placed randomly (with the aid of a random number generator, and a grid system) within the 400 m^2 study quadrat. The percent cover of each species was estimated visually within each of the 1 m^2 quadrats. For species present in the higher layers, the percent cover was estimated within each of the four 100 m^2 quadrats of the 400 m^2 study quadrat. As percent cover was estimated for each species and many species overlapped in space, total cover could be greater than 100%. All plants were identified to species. Plant species were grouped into broad categories (e.g., ferns, herbaceous plants, shrubs, trees [coniferous or deciduous]).

Surveys of forest breeding birds

In both years, breeding birds were monitored using a ten minute, unlimited distance point count (Ralph et al. 1993). Two counts were made at each point, between dawn and 09:30 EDT, during weather other than rain, hail or appreciable wind, all of which would affect the ability to hear birdsong. Counts included birds both seen and heard. To reduce problems associated with observer bias, only two comparably experienced observers performed surveys, and they were given approximately equal numbers of stands in each treatment to census, the same observer visiting the same set of plots for both of the two visits. The order in which the stands were surveyed was determined using a random number table. Totals of birds in the count circle were used as an index of relative abundance for a stand.

To determine whether the two years' bird data differed significantly we compared relative abundances using a one-way ANOVA for each of the three treatments. Results differed between years only for Ovenbirds (Kingsley 1998); here we focus primarily on the 1996 results. One-way ANOVA was also used to determine if there were significant differences in the relative abundance of species among treatments, only for species that had occurred in a minimum of eight different plots in any of the treatments. We used the Least Significant Difference (LSD) Multiple Comparison test to determine where the difference(s) occurred. Where data on relative abundances were not normally distributed, we used the Kruskal-Wallis ANOVA. We used cluster analysis (UPGMA) with Euclidean distances on the relative abundance data to determine the pattern of clustering of the stands with different regeneration ages and a principal components analysis on the vegetation percent cover data to determine whether the data could be reduced to a smaller number of explanatory variables. We also used stepwise multiple regression to determine which principal components from the vegetation cover data explained variation in the relative abundance of bird species or selected habitat categories of birds.

Scientific names of all bird species mentioned in the text and tables are given in Appendix 1.

Results

Basal area, plant species richness and vegetation cover

As expected, average basal area of white pine, and of all species, was highest in the old-cut treatment, and lowest in the recently cut treatment (Table 1), although the basal area of snags did not vary significantly among treatments. The total number of stems of white pine, snags and all species was highest in the old cut treatment and lowest in the recently cut treatments. Plant species richness was highest in the 10-18 year cut treatment, because of the presence of species common to both open and closed canopies (Kingsley 1998).

We found few significant differences among treatments in the percent cover of different vegetative layers. Old-cut and 10-18 year cuts had significantly greater amounts of coniferous and total cover in the canopy than the 2-9 year cuts (Table 2), and percent cover of ferns in the <2m forest layer was significantly greater in the 2-9 year cuts than the remaining treatments (Kingsley 1998). Principal components

Table 1. Comparison of plant species richness, basal area and stem density of white pines, snags and all plant species, for each treatment. Basal areas in m^2/ha, per plot; numbers in stems/ha.

Measure	Old cut	10-18 year cut	2-9 year cut
Mean basal area white pine *	24.7	22.8	10.7
Mean basal area of snags**	9.6	4.7	4.3
Mean basal area of all tree species**	40.8	35.1	18.8
Number white pine stems per ha	305.6	263.9	142.5
Number snag stems per ha	69.4	55.6	32.5
Total Number stems per ha	663.9	605.6	345
Total number plant species (unique species)	52 (6)	66 (9)	51 (3)

* $p < 0.05$, ** $p < 0.01$

analysis on the 13 variables describing percent cover of the vegetation layers resulted in four principal components (PC's) explaining 62% of the observed variance. The first PC (explaining 21.3% of the variance), contrasted stands with a high degree of deciduous cover in the canopy and subcanopy (positive values) and a large herbaceous layer (negative values, Table 3). Positive values of the second PC (20.3% variance explained) indicated stands with full coniferous sub- canopy and canopy layers and a sparse shrub layer, a situation typical of the old-cut stands (Tables 2 and 3). Recent cuts had high negative values, indicating a dense shrub layer and less coniferous canopy cover (Table 2). Positive values of PC4 (12.3% variance explained) indicated, by contrast, a high percent cover of the coniferous component in the 2 to 5, and 5 to 10 m heights (positive values), and a dense ground vegetation layer (negative values). Positive values of PC4 (8.7% of variance) appeared to describe stands with a well-developed herbaceous layer and a well developed coniferous sub-canopy, features seen primarily in the most recently cut stands (Table 2). The remaining principal components each explained less than 8% additional variance among vegetation variables.

