

EFFECTS OF SELECTION CUTTING ON BIRD COMMUNITIES IN CONTIGUOUS EASTERN HARDWOOD FORESTS

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Abstract: We used point counts to sample bird communities in hardwood forest stands following single-tree selection harvest to determine the impacts on birds of this harvesting system. We sampled at 1–5 years post-harvest ($n = 24$), 15–20 years post-harvest ($n = 23$), and in reference stands subjected only to natural disturbances for >30 years ($n = 24$). White-throated sparrow (*Zonotrichia albicollis*), chestnut-sided warbler (*Dendroica pensylvanica*), and mourning warbler (*Oporornis philadelphia*) abundances were significantly higher in recently logged stands than in other treatments. Ovenbird (*Seiurus aurocapillus*) abundance was about 50% lower in recently logged stands and in stands logged 15–20 years previous than in reference stands. Black-throated blue warbler (*Dendroica caerulescens*) and yellow-bellied sapsucker (*Sphyrapicus varius*) abundances were similar in reference and recently logged stands but significantly lower in stands harvested 15–20 years previously. Redundancy Analysis (RDA) identified 6 habitat variables associated with changes in avian abundances. Percent shrub and slash cover were higher in recently logged stands than in older logged and reference stands. Deciduous canopy cover and basal area of living deciduous trees were greater in reference stands than in both logged treatments. Although the abundance of some bird species were statistically lower in selection cut stands, the implications to population persistence will require data on reproductive success in combination with population modeling with varying proportions of the forested landscape committed to selection cutting.

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Forestry activities may result in significant habitat loss on the breeding grounds of forest-dependent passerines (Pimm and Askins 1995), reductions in richness and diversity of forest birds, and shifts in community composition and relative abundances (Probst et al. 1992, Thompson et al. 1992, Annand and Thompson 1997, Robinson and Robinson 1999). The 4 primary silvicultural systems currently employed in North American forestry are clearcutting, shelterwood, seed tree, and group or single-tree selection cutting (Thompson et al. 1995). Selection cutting attempts to emulate small-scale, gap-phase disturbances associated with single-tree or small-group blowdowns and natural senescence, and selection cutting often is used in the management of shade-tolerant tree stands across eastern North America (Lorimer 1989, Hunter 1990). Single-tree selection cutting removes a portion of the hardwood component of the basal area of the forest every 20–25 years. This method is assumed to be sustainable for hardwood forest ecosystems (Robinson and Robinson 1999).

Most studies on silvicultural system impacts on birds have focused on even-aged management techniques, particularly clearcutting (Sallabanks et al. 2000, but see Flaspohler et al. 2002). Because of

its importance as a management technique in eastern hardwood forests (Seymour 1995), we chose to examine potential changes in bird communities and habitat structure that result from single-tree selection harvesting in central Ontario, Canada. Our goal was to determine whether this silvicultural system maintained suitable breeding habitat for species that require mature, closed-canopy hardwood forest for nesting or for species exhibiting long-term population declines. We compared stands that had been harvested during the previous 5 years with stands harvested 15–20 years prior to our censuses and to reference forest stands that had not been harvested for at least 30 years.

We predicted increased abundances of edge- or shrub-associated species and reduced abundances of forest interior species in the most recently cut stands as a result of decreased canopy cover and increased shrub growth. We also predicted that differences in vegetative structure resulting from single-tree selection cutting would be short-lived and that regeneration of habitat features would result in a return to pre-harvest bird composition and abundances within the 20- to 25-year cutting cycle (Ontario Ministry of Natural Resources 1998).

STUDY AREA

We conducted our study June–August 1998 in Algonquin Provincial Park, a 7,725-km² park in

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central Ontario, Canada (45Y32'N, 78Y36'W). We conducted repeated bird surveys to document yearly variation in June 1999 and June 2000. The park is characterized by rocky ridges interspersed with numerous small and large lakes, with elevations ranging from 297 to 537 m (mean = 396 m). Forest cover is primarily sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with some white spruce (*Picea alba*), eastern hemlock (*Tsuga canadensis*), and balsam fir (*Abies balsamea*; Wickware and Rubec 1989). Most of Algonquin Provincial Park was logged for white pine (*Pinus strobus*) in the 1800s, and parkwide harvesting for hemlock and yellow birch occurred in the 1930s and 1940s (Tozer and Strickland 1980). About 12% of the park is designated as a Wilderness Zone and was withdrawn from harvesting activities in 1974. About 57% of the park is managed for timber production, and selection cutting is applied in stands containing >60% hardwood species. About 25% of the hardwood component of the basal area is removed at each selection cut. We conducted our study in an approximately 750-km² portion of the park. Fire suppression is practiced throughout the study area. With the exception of fire, all forests in the park are subject to the same natural disturbance regimes. Our study was restricted to responses of birds in upland forest areas, as the small riparian zones adjacent to first- and second-order streams are not normally subjected to selection cutting.

