Research Paper

Numerical Response of Breeding Birds Following Experimental Selection Harvesting in Northern Hardwood Forests

Réponse numérique de huit espèces d'oiseaux nicheurs à la suite d'une coupe de jardinage expérimentale en forêt feuillue septentrionale

*Samuel Hache*¹, *Thibaut Pétry*² and *Marc-André Villard*²

ABSTRACT. Silvicultural treatments have been shown to alter the composition of species assemblages in numerous taxa. However, the intensity and persistence of these effects have rarely been documented. We used a before-after, control-impact (BACI) paired design, i.e., five pairs of 25-ha study plots, 1-control and 1-treated plot, to quantify changes in the density of eight forest bird species in response to selection harvesting over six breeding seasons, one year pre- and five years postharvest. Focal species included mature forest associates, i.e., Northern Parula (*Setophaga americana*) and Black-throated Green Warbler (*Setophaga virens*), forest generalists, i.e., Yellow-bellied Sapsucker (*Sphyrapicus varius*) and Swainson's Thrush (*Catharus ustulatus*), early-seral specialists, i.e., Mourning Warbler (*Geothlypis philadelphia*) and Chestnut-sided Warbler (*Setophaga pensylvanica*), species associated with shrubby forest gaps, i.e., Black-throated Blue Warbler (*Setophaga caerulescens*), and mid-seral species, i.e., American Redstart (*Setophaga ruticilla*). As predicted, we found a negative numerical response to the treatment in the Black-throated Green Warbler, no treatment effect in the Yellow-bellied Sapsucker, and a positive treatment effect in early-seral specialists. We only detected a year effect in the Northern Parula and the American Redstart. There was evidence for a positive treatment effect on the Swainson's Thrush when the regeneration started to reach the pole stage, i.e., fifth year postharvest. These findings suggest that selection harvesting has the potential to maintain diverse avian assemblages while allowing sustainable management of timber supply, but future studies should determine whether mature-forest associates can sustain second- and third-entry selection harvest treatments.

RÉSUMÉ. Les traitements sylvicoles modifient la composition des assemblages d'espèces de nombreux taxons. Toutefois, l'intensité et la durée des effets de ces traitements ont rarement été évaluées. Notre étude visait à quantifier le changement observé dans la densité de huit espèces d'oiseaux à la suite d'une coupe de jardinage. Pour ce faire, nous avons utilisé un plan d'échantillonnage apparié du type BACI (pour *before-after control-impact* en anglais) consistant en cinq paires de sites (un témoin et l'autre expérimental) de 25 ha chacun. Nos résultats portent sur six saisons de nidification, la première avant la coupe et les cinq suivantes, après la coupe. Les espèces étudiées comprenaient des spécialistes de forêts matures, c.-à-d. la Paruline à collier (*Setophaga americana*) et la Paruline à gorge noire (*Setophaga virens*), des espèces forestières généralistes, c.-à-d. le Pic maculé (*Sphyrapicus varius*) et la Grive à dos olive (*Catharus ustulatus*), des spécialistes de début de succession, c.-à-d. la Paruline triste (*Geothlypis philadelphia*) et la Paruline à flancs marron (*Setophaga pensylvanica*), une spécialiste des trouées forestières, la Paruline bleue (*Setophaga caerulescens*), et une spécialiste du stade intermédiaire de succession, la Paruline flamboyante (*Setophaga ruticilla*). Tel qu'attendu, le traitement sylvicole a eu un effet négatif chez la Paruline à gorge noire, aucun effet chez le Pic maculé et un effet positif chez les spécialistes de début de succession. Nous avons observé un effet de l'année seulement chez les Parulines à collier et flamboyante. Un effet positif chez la Grive à dos olive a été détecté lorsque la régénération a atteint le stade de gaulis, c.-à-d. à la cinquième année après la coupe. Nos résultats montrent que la coupe de jardinage a le potentiel de maintenir divers assemblages aviaires tout en permettant une récolte forestière durable. Toutefois, les futures études devraient chercher à déterminer si les spécialistes des forêts matures peuvent supporter une deuxième ou une troisième rotation de coupe de jardinage.