Table 2. Percent cover of the 13 vegetation variables, and PC scores in each treatment from white pine forest stands in Algonquin Park in 1996.

Vegetation layer	Old cut	10-18 year cut	2-9 year cut
Tree seedlings	6.5	6.6	6.8
Ground layer	31.9	30.6	43.1
Herbaceous	31.7	40.6	46.8
Trees < 2 m	35.2	23.9	19.6
Shrubs < 2m	20.2	23.1	28.7
Deciduous shrubs 2-5m**	16.3	28.2	19.4
Coniferous shrubs 2-5m	34.8	33.3	13.4
Deciduous 5-10m	11.6	8.4	5.1
Coniferous 5-10m	16.5	16.2	14.6
Deciduous sub-canopy	10.1	5.8	1.9
Conifer sub-canopy	59.5	56.9	48.8
Deciduous canopy	4.7	3.4	0.7
Conifer canopy*	37.4	37.2	19.8
Sum	306.5	308.3	268.7
PC1	0.38	-0.13	-0.97
PC2	0.92	0.29	-0.32
PC3	0.08	0.10	-0.56
PC4	-0.44	0.09	0.14

* $p < 0.05$, ** $p < 0.01$

Bird species richness and relative abundance

We recorded a total of 61 bird species in the two years of study. Of this total, the greatest number observed in any one treatment (all stands combined) during one year was 52, in 1995 in the old-cut treatment (Table 3, Appendix 1). Nineteen species were completely absent from all plots in one of the three treatments in the study period: eight of these were absent from the recent (2-9 year) cut stands (Downy Woodpecker, Olive-sided Flycatcher, Gray Jay, Ruby-crowned Kinglet, Swainson's Thrush, Cedar Waxwing, Common Yellowthroat, Pine Siskin) and present in the other treatments, two species were absent from the 10-18 year plots (Hairy Woodpecker, Eastern Wood-pewee) and present in the other treatments, and one species (Yellow Warbler) was absent from the old-cut plots and present in the other treatments. Five species (Common Grackle, White-breasted Nuthatch, Cape May Warbler, Scarlet Tanager, Song Sparrow) occurred only once in one treatment and only one year.

Table 3. Eigenvectors for principal components (PC) 1-4 on percent cover vegetation data from Algonquin Park white pine stands.

Variable (% cover)	PC1	PC2	PC3	PC4
Tree seedlings	0.23	0.33	0.07	0.28
Ground shrubs	-0.28	0.22	-0.34	-0.34
Herbaceous layer	-0.30	-0.09	0.09	0.44
Trees < 2 m	0.20	0.42	0.12	-0.19
Shrubs < 2m	-0.15	-0.41	-0.06	-0.05
Deciduous trees 2-5 m	0.33	-0.32	0.04	0.16
Coniferous trees 2-5 m	-0.12	0.07	0.61	-0.33
Deciduous trees 5-10 m	0.47	-0.15	0.03	0.22
Coniferous trees5-10 m	0.03	0.07	0.65	-0.009
Deciduous sub-canopy	0.45	0.03	-0.08	0.04
Coniferous sub-canopy	-0.17	0.39	0.01	0.43
Deciduous canopy	0.37	0.16	0.17	0.33
Coniferous canopy	-0.03	0.42	-0.16	0.18

Yellow-bellied Sapsuckers, Red-breasted Nuthatches, Nashville Warblers, Yellow-rumped Warblers, Blackburnian Warblers, and Ovenbirds occurred in at least 50% of the plots per treatment in both years, and were the most common species in the study area. Of these, Ovenbirds were the most ubiquitous species occurring in 61 of 62 point counts (98.3%, Appendix 1). Only a few species had a high frequency of occurrence in some treatments and substantially lower occurrence in another treatment: Blue Jay occurred in all recent cut plots and all 10-18 year cut plots in 1996, but only 40% of these plots in 1995; Black-capped Chickadees occurred in over 90% of old-cut plots and fewer than 20% of recently-cut plots; White-throated sparrows occurred in over 70% of 10-18 year cut, and 2-9 year cuts but less than 60% of old-cut plots. Evening Grosbeak occurrence varied from 35.7% to 93.3% between plots within a treatment (Appendix 1). Most species occurred in a similar proportion of plots in 1995 and 1996, although Solitary Vireo and Evening Grosbeak occurred on many more plots in 1996 than in 1995, and Red-eyed Vireo occurred in over 90% of old-cut plots in 1995, but less than 35% of these plots in 1996.