METHODS

Site Selection

We completed our site selection a priori by randomly selecting 71 points in different stands at a 1-ha resolution using 1:15,840 Forest Resource Inventory (FRI) maps (Ontario Ministry of Natural Resources 1978) and 1:25,000 and 1:20,000 Geographic Information System-generated FRI maps (Ontario Ministry of Natural Resources 1996). Stands were delineated on FRI maps by the percent composition of trees. We chose only stands within which any combination of tolerant hardwoods (sugar maple, American beech, yellow birch, eastern hemlock) comprised >60% of the trees. We determined stand boundaries by changes to forests with different tree composition (e.g., >50% white pine) or lakes, rivers, riparian zones, and roads. Coniferous stands are rare and patchy in the western half of the park (Strickland 1993). To be accepted for use, points had to be (1) >400 m apart to ensure independence of results in bird sampling

(Ralph et al. 1993; actual distance: range = 447 m to 26.7 km, mean = 12.2 km, SD = 7.3 km), (2) >100 m from significant water bodies to reduce the influence of riparian bird communities on bird survey results, and (3) <1.5 km from established access routes. Most points were >50 m from logging road edges. Twenty-four of the points were reference stands in the park's Wilderness Zone (hereafter referred to as Reference [RE]). Twenty-four stands were harvested 1–5 years ago (hereafter Logged–Recent [LR]). Twenty-three stands had been regenerating for 15–20 years following their first harvest, and were approaching their second harvesting cycle (hereafter Logged–Old [LO]).

Field Data Collection

Bird Communities.—We conducted a single 10-min, unlimited-distance, point-count survey in the approximate center of each of the 71 stands. Surveys were conducted by 1 of 2 observers, equal in visual and aural identification ability, between 0530 and 0741 hr, 1–19 June 1998 (Ralph et al. 1993, Smith et al. 1998). We found no significant observer effect on species richness, Shannon's species diversity index, or individual species relative abundances. We therefore combined data from the 2 observers. We chose unlimited distance counts because of the difficulty in estimating distances in forests with different vegetation structure. Point counts were conducted in 12 reference stands in each of 3 successive years (1998–2000) to determine the degree to which the species that we studied fluctuated in abundance annually. We chose to test for annual variability in reference stands because successional changes (especially growth of understory vegetation) were assumed to be small. For 14 of the 15 bird species for which we had sufficient data, we found no significant change in point-count abundances over the time period ($n = 12$ stands in the reference treatment, repeated-measures Analysis of Variance [ANOVA]; Appendix A). We therefore assumed that annual variation in abundance of individual species was minimal and hereafter report only results from 1998, the year that we have point-count data from all 3 treatments. This confirms Boulinier et al.'s (1998a) results that showed little temporal variability in bird abundance measures in landscapes with a high proportion of forest cover. For comparisons of relative abundance, Ralph et al. (1993) recommend 10–12 points per treatment. We sampled about twice this amount (23–24 points per treatment), choosing to sample more points rather than fewer points more intensively. As pairing and nesting occurs very syn-

chronously at this latitude, we chose to survey birds during the peak period, without a second count. Surveys were not conducted during rain or if winds were stronger than Beaufort 3. We followed a sampling schedule that rotated systematically among logging treatments and reference point stands.

Habitat Structure.—Habitat structure was quantified from 21 July to 21 August 1998. We centered a 400-m² circular plot (11.3-m radius) on a randomly selected subsample of 55 of 71 bird-survey points (18 in RE, 18 in LR, 19 in LO) because of time limitations. In each 400-m² vegetation plot, 3 4-m² subplots (1.13-m radius) were sampled. We centered 2 perpendicular 25-m ropes on the bird-census point to divide the plot into 4 100-m² sections and improve accuracy in measuring percent cover.

In the 400-m² plots, 2 observers estimated visually deciduous and coniferous tree and shrub percent cover for 6 vertical strata (0–0.5 m, 0.5–2 m, 2–5 m, 5–10 m, subcanopy, canopy). We averaged the observer estimates for each stratum in each of 4 sections of the plot. All living trees >3.0 cm in diameter at breast height (dbh) were tallied as deciduous or coniferous in 10-cm-diameter classes (beginning with 3–10). Snags (dead trees >3.0 cm dbh and >1.0 m tall) were assigned a decay class (0 = leaves present to 5 = no coarse branches, no bark; Jobes 1998) and measured (height and 10-cm-diameter classes). Downed woody debris >3.0 cm in diameter that crossed 1 of the 2 perpendicular ropes (45.1 m total) was tallied in 10-cm-diameter classes. We determined percent cover and decay class for crowns left on the ground in the plot. Basal area (m²/ha) was determined for living and dead deciduous and coniferous trees with a 2-factor basal area prism. We measured height of a single tree similar in height to the canopy average in each plot with a clinometer.

In each of the 4-m² subplots, we counted living trees <3.0 cm dbh and tallied them as coniferous or deciduous. Percent cover was determined for herbs, ferns, graminoids, lycopods, leaf litter, logs (>10 cm diameter), and slash (<10 cm). We averaged litter depth from 12 measurements taken to the nearest 0.5 cm in each subplot.