Key Words: *BACI design; bird communities; forest management; partial harvesting; spot mapping*

¹University of Alberta, ²Université de Moncton

Sponsored by the Society of
Canadian Ornithologists and
Bird Studies Canada

Parrainée par la Société des
ornithologues du Canada et
Études d'oiseaux Canada

BIRD STUDIES
ÉTUDES D'OISEAUX CANADA

INTRODUCTION

The effects of forest management on biodiversity are complex because they are highly species specific and silvicultural treatments themselves vary in intensity and spatial extent. Partial harvesting treatments have been shown to cause habitat degradation in various taxa, such as wood-decaying fungi (Edman et al. 2004), epiphytic lichens and bryophytes (Edman et al. 2008, Löhmus and Löhmus 2010), carabid beetles (Martikainen et al. 2006, Work et al. 2010), salamanders (Homyack and Haas 2009), songbirds (Craig 2002, Gram et al. 2003, Vanderwel et al. 2007, Eng et al. 2011), and mammals (Lindenmayer and Franklin 1997, Gitzen et al. 2007). However, early-seral species are generally favored by partial harvesting (Gram et al. 2003, Guénette and Villard 2005, Heltzel and Leberg 2006, Gitzen et al. 2007). The intensity and persistence of these effects may vary as a function of timber volume harvested, type and rate of postharvest regeneration, and time interval between harvest entries (Vanderwel et al. 2007, 2009). Hence, the numerical response of several species to postharvest stand structure is required to model the range of ecological effects of partial harvesting on avian communities at a regional scale.

Although several studies have reported variations in songbird abundance along gradients in habitat alteration, i.e., different intensities of forest disturbance (Guénette and Villard 2005, Vanderwel et al. 2007), or in response to specific silvicultural prescriptions (Doyon et al. 2005, Tozer et al. 2010, Straus et al. 2011), temporal variations in the density of particular bird species as stands regenerate remain largely undocumented (but see Gram et al. 2003, Campbell et al. 2007). The latter studies had experimental designs that were either characterized by relatively small plots, i.e., low numbers of bird territories, or that featured control plots adjacent to treated plots, which may have yielded misleading information about the magnitude of treatment effects. In other studies, bird abundance was estimated using point counts (Tittler et al. 2001, Tozer et al. 2010, Kardynal et al. 2011, Holmes et al. 2012), which do not necessarily correlate with density estimates from spot mapping of species with relatively large territories (Toms et al. 2006). Point-count data also tend to overestimate population size, i.e., provide estimates of “superpopulations” (Hunt et al. 2012). Hence, well-replicated study designs based on large plots hosting many territories of focal species are needed to provide accurate estimates of the numerical response, i.e., density, of birds to partial harvesting.

In this study, we used a before-after, control-impact paired design (BACI) to monitor the effects of selection harvesting on densities of focal species that are common in eastern Canada’s northern hardwoods. This harvest treatment was designed to develop multiage stands and to increase the overall quality of the growing stock (Nyland 2003). Through the retention of approximately 60-70% of the basal area, selection harvesting offers the possibility of maintaining species

associated with late-seral forest while stimulating regeneration and, thus, potentially meeting the requirements of forest species associated with a dense shrub layer. We measured the numerical response of eight bird species representing a broad range of habitat associations and common enough to allow statistical analyses (Table 1). We documented the direction, magnitude, and timing of changes in density, or lack thereof, during the first five years following a selection harvest treatment.

We predicted the response of each focal species based on its habitat requirements documented in the literature. Specifically, we predicted that the postharvest density of mature forest associates, Northern Parula (*Setophaga americana*) and Black-throated Green Warbler (*Setophaga virens*) would decrease relative to that of control plots (Morse and Poole 2005, Moldenhauer and Regelski 2012), whereas no treatment effect was expected for species considered to be forest generalists, Yellow-bellied Sapsucker (*Sphyrapicus varius*) and Swainson’s Thrush (*Catharus ustulatus*; Mack and Yong 2000, Walters et al. 2002, Straus et al. 2011). However, the Yellow-bellied Sapsucker could benefit from the creation of snags as a result of wounds sustained by trees retained during harvest operations (Thorpe et al. 2008). Finally, we predicted a positive response of species associated with a dense shrub layer, i.e., Mourning Warbler (*Geothlypis philadelphia*), Chestnut-sided Warbler (*Setophaga pensylvanica*), and Black-throated Blue Warbler (*Setophaga caerulescens*), or dense midstory vegetation, i.e., American Redstart (*Setophaga ruticilla*), as the stands regenerated after the treatment (Richardson and Brauning 1995, Sherry and Holmes 1997, Holmes et al. 2005, Pitocchelli 2011).