When we examined average richness of the plots among treatments (number of species/plot), we found no significant differences in species richness among treatments (Table 4), in either 1995 ($F = 0.66$, $p = 0.42$) or 1996 ($F = 0.38$, $p = 0.68$). When we examined the proportion of species from different ecological guilds, among treatments, we also found no differences; in general species from each ecological community were present in each of the three treatments (Table 5). When comparing relative abundance among these categories, we found significantly greater numbers of individuals of open shrub nesting species in the recently cut treatments, and significantly greater numbers of closed canopy and cavity nesting species in the old-cut plots (Table 6). When we compared the number of individuals heard in the point counts among treatments we also found no significant difference (Table 6).

Cluster analysis using relative abundance of bird species from the different treatments indicated that, in general, old-cut stands clustered together, but some stands cut either recently or 10-18 years ago also clustered with old-cut stands (Figure 1). The old-cut

Table 4. Bird species richness data for three treatments from Algonquin Park, in 1995 and 1996.

Measure	Old-cut		10-18 year cut		2-9 year cut
	1995	1996	1995	1996	1996[a]
Mean (±SE)number of species/stand	17.8 (0.75)	20.7 (0.75)	16.8 (0.99)	21.2 (1.17)	20.1 (0.66)
Total number of species	52	46	44	51	46
Number of unique species	3		3		1
Total number of species in study period (% of 61)	55 (90.2)		55 (90.2)		46 (75.4)

[a] The 2-9 year cuts were not sampled in 1995.

Table 5. Number of species in each treatment belonging to 12 different habitat associations in the three treatments. Some species belong to two groups (e.g., coniferous and canopy; see Appendix 1 for categorization).

Habitat	Old cut	10-18 year cut	2-9 year cut
Open (O)	6	6	7
Canopy	15	15	13
Coniferous (CO)	16	16	12
Generalists (G)	6	4	5
Mixed (MX)	5	5	4
White Pine (WP)	1	1	1
Deciduous (D)	8	5	6
Understory (U)	3	3	3
Spruce Budworm (SB)	1	3	1
Cavities (CV)	7	6	6
Edge (E)	1	2	1
Wetland (W)	1	1	0

stands were significantly more similar to each other, and hence more uniform in their bird communities, than the stands cut either 2-9 or 10-18 years ago (mean [SE] of Euclidean distances; old-cut to old-cut: 12.8 [0.17], 10-18 year cut to 10-18 year cut: 14.6 [0.23], 2-9 year cut to 2-9 year cut: 16.2 [0.43], $F = 42.1$, $p < 0.00001$). Across treatments, the greatest difference between treatments was between the bird communities in stands cut 10-18 years ago, and those cut 2-9 years previously (mean [SE] Euclidean distance = 15.6 [0.27]). The least difference was between old-cut stands and stands cut 10-18 years previously (14.18 [0.17]), whereas bird communities from old-cut stands and those cut 2-9 years ago were intermediate in average similarity (14.7 [0.20], not significantly different than distance between old-cut and 10-18 years stands, $p = 0.14$, LSD multiple comparison test).

Of the 32 species that were present in at least 8 stands, only six varied significantly (or nearly so) in relative abundance among treatments (Table 7). In all cases but Ovenbird, both years showed similar trends (Kingsley 1998). Ruffed Grouse were in higher relative abundance (although not significantly so) in recently cut stands than in the other treatments. Old-cut stands contained significantly higher relative abundance of Black-capped Chickadees than the other stands. Chestnut-sided and Mourning Warblers were found seldom or not at all in old-cut stands and were common in recently cut stands. In 1995, there was no significant difference between treatments for Ovenbirds (ANOVA, $F = 1.96$, $p = 0.16$), but in 1996, there were significant differences among treatments with the 10- 18 year cuts having significantly lower numbers of birds than the old-cut treatment (Table 7). White-throated Sparrows were significantly more abundant in the 2-9 year cuts than the old-cut stands.