Data Analysis

We tested data for normality and homoscedasticity using Kolmogorov-Smirnov and Levene's Test, respectively. We normalized non-normal and/or heteroscedastic data through transformation when possible to allow for parametric testing. Although point-count estimates for most species deviated significantly from normality, treatment

effects were always consistent between ANOVAs and Kruskal-Wallis ANOVAs by ranks, so we presented means and standard errors—as well as ranges—for ease of comparison with data in the literature. We used Tukey's HSD tests for post hoc testing to identify specific inter-treatment differences when ANOVAs revealed significant factor effects (Zar 1999). Stands were treated as statistically independent sampling units. We performed analyses using STATISTICA™ or SAS (SAS Institute 1999). Significance was assumed at Bonferroni-corrected *P*-values <0.05, but we also reported results for corrected *P*-values <0.10.

Bird Communities.—We used 1-way ANOVAs on species richness, Shannon's and log-series diversity indices, and abundance data (grouped by treatment) to test for inter-observer variability (by observer), time-of-day effects (by first or second hr after sunrise), and seasonal effects (by 6- and 9-day groupings; Boulonier et al. 1998b). Since none of these effects were significant, we combined all data and reported only treatment effects.

We used 1-way ANOVAs on species richness and Shannon's and log-series diversity indices by logging treatment to identify inter-treatment variability. Abundances of 17 species present in >20% of all point counts (i.e., 14/71) were compared among treatments using 1-way ANOVA or Kruskal-Wallis ANOVA. Although only present in 13 of 71 point counts, blue jay abundances also were tested because blue jays are a potential nest predator and may therefore affect reproductive success within treatments. To provide an assessment of the degree of community variability among treatments, we performed unweighted pair-group average cluster analysis on Euclidean distance matrices of the mean number of singing males of each species for all 71 points, grouped by treatment (Manly 1994).

Habitat Relations of Birds.—We used Detrended Correspondence Analysis (DCA) to explore which of the habitat variables we measured were potentially most important in explaining differences in bird communities among treatments. The DCA conducted on point-count data revealed a linear response of species to environment. We therefore identified relationships between bird species' abundances and habitat variables using RDA (ter Braak and Smilauer 1998). We used forward stepwise selection with 999 Monte Carlo permutations (CANOCO; ter Braak and Smilauer 1998) to identify habitat variables that contributed significantly to the ordination of habitat features and the abundances of the 18 birds species included in our analysis. Percent grass and sedge cover

Table 1. Species richness, number of individuals, number of unique species, and means (95% CI) of species richness, Shannon's diversity index, and log-series diversity of birds from 71 unlimited point count stations in 71 stands at 31 temporal stages in single-tree selection cutting rotation and reference stands in Algonquin Provincial Park, Ontario, Canada, June–August 1998.

Variable	Treatment		
	Reference (RE)	Logged–recent (LR)	Logged–old (LO)
Total species	39	39	37
Mean richness (95% CI) ^a	10.6 (9.65 to 11.51)	12.1 (11.02 to 13.23)	8.7 (7.42 to 9.97)
No. of unique species	6	4	4
No. of individuals	406	448 (+)	287 (-)
Shannon's diversity	3.14 (3.00 to 3.29)	3.39 (3.26 to 3.53)	2.81 (2.55 to 3.07)
(bits per individual, CI, N) ^{b,c}	8.86 species	10.48 species	7.01 species
Log-series diversity ^d	13.8 (10.85 to 16.79)	18.1 (13.92 to 22.34)	19.4 (11.84 to 26.87)

^a $F_{2,68} = 6.81$, $P < 0.0001$; multiple comparisons: RE-LR $P < 0.10$; RE-LO $P < 0.04$; LR- LO $P < 0.0001$, Tukey's HSD test.

^b $F_{2,68} = 10.5$, $P < 0.0001$; multiple comparisons: RE-LR $P < 0.13$; RE-LO $P < 0.03$; LR- LO $P < 0.0002$.

^cNumber of equally common species that would produce the same diversity as H' , MacArthur 1965.

^d $F_{2,68} = 1.26$, $P = 0.29$.

had a disproportionately large and apparently stochastic influence on the ordination. We believed that this was the result of high variability from clumping all grass and sedge species into a single variable, so we removed this variable prior to conducting the ordination.

We used 1-way ANOVAs to identify specific differences among treatments in the habitat variables identified by RDA as significant ($P < 0.10$). Chi-squared analysis was used on the categorical diameter class data.

We tallied the number of species in each logging treatment for 3 life-history categories and 2 population-trend indices, and we conducted chi-squared analyses to identify among treatment effects. The forest habitat association (edge, interior, generalist) and nesting ecology (cavity, tree, shrub, ground) of each species surveyed were determined from Ehrlich *et al.* (1988), and the migration ecology (resident, short-distance migrant, long-distance migrant) of each species was derived from National Geographic Society (1987). We obtained long-term (25–35 yr) Canadian and Ontario population trends for each species sampled from Dunn (1997).