METHODS

Study area and experimental design

The study was conducted in the Black Brook District, northwestern New Brunswick, Canada (47°23’N, 67°40’W). This 2000 km² private forest is managed by J. D. Irving Ltd. Dominant species in hardwood stands are sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), along with relatively sparse coniferous species (balsam fir, *Abies balsamea*; spruces, *Picea* spp.).

Over the past 30 years, J. D. Irving Ltd. has managed most of its hardwood stands and hardwood-dominated mixedwoods through selection harvesting. Typically, this silvicultural treatment removes 30-40% of the basal area, i.e., cross-sectional area at breast height, 1.35 m, of all stems with a diameter ≥ 10 cm, under a 20-25 year rotation. Skid trails, 5 m wide, account for 20% of the harvested basal area, with the remaining 10-20% being removed within the residual forest between skid trails. Foresters aim to harvest stems in each diameter class as a function of a predetermined multiage distribution (Nyland 1998), although there is a positive bias

Table 1. Numerical responses to partial harvesting in northern hardwood forests and territory sizes of focal bird species according to the literature.

	Numerical response to partial harvesting [†]	Parameter	Territory size (ha) [‡]	Method used for estimating territory size	Sources for territory sizes
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	Negative or no effect	Abundance/Density	2-3	N/A	Walters et al. 2002
Swainson's Thrush (<i>Catharus ustulatus</i>)	Negative or no effect	Abundance	2	Spot mapping	Sabo 1980
Mourning Warbler (<i>Geothlypis philadelphia</i>)	No effect (early) or positive (later)	Abundance	1-2	Spot mapping	Cox 1960
American Redstart (<i>Setophaga ruticilla</i>)	No effect (early) or positive (later)	Abundance	0.5-1	Spot mapping	Hunt 1996, Sherry and Holmes 1989
Northern Parula (<i>Setophaga americana</i>)	Negative	Abundance	0.5-1.0	N/A	Moldenhauer and Regelski 2012
Chesnut-sided Warbler (<i>Setophaga pensylvanica</i>)	Positive	Abundance	1-2	Spot mapping	Kendeigh 1945
Black-throated Blue Warbler (<i>Setophaga caerulescens</i>)	Negative (early) or positive (later)	Abundance/Density	1-3	Spot mapping	Steele 1992
Black-throated Green Warbler (<i>Setophaga virens</i>)	Negative or no effect	Abundance/Density	0.5-1.5	Spot mapping	Sabo 1980, Robichaud and Villard 1999

[†]Sources reporting effects of partial harvesting on our focal species: Norton and Hannon 1997, Bourque and Villard 2001, Gram et al. 2003, Jobes et al. 2004, Guénette and Villard 2005, Campbell et al. 2007, Holmes and Pitt 2007, Tozer et al. 2010, Straus et al. 2011.

[‡]Values are based on estimates provided from the literature and our field observations.

toward larger trees that would not be merchantable at the next harvest entry.

The study was conducted over six successive breeding seasons, i.e., 2006-2011, one year preharvest and five years postharvest, in 5 pairs of 25 ha study plots in which there was 1 control and 1 plot treated through selection harvesting. Paired plots were located 3-6 km apart and the average distance between pairs of plots was 23.8 km (± 9.1 SD). Prior to the treatment, study plots had not been disturbed for at least 30 years and comprised trees of at least 120-150 years of age. Please refer to Haché and Villard (2010) for further details on the experimental design and harvest treatment.