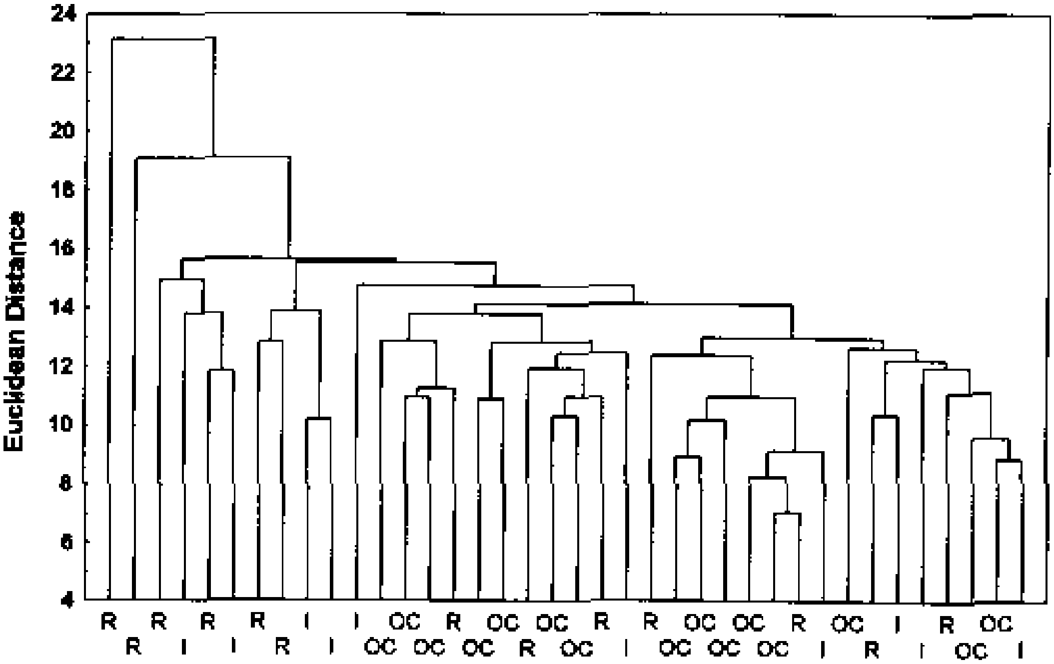
Vegetation and bird relationships

The principal components of the vegetation data explained variation in relative abundance for only a small number of bird species, and not necessarily those that showed significant differences among treatments. Blue Jay relative abundance was higher in stands with low values of PC 1, the component indicating thick deciduous cover in the canopy and subcanopy (Table 8). Brown Creeper abundance was positively correlated with PC4 (greater herbaceous layer and coniferous subcanopy), Black-throated Blue Warblers were negatively associated with both PC1 and PC4 and

Table 6. Mean and (standard error) relative abundance of birds from seven habitat categories occurring in each of the three treatments in Algonquin Park.

Habitat preference	Old-cut	10-18 year cut	2-9 year cut	F	p
Cavities	5.8 (0.49)	3.7 (0.85)	3.5 (0.36)	5.2	0.01
Conifer	13.4 (1.27)	13.2 (1.89)	11.7 (2.08)	0.28	0.76
Closed Canopy	31.3 (1.34)	28.3 (1.85)	26.0 (0.70)	3.58	0.04
Open shrubs	4.1 (0.56)	7.5 (1.36)	14.8 (2.60)	11.45	0.0001
Understory	3.5 (0.51)	4.0 (0.86)	2.5 (0.61)	1.31	0.28
Ground vegetation	10.9 (0.78)	8.7 (0.68)	9.9 (0.94)	1.83	0.18
Generalists	14.3 (1.31)	14.2 (1.37)	15.8 (1.86)	0.35	0.70
Total individuals	57.5 (1.85)	59.6 (3.15)	61.0 (1.97)	0.29	0.74

Figure 1. Cluster diagram resulting from UPGMA on Euclidean distances of stands, based on relative abundance of bird species. OC = old-cut stands, R(ecent) = 2-9 year cuts, I(ntermediate) = 10-18 year cuts.



Black-throated Green Warblers were negatively associated with PC4. Veery abundance was higher in stands with high amounts of deciduous cover (PC1) and low amounts of coniferous cover (PC2). Mourning Warblers also were more abundant in stands with higher scores on PC4. White-throated Sparrow abundance was negatively related to PC1, the deciduous component of the forest. The relative abundance of no other species was related to these vegetative features. PC1 also explained a small, but significant amount of variation in the relative abundance of all open shrub species (negative partial correlation, Table 8). The relative abundance of dense understory species was explained by PC2 (negative partial correlation). No principal component explained significant variation in the relative abundance of any other ecological group., although the total number of individuals was weakly (negatively) related to variation in PC2.

Table 7. Mean and (standard error) relative abundance of six species of birds in White Pine forests at different stages of cutting, in Algonquin Park.

Species	**Old-cut**	**10-18 year**	**2-9 year**	**Statistic**[a]	**p**
Ruffed Grouse	1.5 (.41)	1.3 (0.42)	2.7 (0.55)	3.20[a]	0.053
Black-capped Chickadee	1.5 (0.34)	0.5 (0.40)	0.2 (0.10)	16.9[b]	0.001
Chestnut-sided Warbler	0.5(0.24)	3.2(1.00)	5.5(1.54)	22.3[b]	0.001
Mourning Warbler	0	0.3(0.23)	1.1(0.49)	13.1[b]	0.005
Ovenbird	9.5(0.71)	6.6(0.85)	8.2(0.92)	3.93[a]	0.029
White-throated Sparrow	2.1(0.61)	3.2(0.36)	4.5(1.17)	3.22[a]	0.052

[a] Anova (F)

[b] Kruskal-Wallis χ^2

Table 8. The relationship between vegetative features and relative abundance for 6 species of birds and 3 ecological categories of birds found in White Pine forests in Algonquin Park, Ontario. Equations presented only when significant predictors of relative abundance were detected ($p < 0.10$).