RESULTS

Bird Communities

We detected 52 species across all treatments during point counts. Shannon's diversity index and mean species richness per count did not differ between RE and LR stands ($P > 0.10$; Table 1) but was higher in RE and LR stands than in LO stands (Tukey probabilities: $P_{RE-LO} = 0.041$, $P_{LR-LO} < 0.001$). Log-series Diversity did not differ significantly among treatments. Total number of individuals of all species was higher than expected in LR stands and lower than expected in LO stands based on a uniform expected distri-

bution ($\chi^2_1 = 36.7$, $P < 0.001$; Table 1). Each treatment had at least 4 unique species, all of which were seen and/or heard < 3 times.

Abundances did not differ among treatments for 12 of the 18 species tested (Table 2). Yellow-bellied sapsuckers were marginally more abundant in RE and LR than LO stands (Tukey probability: $P = 0.082$). White-throated sparrows, mourning warblers, and chestnut-sided warblers were significantly more abundant in LR stands than RE and LO stands (Tukey probability: $P < 0.001$), with mourning warblers not recorded in RE stands. Ovenbirds were less than half as abundant in LO and LR than RE stands (Tukey probability: $P < 0.001$). Black-throated blue warblers were less abundant in LO stands than LR and RE stands (Tukey probability: $P < 0.02$).

Using a cluster analysis on the distance matrix of mean numbers of singing males of each species, LR stands were 14% more dissimilar from RE and LO stands in overall bird community composition than RE and LO stands were to one another (RE–LO, Euclidean distance = 2.01; RE–LO cluster to LR, Euclidean distance = 2.35).

Habitat Relations of Birds

Redundancy analysis identified 13 habitat variables that contributed significantly ($P < 0.10$) to the abundances of the 18 bird species tested. One-way ANOVAs on these variables (χ^2 on diameter data) revealed no significant differences among logging treatments for 7 of the 13 variables tested. Five of the 8 habitat variables that differed among treatments related to vertical deciduous structure (percent cover; Table 3). The first 2 axes generated by RDA explained 50.6% of the variability in the species–environment relationship. The main environmental gradient identified by RDA corresponded to the logging effects on habitat structure (Fig. 1a), with

Table 2. Means, standard errors, and ranges of unlimited-distance point counts for 22 common species sampled at 2 temporal stages in single-tree selection cut stands and reference stands in contiguous tolerant hardwood forests in central Ontario, Canada, 1998. Species are listed in order of decreasing abundance in the reference treatment.

Species	Reference (n = 24)	Logged-recent (n = 24)	Logged-old (n = 23)	F _{2,22}	P ^a
Red-eyed vireo	3.21 ± 0.34	2.65 ± 0.32	2.95 ± 0.32	0.79	0.46
<i>Vireo olivaceus</i>	1-6	0-7	1-6		
Ovenbird	2.37 ± 0.17	1.08 ± 0.22	1.00 ± 0.23	13.4	0.0001
	1-4	0-3	0-4		
Black-throated blue warbler	1.21 ± 0.17	1.38 ± 0.21	0.52 ± 0.11	7.16	0.001
	0-3	0-4	0-1		
Black-throated green warbler	1.13 ± 0.18	1.04 ± 0.21	0.87 ± 0.19	0.43	0.65
<i>D. virens</i>	0-3	0-4	0-3		
Yellow-bellied sapsucker	0.83 ± 0.18	0.66 ± 0.14	0.17 ± 0.08	5.84	0.004
	0-3	0-2	0-1		
Winter wren	0.75 ± 0.17	1.00 ± 0.16	0.65 ± 0.16	1.18	0.31
<i>Troglodytes troglodytes</i>	0-2	0-3	0-3		
Least flycatcher	0.67 ± 0.29	0.67 ± 0.28	0.09 ± 0.06	1.96	0.15
<i>Empidonax minimus</i>	0-6	0-6	0-1		
American redstart	0.67 ± 0.15	0.50 ± 0.15	0.74 ± 0.20	0.52	0.6
<i>Setophaga ruticilla</i>	0-2	0-2	0-3		
Swainson's thrush	0.63 ± 0.18	0.33 ± 0.11	0.48 ± 0.12	1.06	0.35
<i>Catharus ustulatus</i>	0-3	0-2	0-2		
Blackburnian warbler	0.58 ± 0.13	0.63 ± 0.16	0.91 ± 0.14	1.53	0.22
<i>D. fusca</i>	0-2	0-2	0-2		
Rose-breasted grosbeak	0.42 ± 0.10	0.67 ± 0.13	0.65 ± 0.13	1.31	0.27
<i>Pheucticus ludovicianus</i>	0-1	0-2	0-2		
Veery	0.42 ± 0.12	0.46 ± 0.16	0.30 ± 0.10	0.38	0.69
<i>C. fuscescens</i>	0-2	0-3	0-1		
Yellow-rumped warbler	0.38 ± 0.12	0.58 ± 0.17	0.43 ± 0.15	0.53	0.59
<i>D. coronata</i>	0-2	0-3	0-2		
Brown creeper	0.33 ± 0.09	0.21 ± 0.10	0.09 ± 0.06	1.84	0.17
<i>Certhia americana</i>	0-1	0-2	0-1		
Chestnut-sided warbler	0.33 ± 0.15	1.62 ± 0.24	0.52 ± 0.18	13.04	0.0001
	0-3	0-4	0-3		
Hermit thrush	0.29 ± 0.09	0.21 ± 0.10	0.17 ± 0.14	0.29	0.75
<i>C. guttatus</i>	0-1	0-2	0-3		
Scarlet tanager	0.25 ± 0.13	0.67 ± 0.19	0.17 ± 0.11	3.46	0.04
<i>Piranga olivacea</i>	0-1	0-2	0-1		
White-throated sparrow	0.21 ± 0.08	1.17 ± 0.17	0.22 ± 0.11	18.07	0.0001
	0-1	0-3	0-2		
Eastern wood-pewee	0.21 ± 0.08	0.21 ± 0.08	0.04 ± 0.04	1.62	0.2
<i>Contopus virens</i>	0-1	0-1	0-1		
Red-breasted nuthatch	0.17 ± 0.08	0.13 ± 0.07	0.09 ± 0.06	0.32	0.72
<i>Sitta canadensis</i>	0-1	0-1	0-1		
Blue jay	0.13 ± 0.07	0.50 ± 0.18	0.13 ± 0.07	3.22	0.04
<i>Cyanocitta cristata</i>	0-1	0-3	0-1		
Mourning warbler		0.75 ± 0.15	0.04 ± 0.04	21.4	0.0001
		0-2	0-1		