Bird survey method

We estimated the density of all focal bird species using the spot-mapping method (Bibby et al. 2000) by walking flagged transects spaced every 100 m. In each study plot, territories were delineated using all detections and instances of countersinging during eight morning visits conducted between sunrise and 1000 AST when rain or wind did not interfere with the detection of bird vocalizations. This information, combined with territory size estimates from the literature (Table 1), was used to draw ellipses around clusters of detections. Territories required a minimum of 2 detections separated by at least 10 days (Bibby et al. 2000), but most

territories comprised detections from at least 4 different plot visits (4.1 ± 1.5 detections; mean $\pm$ SD). We only considered territories that overlapped study plots by $\geq 25\%$ when estimating density. In each plot, we added territory fractions that overlapped the study plot, i.e., 0.25, 0.33, 0.50, 0.66, and 0.75, to the number of complete territories to estimate density.

Habitat monitoring

We characterized forest stand composition using 25 habitat sampling plots, 0.04 ha each, systematically located in each bird study plot. Sampling was conducted during the preharvest year (treated plots) and the first (all 10 plots), fourth (treated plots), and fifth years postharvest (control plots). Although we did not measure the preharvest condition in controls, there is no a priori reason to expect important year-to-year variation in stand structure. During each inventory, we measured the diameter at breast height (dbh) of all trees and snags present within each sampling plot to estimate the basal area (m^2/ha) of all living trees with ≥ 10 cm dbh and the densities of live trees and snags.

Each year, we also quantified changes in canopy closure, shrub cover, and litter depth in four of the five treated plots and two of the five controls. Specifically, we measured shrub cover, canopy closure, and litter depth at 400 uniformly distributed points per study plot. Canopy closure was estimated using a

transparent plexiglass sheet (25 × 25 cm, split into a 5 × 5 grid) held overhead. We measured litter depth down to the mineral soil, to the nearest 1 mm, and estimated shrub cover (0.1–1.3 m high within a 2.5 m radius) using a semiquantitative scale (0–10, 10–25, 25–50, 50–75, 75–90, and 90–100%).

Statistical analyses

We used linear mixed models (LMM) to test for the effects of treatment, year, and year × treatment interactions on density of each focal species. We included random effects to control for the spatial structure of our experimental design, i.e., study plots nested within treatment and landscape context (paired plots; 0–5), and accounted for repeated measurements by specifying a first-order autoregressive structure to each model. After adding 0.001 to all sites with a density of 0, we applied a natural logarithmic transformation to densities of Mourning Warbler, Chestnut-sided Warbler, and American Redstart to meet the assumptions of normality and equal variances. In these analyses, the five harvested plots were considered as treated during the preharvest year to allow distinguishing treated plots from controls throughout the study. Therefore, a significant treatment × year interaction was required to infer an overall treatment effect. We also conducted multiple comparison analyses to test for year-specific treatment effects. We used the same modelling approach to test for treatment and year effects on the total density and basal area of trees, conifers, and snags (only density) separately. Those models included the same random effects as the bird models. However, the interaction term could not be included in these models because data were only collected simultaneously in both treated plots and controls during the first year postharvest. We still used LMM to provide insight into treatment and year effects although multiple comparison analyses were used to pinpoint year-specific treatment effects. We tested for a treatment effect on density and basal area of conifer trees because it might have influenced some of the focal species in hardwood-dominated stands, e.g., Black-throated Green Warbler (Robichaud and Villard 1999). Lastly, we tested for effects of treatment, year, and year × treatment interactions on litter depth, shrub cover, and canopy closure using LMM. In these models, random effects accounted for habitat sampling points (HSP; 400 per plot), which were nested within study plots. However, for these three models, we could not specify a first-order autoregressive structure and the additional hierarchical levels, i.e., treatment and landscape context, because model convergence was problematic.

To avoid adding parameters that would not substantially improve the fit of the models, we used an Akaike's information-theoretic approach for model selection (AIC) to compare the relative importance of models (1) without random effects and an autoregressive term, (2) with only the autoregressive term, and (3) with the autoregressive term and all potential combinations of random effects. They included HSP, HSP(Site), HSP(Site) + Site, and Site for litter depth,

shrubs cover, and canopy closure (six a priori models), and for all other models, Site, Site(Treatment), Site(Landscape), Site (Landscape) + Landscape, and Landscape were considered (seven a priori models). Results from the model without random effect and the autoregressive term were presented if $\Delta AIC < 2$. Otherwise results from the model with $\Delta AIC < 2$ that had the fewer random effects were reported, or model with the lowest AIC value when multiple models had $\Delta AIC < 2$ and a similar number of parameters. All analyses were performed using the MIXED procedure in SAS 9.2 (Statistical Analysis Systems, Cary, North Carolina).