Species	Equation	r^2	p
Brown Creeper	1.37+0.69PC	20.8	0.02
Blue Jay	2.15-0.38PC1	24.8	0.01
Veery	1.65+0.33PC	13.6	0.063
Mourning Warbler	0.24+0.35PC	32.9	0.002
Black-throated Blue Warbler	4.66-	29.8	0.017
Black-throated Green	4.75-0.60PC4	12.7	0.075
Rose-breasted Grosbeak	1.16+0.39PC	13.2	0.068
White-throated Sparrow	3.16-	34.5	0.007
Open shrub species	7.56-1.19PC1	13.4	0.066
Dense understory species	3.09-0.66PC2	21.2	0.018
Number of individuals	58.0-1.75PC2	13.5	0.065

Discussion

The uniform shelterwood logging system for white pine is an excellent system for pine regeneration on sandy soils characteristic of the region in the east side of Algonquin Park in central Ontario (Chapeskie et al. 1989). White pine regeneration in our study, judging by the stands cut 10-18 years ago, was good, with the basal area of white pine approaching that found in our old-cut stands. In other locations, where soils have greater organic content, white pine regeneration requires scarification through fire (Corbett 1994), a much more extreme disturbance to land bird communities, with large changes in both species composition and relative abundance of canopy dependent species (Dickson et al. 1983).

Our old-cut stands that had no record of cutting are presumably the closest in vegetation structure and bird communities to original old-growth white pine forests in central Ontario. The major impact of the timber harvesting appears to be a change in composition of a few bird species, with a slight reduction in the number of closed-canopy and coniferous associates, as predicted, and an increase of one open-shrub nesting species. Although the older cuts (both old-cut and 10-18 year cuts) contained almost 10 more species over the two years than the recently cut stands, there was substantial yearly variation in the total number of species found in one year in one treatment. Therefore, a second year of surveying in the recently cut stands could possibly have resulted in similar species richness values in the 2-9 year cut and the detection of greater numbers of species (Smith et al. 1995). Unlike other studies where logging results in an increase in edge-related species, and an increase in overall species richness (Thompson and Capen 1988; Welsh and Healy 1993), the uniform shelterwood system, presumably because of the absence of intrusion of many edge species, resulted in no net change or possibly a slight reduction in richness across the landscape.

The relative abundance of birds from different ecological categories, and the relative abundance of particular species, were affected by this silvicultural method, particularly when comparing the bird communities in the recently cut stands with those from the old-cut stands. There was, as predicted, a decline in the relative abundance of species preferring closed canopy, and a substantial increase in the relative abundance of individuals from species preferring open shrubs for nesting. Unlike clearcutting, where both species composition and abundance are usually affected, we found that most of the closed-canopy species that occurred in the old cut stands were also present in the recently-cut stands, but in substantially smaller numbers. The loss of individuals of cavity-nesting species from both the intermediate aged stands and the recently cut stands is due primarily to the loss of Black-capped Chickadees, although the relative abundance of both Pileated Woodpeckers and Brown Creepers (the latter an occasional cavity user, Gauthier and Aubry 1996) was also lower in the recently cut stands.

Our intermediate treatment, where 10-18 years had elapsed for regeneration, demonstrates the relatively benign nature of this silvicultural technique, as most bird species that were not present in the more recent cut were present in this treatment, and the relative abundance of all species and ecological groups affected significantly by the cutting had approached that seen in the old-cut treatments. According to the silvicultural guidelines for the east side of Algonquin Park, the stands that were cut 18 years ago would undergo the next stage of cutting in two years (Chapeskie et al. 1989; N. Quinn pers. comm.), and these stands are predicted to lose canopy species and favour shrub-nesting species. Shrub-nesting species, in particular, Chestnut-sided Warblers, Mourning Warblers and White-throated Sparrows, generally respond positively to most silvicultural techniques (Titterington et al. 1979; Thompson and Capen 1988; Freedman et al. 1981; Falls and Kopachena 1994), including the uniform shelterwood system. These species have healthy populations particularly outside of Algonquin Park (Cadman et al. 1988), where early successional stages predominate (Chapman and Putman 1984).