^a All significant P-values remain significant after Bonferoni corrections except for blue jay.

RE stands generally to the lower left portion of the ordination biplot and LR stands to the upper right side. Logged-old stands were more similar to RE stands, but tended more toward the upper left portion of the ordination (Fig. 1a). The dispersion of points in the ordination from both logging treatments suggests greater variability among stands in habitat characteristics than among reference stands. Bird species abundances were congruent with habitat structural variation among treatments (Fig. 1b). The ovenbird was positioned at the end of the gradient positively associated with deciduous canopy cover and density of living deciduous trees in the 10–20-cm-diam-

eter class. Chestnut-sided and mourning warblers and the white-throated sparrow were positioned at the other end of the gradient, positively associated with percent cover of slash and deciduous shrubs (0–0.5-m strata). The black-throated blue warbler was associated with coniferous cover and fell in the lower right-hand portion of the biplot, which was shared primarily by LR and RE stands (Fig. 1b). Species whose abundances did not vary among treatments generally were positioned along the second axis of the ordination. Blackburnian, black-throated green, and myrtle warbler abundances were associated with small conifers, and red-eyed vireo and American red-

Table 3. Means and 95% confidence intervals of 8 habitat variables that showed significant or near significant treatment effects and were identified by redundancy analysis as being significantly associated with bird species' abundances in contiguous tolerant hardwood forests in central Ontario, Canada, 1998.

Habitat variable	Treatment		
	Reference (<i>n</i> = 18)	Logged-recent (<i>n</i> = 18)	Logged-old (<i>n</i> = 19)
Percent deciduous cover at:			
0–0.5 m ^a	13.3 (12.3 to 14.4)A	31.3 (28.5 to 34.0)B	12.0 (10.8 to 13.3)A
0.5–2 m ^b	30.5 (29.0 to 32.0)A	39.8 (41.0 to 49.9)B	22.9 (22.5 to 26.7)A
2–5 m ^c	27.3 (25.2 to 29.4)A	11.8 (10.9 to 12.6)B	42.8 (40.0 to 45.5)C
5–10 m ^d	24.9 (22.6 to 27.2)A	15.5 (14.2 to 16.8)A	38.6 (36.0 to 41.1)B
Canopy ^e	62.6 (59.7 to 65.6)A	22.8 (20.3 to 25.3)B	27.9 (25.8 to 30.0)B
Slash (%) ^f	3.4 (3.2 to 3.6)A	8.2 (7.3 to 9.0)B	3.2 (2.7 to 3.6)A
Stems/ha ^g	14,283 (14,147 to 14,419)A	26,643 (34,576 to 38,710)B	42,775 (37,512 to 48,038)B
Basal area ^h of living deciduous trees (m ² /ha)	19.1 (18.1 to 20.2)A	10.3 (9.7 to 11.0)B	12.3 (11.7 to 13.0)B

^a $F_{2,51} = 8.75, P < 0.0005$.

^b $F_{2,51} = 3.12, P = 0.053$.

^c $F_{2,51} = 15.6, P < 0.0001$.

^d $F_{2,51} = 7.58, P < 0.002$.

^e $F_{2,51} = 16.9, P < 0.00001$.

^f $F_{2,51} = 6.91, P < 0.002$.

^g $F_{2,51} = 7.05, P < 0.002$.