RESULTS

On average, the treatment removed 12.3 m² of the preharvest basal area (41.9 %). In the first year postharvest, basal area in treated plots was significantly lower than in controls ($t_{12} = 4.22$, $P = 0.001$). This difference was still present by the fourth year postharvest ($t_{12} = 3.58$, $P = 0.004$; fourth year postharvest, treated plots vs fifth year postharvest, controls; Table 2, Fig. 1A) with little change in the basal area for both controls (-1.5 m²) and treated plots (-0.4 m²) between the first and the fourth/fifth years postharvest. A similar pattern emerged for total tree density, which decreased by 41% in treated plots compared to controls ($t_{12} = 4.15$, $P = 0.001$; Table 2, Fig. 1B). Total tree density increased by 8.3% in treated plots between the first and the fourth years postharvest, but there was still a trend for a treatment effect ($t_{12} = 2.05$, $P = 0.062$; fourth year postharvest, treated plots vs fifth year postharvest, controls). When considering the treatment effect on basal area and density of conifer trees, the same pattern emerged, but no significant effect was detected owing to the large variation among control plots (Table 2, Fig. 1C–D). Similarly, there was no evidence for year or treatment effects on the density of snags (Table 2, Fig. 1E). Mean values remained stable in treated plots between the first and fourth years postharvest although mean snag density increased by 25.4 stems/25 ha in controls from the first to the fifth year postharvest ($t_{12} = 1.91$, $P = 0.081$). The model predicting the total tree density with the lowest AIC value included the autoregressive term and Site(Landscape) + Landscape as random effects. The second best-ranked model had a $\Delta AIC = 3.7$. Models with the lowest AIC value for the other response variables only included the autoregressive term, whereas models without random effects or the autoregressive term had a $\Delta AIC > 3.8$.

Selection harvesting reduced canopy closure by approximately 20% and this reduction lasted for the duration of the study. There was a significant treatment × year interaction effect on this variable (Table 2, Fig. 2A), as well as on litter depth (Table 2, Fig. 2C). During the first year postharvest, litter depth decreased by approximately 30% (12.1 mm; $t_{12000} = 14.75$, $P < 0.001$), but the importance of the treatment effect decreased gradually through time, and litter depth was 16.5% (5.9 mm) thinner in treated plots than in controls by the fifth year postharvest ($t_{12000} = 7.51$, $P < 0.001$). In the case of shrub cover,

Fig. 1. Mean ($\pm$ SD) total basal area (A), density of live trees (B), basal area (C), and density of live conifers (D), and density of snags (E) in plots treated by selection harvesting and controls during the preharvest year, first year postharvest, and the fourth year postharvest. The solid line delineates the pre- from the postharvest and asterisks (*) indicate significant year-specific treatment effects.

Table 2. Linear mixed models relating habitat variables to treatment (selection harvesting), year, and their interaction. Values in bold indicate significant effects, i.e., P -values < 0.05 .

Habitat variable	Predictors	DF (numerator, denominator)	F-value	P-Value
Total basal area	Treatment	1,8	17.85	0.003
	Year	3,12	69.59	< 0.001
Density of trees	Treatment	1,12	17.21	0.003
	Year	3,12	203.13	< 0.001
Basal area of conifers	Treatment	1,8	1.82	0.213
	Year	3,12	28.42	< 0.001
Density of conifers	Treatment	1,8	0.86	0.381
	Year	3,12	12.17	< 0.001
Density of snags	Treatment	1,8	0.74	0.415
	Year	3,12	2.07	0.158
Canopy closure	Treatment	1,12000	820.98	< 0.001
	Year	5,12000	46.74	< 0.001
	Treatment $\times$ Year	4,12000	58.73	< 0.001
Shrub cover	Treatment	1,11000	190.75	< 0.001
	Year	5,11000	93.3	< 0.001
	Treatment $\times$ Year	4,11000	247.68	< 0.001
Litter depth	Treatment	1,12000	424.99	< 0.001
	Year	5,12000	70.65	< 0.001
	Treatment $\times$ Year	4,12000	16.30	< 0.001