Our results indicated that the old-cut treatment had the highest degree of similarity among stands in bird communities, whereas the recently cut stands had the lowest degree of similarity. These results support the old idea that undisturbed ecological communities are more stable, or more predictable, than transitional communities (Horn 1975), despite the uniformity of the logging disturbance. The logged treatments would include, in some stands, both bird species from the undisturbed closed-canopy forest, as well as species that have newly colonized these stands. The underlying factors determining population colonization and extinction from forest patches is a research area that is relatively unexplored (Blake et al. 1994; Villard et al. 1995), but our data, showing very similar relative abundance of most species over two years of study, suggest relative stability of avian communities in successive breeding seasons across each treatment landscape.

Our measure of structural heterogeneity of the vegetation community, the sum of the vegetation layers, was not an important predictor of species richness at the stand level, a result contradictory to many other studies on bird communities (MacArthur et al. 1962; Karr and Roth 1971; James and Warmer 1982; Niemi and Hanowski 1984; Steffen 1985; Thompson et al. 1995). The relative abundance of a small number of species was explained by particular features of the plant community; the most common explanatory variables were those that reflected the amount of deciduous and canopy cover and the extent of the herbaceous layer. These habitat variables explained the variation in relative abundance of Mourning Warblers and White-throated Sparrows. The gradual decrease in numbers of these species as the stand regenerated corresponded to the increase in canopy cover in the forest stands.

Some species, for which we found no significant vegetative feature that explained relative abundance, varied significantly in abundance among stands. The Black-capped Chickadee, a cavity-nester (primarily in small deciduous snags), was significantly more abundant in the old-cut treatments than in the other treatments. Unfortunately, we did not measure the density of small deciduous versus coniferous snags, and these were probably more common in the old-cut stands, as they would be lost through the logging operations in the more recently cut stands. Chickadees prefer to excavate their nests in standing deciduous tree stumps with an average diameter of 10 to 18 cm at breast height (Peck and James 1987) and suitable nesting snags may limit population densities of this species (Smith 1993).

Several species had significant vegetative predictors but did not vary significantly among treatments, including Blue Jays and Brown Creepers. Presumably this result occurred because of the heterogeneity of vegetation features even within a single treatment. Blue Jays were negatively associated with habitats with a high degree of deciduous cover (PC1) in the subcanopy of the forest, features present to some degree in both the recent cuts and the 10-18 year cuts. Selective removal of this layer of the forest might result in vegetation characteristics that reduce the numbers of Blue Jays, a management technique that could be used to increase breeding success of some neotropical migrants that suffer extremely high rates of predation by this species (e.g., Red-eyed Vireo, Hanski et al. 1996; Burke 1998).

When analysed as ecological categories, the relative abundance of all open shrub species was explained by a negative partial correlation with the amount of deciduous cover, whereas relative abundance of dense understory species, like the Veery, was explained by principal components describing both deciduous and coniferous canopy cover. Although composition was affected, the relative abundance of conifer-associated species did not vary significantly among treatments, probably because most of these species were associated with conifers other than white pines (e.g., Golden-crowned Kinglets are associated with white spruce *(Picea glauca)* and balsam fir (*Abies balsamea*); Gauthier and Aubry 1996). Generalists, as might be expected, were not affected by the silvicultural treatments, and their relative abundance was not related to any specific vegetation feature, indicating their very broad habitat preferences.

Point count data, although satisfactory for determining relative abundance (Ralph et al. 1993), do not provide an accurate assessment of the productivity of bird communities (Robinson et al. 1995). As Brown-headed Cowbirds (*Molothrus ater*) were never seen in the study area, cowbird parasitism is probably not an issue in the relatively continuous forest cover throughout Algonquin Park, a conclusion supported by other studies in eastern North America on bird communities in forested landscapes (Welsh and Healy 1993; Hanski et al. 1996; King et al. 1996; Sabine et al. 1996). Relative abundance data from point counts can also overestimate productivity if predators respond positively to changes in vegetation structure as a result of timber harvesting (Welsh and Healy 1993; Hanski et al. 1996). Predators can greatly reduce the productivity of the habitat for breeding birds (Wilcove 1985; Andren and Angelstram 1988; Rudnicky and Hunter 1993; Hanski et al. 1996). Although we do not have any information on mammalian predators, our data indicate that the egg predator, the Blue Jay, is not more common on the recently logged plots than in the old-cut plots, a result also similar to results from two other studies on timber harvesting and forest bird communities (Thompson et al. 1992; Welsh and Healy 1993).

Many species were not adversely affected by uniform shelterwood logging, including Winter Wrens and Ovenbirds, both species that use the forest floor for feeding and nesting, and most cavity-nesting species (e.g., woodpeckers, but not Black-capped Chickadees). This result is encouraging as woody debris, herbaceous plants, mosses, leaf litter and snags are often disrupted in clearcuts, and are important sources of food and nesting habitat for these groups of birds (Cadman et al. 1988; Van Horn and Donovan 1994; Naylor et al. 1996; Burke and Nol 1998). The provisions by the Algonquin Forest Authority for protecting these features in applying this method of timber management seem to be adequate for these species, although chickadee abundance suggests that smaller deciduous snags appear to have been reduced by logging.