^h $F_{2,51} = 7.50, P < 0.001$.

start abundances with sapling density (percent deciduous cover in 2–5-m strata; Fig. 1b).

We found no differences in number of species belonging to the different life-history (migration ecology, nesting substrate, habitat association) or long-term population trend (Ontario or Canada) categories (χ^2_1 , all P s > 0.56).

DISCUSSION

Bird Response

Our results support other studies that suggest selectively cut stands generally retained mature forest bird communities (Thompson et al. 1995, Annand and Thompson 1997, Robinson and Robinson 1999), with some exceptions. Cluster analysis on abundance data suggested that LO stands were more similar to reference stands than LR stands in overall community composition. Some changes in abundance associated with logging were short term, but if we assume that the stands represented a potential time series, long-term reductions in abundance were experienced by at least 3 species in our study area. We found a significant reduction of both species and number of individuals in LO stands as compared to RE stands. The combination of reduced shrub layer and reduced canopy cover in LO stands may work together to limit the availability of habitat suitable to both edge/shrub-associated species and forest interior species.

The identification of among-treatment differences in diversity by Shannon's index and not by

the log-series index may be attributable to the Shannon's index's sensitivity to differences in abundances of a few common or rare species. Although widely used, the ecological applicability of the Shannon's diversity index is often brought into question, largely due to this sensitivity (Taylor et al. 1976, Magurran 1988). The log-series index is based more on the abundances of the most common species, making it more robust overall (Taylor et al. 1976, Magurran 1988). Therefore, a lack of differences among logging treatments in this measure of biodiversity is encouraging.

Our prediction of a change in bird communities as a result of selection cutting was supported for some species but not for others. In general, in the reference stands, we recorded no annual variation over 3 years of point counts, suggesting a relatively stable avifauna in the absence of anthropogenic disturbances. Within a year, the habitat ordination for these stands was also more clustered than habitat ordination of logged stands. Three of the 6 species that exhibited significant or marginally significant inter-treatment differences in abundance were edge/shrub-associated species (white-throated sparrow, chestnut-sided and mourning warblers). As predicted, the abundances of these species were higher in LR stands, relative to RE stands, but similar to abundances in reference stands in LO stands. Our findings are consistent with those of Robinson and Robinson (1999), who reported that edge-species abundances peaked 2–3 years following selection cutting, began to decrease 4–5 years

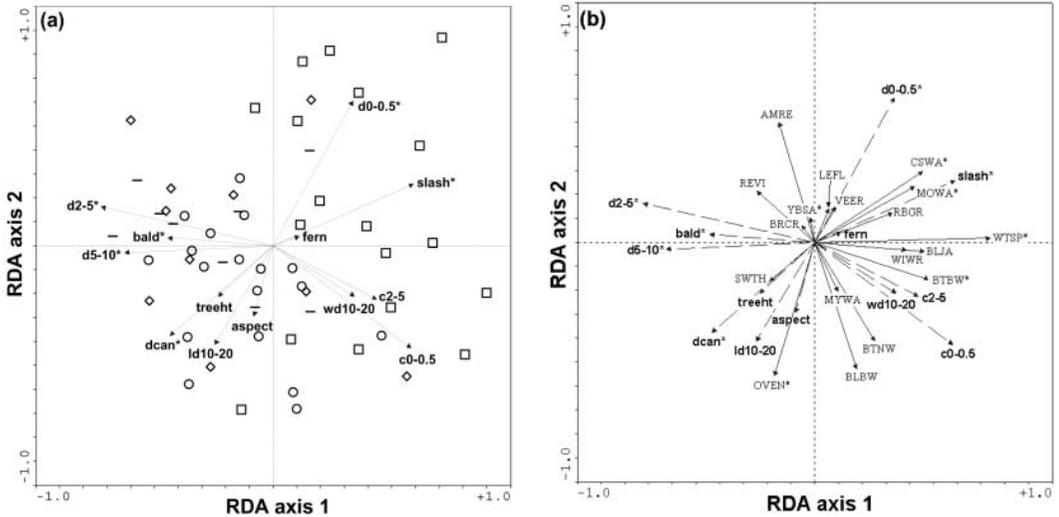


Fig. 1. Ordination biplots of (a) sites (Reference = circles, Logged-recent = squares, Logged-old = diamonds) and (b) bird species abundances with 13 habitat structure variables identified by redundancy analysis (RDA) as significantly contributing to the abundances of 18 forest bird species in a contiguous tolerant hardwood forest in central Ontario, Canada, 1998. Axis 1 explains 28.1% of variability in species–environment relationship; axis 2 explains 22.5% (cumulative = 50.6%). Habitat structure variables were basal area, living deciduous trees (bald); aspect (degrees) of plot (aspect); percent conifer cover: 0–0.5 m stratum (c0–0.5) and 2–5 m stratum (c2–5); percent deciduous cover: 0–0.5 m stratum (d0–0.5), 2–5 m stratum (d2–5), and 5–10 m stratum (d5–10); percent deciduous canopy cover (dcan); percent fern cover (fern); number of living deciduous trees, 10–20 cm dbh class (ld10–20); percent slash cover (slash); height (m) of canopy trees (treeht); and number of downed logs, 10–20 cm diameter (wd10–20). Bird species in the analysis were American redstart (AMRE), blackburnian warbler (BLBW), blue jay (BLJA), brown creeper (BRCR), black-throated blue warbler (BTBW), black-throated green warbler (BTNW), chestnut-sided warbler (CSWA), least flycatcher (LEFL), mourning warbler (MOWA), myrtle warbler (MYWA), ovenbird (OVEN), rose-breasted grosbeak (RBGR), red-eyed vireo (REVI), Swainson's thrush (SWTH), veery (VEER), winter wren (WIWR), white-throated sparrow (WTSP), and yellow-bellied sapsucker (YBSA).