a significant treatment $\times$ year interaction was also detected (Table 2), but the opposite pattern was observed. Initially, shrub cover was similar between treated plots and controls but it was 13.7% lower in treated plots than in controls during the first year postharvest ($t_{11000} = 11.6$, $P < 0.001$; Fig. 2B). By the second year, shrub cover in treated plots returned to the original values and it increased steadily thereafter, being approximately 29.5% higher in treated plots than in controls by the fifth year postharvest ($t_{11000} = -26.6$, $P < 0.001$). The best ranked models for the three response variables included HSP(Site) as a random effect (second best-ranked models had $\Delta AIC > 15.4$).

The density of Black-throated Green Warbler was influenced by treatment and year (Table 3, Fig. 3B). The density of this species was significantly lower in treated plots than in controls during the second and fifth years postharvest, whereas treatment effect was marginally significant in the third and fourth years postharvest (Table A1.1). Only a year effect was observed on the density of Northern Parula and Yellow-bellied Sapsucker (Table 3, A1.2, A1.3, Fig. 3A, 4A). Differences in Swainson's Thrush density between treated and control plots varied widely over time (Table 3, Fig. 4B). In the first three years postharvest, its mean density tended to be higher in controls, whereas the opposite pattern was observed by the fifth year postharvest (Table A1.4). Early-seral specialists and species associated with shrubby forest gaps exhibited a positive but lagged response to the harvest treatment. Higher densities of Mourning Warbler and Chestnut-sided Warbler in treated plots than in controls were first observed during the third year postharvest, whereas a positive treatment effect on Black-throated Blue Warbler was first detectable in the fourth

Fig. 2. Mean ($\pm$ SD) canopy cover (A), shrub cover (B), and litter depth (C) in treated plots (4 plots) and controls (2 plots) one year preharvest and the first five years postharvest. The solid line delineates the pre- from the postharvest years and asterisks (*) indicate significant year-specific treatment effects.

Table 3. Linear and linear mixed models relating bird density to treatment (selection harvesting), year, and their interaction. Values in bold indicate significant effects, i.e., P -values < 0.05 .

Species	Predictors	DF (numerator, denominator)	F-value	P-Value
Black-throated Green Warbler (<i>Setophaga virens</i>)	Treatment	1,8	6.74	0.032
	Year	5,40	6.04	< 0.001
	Treatment $\times$ Year	5,40	1.01	0.427
Northern Parula (<i>Setophaga americana</i>)	Treatment	1,8	0.73	0.416
	Year	5,40	17.98	< 0.001
	Treatment $\times$ Year	5,40	1.30	0.284
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	Treatment	1,40	0.15	0.702
	Year	5,40	4.10	0.004
	Treatment $\times$ Year	5,40	0.04	0.826
Swainson's Thrush (<i>Catharus ustulatus</i>)	Treatment	1,8	0.28	0.612
	Year	5,40	13.27	< 0.001
	Treatment $\times$ Year	5,40	2.38	0.055
Mourning Warbler (<i>Geothlypis philadelphia</i>)	Treatment	1,48	89.29	< 0.001
	Year	5,48	29.77	< 0.001
	Treatment $\times$ Year	5,48	24.47	< 0.001
Black-throated Blue Warbler (<i>Setophaga caerulescens</i>)	Treatment	1,8	2.42	0.158
	Year	5,40	5.95	0.003
	Treatment $\times$ Year	5,40	2.37	0.057
Chestnut-sided Warbler (<i>Setophaga pensylvanica</i>)	Treatment	1,8	8.38	0.020
	Year	5,40	6.18	< 0.001
	Treatment $\times$ Year	5,40	3.33	0.013
American Redstart (<i>Setophaga ruticilla</i>)	Treatment	1,8	3.58	0.095
	Year	5,40	9.61	< 0.001
	Treatment $\times$ Year	5,40	0.96	0.455

Fig. 3. Mean ($\pm$ SD) density of Northern Parula, *Setophaga americana* (A) and Black-throated Green Warbler, *Setophaga virens* (B) in treated plots and controls during one year preharvest and the first five years postharvest. The solid line delineates the pre- from the postharvest years and asterisks (*) indicate significant year-specific treatment effects.