Management Recommendations

Owing to the loss of closed-canopy species, and lower densities of these species in the landscape, and the relative rarity of forested habitat in eastern Ontario outside of Algonquin Park (Chapman and Putman 1984), we recommend a longer rotation period (30-40 years for each cut, 120-160 year rotation) and the retention of 10% of remaining mature canopy trees in the final cuts in Algonquin Park. This will ensure that healthy populations of species that depend on a closed canopy will be maintained in these forests and in the region generally. Black-capped Chickadee populations in the east side of the park may be maintained by taking greater care, during timber harvesting, not to eliminate small deciduous snags. Continued use of this technique in Algonquin Park, with the above caveats, appears to be compatible with the goal of preserving avian biodiversity.

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Appendix 1. Percentage of plots observed (n) and habitat associations of bird species in the three treatments, in 1995 and 1996 in Algonquin Park.

Species	**Old-cut**		**10-16 year cut**		**2-9 year cut**
	1995	1996	1995	1996	
Ruffed Grouse *Bonasa umbellus* -O	0.286 (4)	0.467 (7)	-	0.272(3)	0.75(9)
Ruby-throated Hummingbird *Archilochus colubris* -G	0.071(1)	0.071(1)	-	-	-
Yellow-bellied Sapsucker *Sphyrapicus varius* -CV	0.642(9)	0.6(9)	0.6(6)	0.636(7)	0.917(11)
Downy Woodpecker *Picoides pubescens* -CV	0.214(3)	0.2(3)	-	0.182(2)	-
Hairy Woodpecker *P. villosus* -CV	0.071(1)	-	-	-	0.25(3)
Black-backed Woodpecker *P. arcticus* -CV	0.142(2)	-	-	0.091(1)	0.25(3)
Northern Flicker *Colaptes auratus* -CV	0.071(1)	0.267(4)	0.1(1)	0.454(5)	0.167(2)
Pileated Woodpecker *Dryocopus pileatus* -CV	0.142(2)	0.467(7)	0.1(1)	0.091(1)	0.25(3)
Olive-sided Flycatcher *Contopus borealis* -CO	0.071(1)	-	0.4(4)	0.091(1)	-
Eastern Wood-Pewee *C. virens* -D	0.071(1)	0.2(3)	-	-	0.25(3)
Least Flycatcher *Empidonax minimus* -D	-	0.071(1)	0.1(1)	0.364(4)	0.083(1)
Great Crested Flycatcher *Myiarchus crinitus* -D	0.214(3)	-	0.3(3)	0.091(1)	0.083(1)
Gray Jay *Perisoreus canadensis* -CO	0.142(2)	0.2(3)	0.2(2)	0.091(1)	-
Blue Jay *Cyanocitta cristata* -G	0.643(9)	0.733(11)	0.4(4)	1.0(11)	1.0(12)
Common Grackle *Quiscalus quiscala* -CO	-	-	0.1(1)	-	-
Common Raven *C. corax* -CO	0.142(2)	0.33(5)	0.2(2)	0.273(3)	0.583(7)
Black-capped Chickadee *Poecile atricapillus* -CV	0.929(13)	0.733(11)	0.8(8)	0.182(2)	0.167(2)
Brown Creeper *Certhia americana* -CO	0.357(5)	0.733(11)	0.3(3)	0.454(5)	0.417(5)
Red-breasted Nuthatch *Sitta canadensis* -CO	0.929(13)	0.867(13)	0.9(9)	0.727(8)	0.833(10)
White-breasted Nuthatch *S. carolinensis* -D	-	0.067(1)	-	-	-
Winter Wren *Troglodytes troglodytes* -CO	0.5(7)	0.467(7)	0.4(4)	0.727(8)	0.667(8)
Golden-crowned Kinglet *Regulus satrapa* -CO	0.357(5)	0.333(5)	0.5(5)	0.545(6)	0.167(2)
Ruby-crowned Kinglet *R. calendula* - CO	0.143(2)	0.133(2)	0.1(1)	0.273(3)	-
Veery *Catharus fuscescens* -US	0.571(8)	0.533(8)	0.6(6)	0.727(8)	0.333(4)
Swainson's Thrush *C. ustulatus* -CO	0.214(3)	-	0.1(1)	-	-
Hermit Thrush *C. guttatus* -MX	0.857(12)	0.8(12)	0.7(7)	0.454(5)	0.75(9)
Wood Thrush *Hylocichla mustelina* -D	0.071(1)	0.067(1)	-	-	-
American Robin *Turdus migratorius* -G	0.643(9)	0.467(7)	0.6(6)	0.273(3)	0.333(4)
Cedar Waxwing *Bombycilla cedrorum* -E	0.071(1)	-	0.3(3)	-	-
Solitary Vireo *Vireo solitarius* -CO	0.357(5)	0.933(14)	0.2(2)	0.636(7)	0.583(7)
Red-eyed Vireo *V. olivaceus* -D	0.929(13)	0.333(5)	0.9(9)	0.364(4)	0.333(4)
Tennessee Warbler *Vermivora peregrina* -SB	-	-	-	0.182(2)	-
Nashville Warbler *V. ruficapilla* -D	0.929 (13)	0.8(12)	0.8(8)	0.909(10)	0.917(11)
Chestnut-sided Warbler *D. pensylvanica* -O	0.286(4)	0.267(4)	0.9(9)	0.727(8)	0.833(10)
Magnolia Warbler *D. magnolia* -U	0.7(7)	0.667(10)	0.4(4)	0.545(6)	0.416(5)
Cape May Warbler *D. tigrina* -SB	-	-	-	0.091(1)	-
Black-throated Blue Warbler *D. caerulescens* -D	0.714(10)	0.733(11)	0.7(7)	0.818(9)	0.75(9)
Yellow-rumped Warbler *D. coronata* -MX	0.857(12)	1.0(15)	0.9(9)	1.0(11)	0.917(11)