post harvest, and that most of these species were not present in stands 11 years following harvest.

Three of the 6 species did not respond to selection cutting as predicted. Ovenbird abundance decreased by over 50% in the LR stands but contrary to prediction, their abundances also were 50% lower in LO stands. This ground-nesting, forest-interior species requires the combination of high canopy closure and low herbaceous and shrub cover for nesting and foraging (Van Horn and Donovan 1994). This combination is rare in LR and LO stands because the former has high shrub cover and both treatments have low canopy cover in our study area, evidently rendering large portions of these stands less suitable for ovenbird nesting and foraging.

The ovenbird demonstrated a marked response to selection cutting in our study. This species has responded to landscape- and site-level habitat modifications through reductions in abundance (Burke and Nol 1998, Flaspohler et al. 2002), territory size (Smith and Shugart 1987, Villard et al. 1993), pairing success (Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998), and productivity (Gibbs and Faaborg 1990, Burke and Nol 2000), making the

ovenbird an ideal indicator of the structural characteristics of mature hardwood forests. Our study, however, only examined relative abundance. Ovenbirds and other species (even those whose abundances did not differ significantly among treatments) may be demonstrating 1 or more of the other demographic responses to selection cutting.

Black-throated blue warbler and yellow-bellied sapsucker abundances did not change shortly after logging, but both species were present in lower abundance in the old-logged stands of 15–20 years post-harvest. This indicates that, as long as recently logged stands exist, these species probably will persist in the Algonquin landscape. The black-throated blue warbler is a shrub-nesting, forest-interior species (Holmes 1994). Reference stands contained small patches with high shrub densities, (in our study area mostly *A. saccharum* saplings) probably created through natural gap-phase disturbances (Runkle 1985). These vegetation patches were sufficient to provide suitable nesting habitat for black-throated blue warblers in these stands. The significant increase in shrub density shortly after logging (in LR stands) appeared to provide more nesting

substrate for the black-throated blue warbler. However, a reduced canopy cover and a dense sapling layer in LO stands may have limited the suitability of much of this habitat for black-throated blue warbler nesting and may explain why their abundance was not higher in these stands. The reduction in shrub density as stands regenerated for 15–20 years was relatively uniform among stands within this treatment category, resulting in an overall loss of suitable nesting habitat for this species.

Yellow-bellied sapsuckers drill holes in live trees to generate a flow of sap that attracts and catches insects (Eberhardt 2000). The yellow-bellied sapsucker therefore requires large living trees for both nest sites and foraging (Thomas et al. 1979, Eberhardt 2000). The significantly lower basal area of living deciduous trees in LO stands might limit the availability of suitable foraging and/or nesting sites, and may account for reduced sapsucker abundance in this treatment. The yellow-bellied sapsucker was close to the center of the ordination biplot, suggesting that a habitat feature not included in the ordination (e.g., tree health; Eberhardt 2000) may have had a greater influence on the abundance of this species than did any of the features in our ordination.

Habitat Relations of Birds

Significant and predictable changes in the vegetation structure of logged stands explained differences in the abundances of 6 bird species among treatments. Percent deciduous canopy cover was significantly higher in RE stands than in LR and LO stands. Reduced canopy closure in LR stands increased light penetration to the forest floor and allowed for the establishment of a dense shrub layer composed primarily of shade-intolerant wild red raspberry (*Rubus idaeus*; Finegan 1984). Increased light penetration also released shade-tolerant sugar maple, American beech, and striped maple (*Acer pensylvanicum*) seedlings, which outgrew the shade-intolerant shrub layer of LR stands and produced the dense sapling layer typical of LO stands (Finegan 1984). Slash abundance increased shortly after logging, but decreased through decay to pre-harvest levels over the next 15–20 years. These results generally are consistent with other studies on the effects of logging on habitat structure (Annand and Thompson 1997, Robinson and Robinson 1999, Flaspohler et al. 2002).

MANAGEMENT IMPLICATIONS

Some bird species demonstrating long-term population declines are associated with open habitats

(e.g., white-throated sparrow; Dunn 1997). The selection cutting system in our study positively affected these species and may benefit their populations by providing small amounts of suitable nesting habitat in an otherwise continuously forested landscape. At least 3 forest-interior species were negatively affected by selection cutting. Timber management might allow both groups of species to coexist in single-tree, selection-cut, tolerant hardwood stands, but decisions will have to be made carefully to avoid trade-offs between open-habitat and forest-interior species (Lent and Capen 1995, Annand and Thompson 1997). Closed-canopy forest could become a limiting factor for some species in selection-cut forests, especially over several rotations.

As Algonquin Provincial Park is heavily used for recreation, aesthetic concerns result in harvesting restrictions that are more strict in our study area than they are in non-park areas (Algonquin Forestry Authority 1994). Therefore, bird community responses to selection cutting that we have identified could potentially be more pronounced in privately owned lands. Because continuously forested landscapes often are considered the benchmark by which the results of forest fragmentation studies should be compared (e.g., Hartley and Hunter 1998, Burke and Nol 2000), ensuring healthy bird populations in park environments to supply less productive populations outside of parks and reserves is critical. Implications for population persistence will require data on reproductive success in combination with population modeling with varying proportions of the forested landscape committed to selection cutting.

Basal area of living deciduous trees decreased significantly after harvest and remained suppressed 15–20 years post-harvest. At that time (late 1970s, early 1980s), cuts, although still considered single-tree selection, were probably heavier than at present. The basal area of a stand's merchantable timber should return to pre-harvest levels in the 20 years between cycles in the selection cutting system, allowing continued harvesting in perpetuity (Ontario Ministry of Natural Resources 1998).

Retention of a closed canopy is another theoretical advantage of selection cutting over other silvicultural systems (Thompson et al. 1995, Ontario Ministry of Natural Resources 1998). Neither a return to pre-harvest levels in basal area nor a closed canopy is present in the managed tolerant hardwood forests that have reached 2 decades in age. Canopy closure was the same in LO stands as LR stands, which was over one-third lower than in RE stands. Total basal area of living trees decreased

between cycles. Logged-old stands are scheduled to be harvested again in 1–5 years. At this time, fewer if any trees can be harvested if the minimum total residual basal area requirement of 20 m²/ha is to be maintained (Ontario Ministry of Natural Resources 1998). Resulting stands will be different in structure from all 3 treatments in this study. We recommend a follow-up study in the next decade to examine bird communities in stands currently in our recently logged treatment, where prescriptions of selection cutting were more closely followed.

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Appendix A. Yearly variation in unlimited point-count estimates (mean \pm SE, range) for the 15 most common species observed in 12 reference stands sampled in each of 1998–2000 in central Ontario, Canada. Species presented in order of decreasing abundance in 1998.

Species	1998	1999	2000	$F_{2,22}$	P
Red-eyed vireo	3.25 \pm 0.49 1–6	4.25 \pm 0.43 2–6	3.5 \pm 0.40 1–6	1.71	0.2
Ovenbird	2.7 \pm 0.22 1–4	2.17 \pm 0.37 0–4	1.83 \pm 0.41 0–5	2.2	0.13
Black-throated blue warbler	1.17 \pm 0.27 0–3	1.08 \pm 0.25 0–2	1.41 \pm 0.33 0–4	0.36	0.7
Black-throated green warbler	1.08 \pm 0.26 0–3	1.41 \pm 0.29 0–2	1.00 \pm 0.21 0–2	1.26	0.3
Winter wren	1.0 \pm 0.27 0–2	0.92 \pm 0.34 0–3	0.33 \pm 0.19 0–2	2.15	0.14
Yellow-bellied sapsucker	0.83 \pm 0.30 0–3	1.33 \pm 0.38 0–5	1.25 \pm 0.39 0–3	1.54	0.24
Blackburnian warbler	0.75 \pm 0.22 0–2	0.58 \pm 0.19 0–2	0.42 \pm 0.19 0–2	1.38	0.27
Least flycatcher	0.67 \pm 0.31 0–3	0.67 \pm 0.35 0–4	0.41 \pm 0.33 0–4	0.37	0.69
Veery	0.50 \pm 0.19 0–2	0.67 \pm 0.26 0–2	0.58 \pm 0.22 0–2	0.16	0.89
Yellow-rumped warbler	0.50 \pm 0.67 0–2	0.58 \pm 0.51 0–1	0.33 \pm 0.65 0–2	0.48	0.63
Rose-breasted grosbeak	0.42 \pm 0.15 0–1	0.50 \pm 0.15 0–1	0.25 \pm 0.18 0–2	0.56	0.58
American redstart	0.33 \pm 0.14 0–1	0.5 \pm 0.26 0–3	0.58 \pm 0.29 0–3	0.52	0.6
Swainson's thrush	0.25 \pm 0.18 0–2	0.33 \pm 0.19 0–2	0.50 \pm 0.15 0–1	0.56	0.57
White-throated sparrow	0.25 \pm 0.25 0–1	0.67 \pm 0.67 0–2	0.42 \pm 0.41 0–2	1.85	0.18
Scarlet tanager	0.25 \pm 0.13 0–1	0.67 \pm 0.19 0–2	0.17 \pm 0.11 0–1	3.46	0.04