Appendix 1 (continued)

Species	**Old-cut**		**10-16 year cut**		**2-9 year**
	1995	1996	1995	1 996	**cut**
Black-throated Green Warbler *D. virens* -CO	0.429(6)	0.533(8)	0.2(2)	0.454(5)	0.083(1)
Blackburnian Warbler *D. fusca* -CO	0.714(10)	1.0(15)	0.7(7)	0.818(9)	0.75(9)
Pine Warbler *D. pinus* -WP	0.429(6)	0.6(9)	0.5(5)	0.727(8)	0.583(7)
Bay-breasted Warbler *D. castanea* -SB		0.071(1)		0.182(2)	0.167(2)
Black-and-white Warbler *Mniotilta varia* -MX	0.5(7)	0.467(7)	0.3(3)	0.455(5)	0.167(2)
American Redstart *Setophaga ruticilla* -O	0.143(2)	-	-	0.182(2)	0.083(1)O1
Ovenbird *Seiurus aurocapillus* - MX	1.0(14)	1.0(15)	0.9(9)	1.0(11)	1.0(12)
Northern Waterthrush *S. noveboracensis* -O	0.214(3)	0.2(3)	-	0.182(2)	0.083(1)
Mourning Warbler *Oporonis philadelphia* -O	0.071(1)	-	-	0.091(1)	0.416(5)
Common Yellowthroat *Geothlypis trichas* -W	0.071(1)	-	0.1(1)	0.273(3)	-
Canada Warbler *Wilsonia canadensis* -U	0.143(2)	0.2(3)	0.1(1)	0.182(2)	0.25(3)
Scarlet Tanager *Piranga olivacea* -O	-	-	0.1(1)	-	-
Rose-breasted Grosbeak *Pheucticus ludovicianus* -G	0.214(3)	0.467(7)	0.2(2)	0.455(5)	0.416(5)
Chipping Sparrow *Spizella passerina* -CO	0.285(4)	0.4(6)	0.3(3)	0.182(2)	0.333(4)
Song Sparrow *Melospiza melodia* -O	-	-	-	-	0.083(1)
White-throated Sparrow *Zonotrichia albicollis* -O	0.357(5)	0.533(8)	0.7(7)	0.833(10)	0.917(11)
Dark-eyed Junco *Junco hyemalis* -CO	0.071(1)	0.133(2)	-	0.273(3)	0.167(2)
Purple Finch *Carpodacus purpureus* -CO	0.286(4)	0.2(3)	0.4(4)	0.545(6)	0.5(6)
Red Crossbill *Loxia curvirostra* -CO	0.143(2)	0.2(3)	0.1(1)	0.091(1)	0.083(1)
Pine Siskin *Carduelis pinus* -CO	0.071(1)	0.067(1)	0.2(2)	0.091(1)	-
American Goldfinch *C. tristis* -G	0.143(2)	0.2(3)	0.1(1)	0.182(2)	0.167(2)
Evening Grosbeak *Coccothraustes vespertinus* -CO	0.357(5)	0.933(14)	0.5(5)	0.818(9)	0.75(9)

[a]- **Habitat Associations:** O = open shrub, G = habitat generalists, CV = cavities, CO = coniferous (non-white pine), D = deciduous forest, MX = mixed woods, E = edge, US = understory, SB = spruce-budworm, WP = white pine, W = wetlands.
[b] No data.