Fig. 4. Mean ($\pm$ SD) density of Yellow-bellied Sapsucker, *Sphyrapicus varius* (A) and Swainson's Thrush, *Catharus ustulatus* (B) in treated plots and controls during one year preharvest and the first five years postharvest. The solid line delineates the pre- from the postharvest years and the asterisk (*) indicates a significant year-specific treatment effect.

Fig. 5. Mean ($\pm$ SD) density of Mourning Warbler, *Geothlypis philadelphia* (A), Chestnut-sided Warbler, *Setophaga pensylvanica* (B), Black-throated Blue Warbler, *Setophaga caerulescens* (C), and American Redstart, *Setophaga ruticilla* (D) in treated plots and controls during one year preharvest and the first five years postharvest. The solid line delineates the pre- from the postharvest years and asterisks (*) indicate significant year-specific treatment effects.

year postharvest (Table 3, Fig. 5A-C, Table A1.5-A1.7). There was only a year effect on the density of American Redstarts (Table 3, Fig. 5D, Table A1.8). The model including the autoregressive term and Site as a random effect had the lowest AIC value for the Yellow-bellied Sapsucker (the second best-ranked model had a Δ AIC = 2.2). In the Mourning Warbler, the model with the lowest AIC value had no autoregressive term or random effects. For all other species, models with the lowest AIC values had included the autoregressive term (models without random effects or the autoregressive term had a Δ AIC > 2.2).

DISCUSSION

Most focal species followed the trends predicted on the basis of their documented habitat requirements. The density of Black-throated Green Warblers decreased in response to selection harvesting, whereas the Yellow-bellied Sapsucker, a forest generalist, only exhibited year-to-year variation, irrespective of treatment. Also as predicted, the three species associated with a dense shrub layer, Chestnut-sided Warbler, Mourning Warbler, and Black-throated Blue Warbler, increased in density following the harvest treatment. The American Redstart did not show the anticipated positive response to the treatment, even in the later years of the study.

However, a late positive response to the treatment was observed in the Swainson's Thrush, even though we considered it to be a forest generalist. The other species that did not respond as expected is the Northern Parula. It showed year-to-year variation in density, irrespective of the treatment. Even though our results are largely consistent with our predictions, what is more insightful is the fact that selection harvesting caused substantial changes in the structure of avian assemblages over a relatively short period. These responses by some of the most abundant forest bird species of eastern Canada's northern hardwoods suggest that decisions taken by forest managers and conservation planners can have a considerable influence on these species and other ecosystem components and, thus, forest management plans should be designed with care.

The selection harvest treatment applied here favored early-seral specialists. Across eastern North America, conservation plans are being implemented to conserve those species (Askins 2001, Chandler et al. 2009, Schlossberg et al. 2010). These authors have identified the Chestnut-sided Warbler as one of the species most threatened by the decline in early-seral forest habitat. At least during the early regeneration stage, selection harvesting seemed to offer high-quality breeding habitat for

this species, as its density increased substantially, and family groups were observed (S. Haché, T. Pétry, M.-A. Villard, *personal observations*). Elsewhere in our study area, this species is mainly found in shrubby edges along forest roads. A similar pattern was observed in the Mourning Warbler. However, selection harvesting did not appear to be as beneficial to the Black-throated Blue Warbler, whose densities were also relatively high in control plots in which treefall gaps were present. The density of Black-throated Blue Warblers decreased in treated plots immediately after harvesting, probably because of the damage to the shrub layer resulting from skidding operations, and it only exhibited a positive response to selection harvesting by the fourth year postharvest. This delayed response to partial harvesting has also been reported elsewhere (Bourque and Villard 2001, Holmes and Pitt 2007, Vanderwel et al. 2009). There is evidence that partially harvested stands may continue to provide suitable habitat to early-seral passerines for many years (Holmes et al. 2012). Patterns in the density of Swainson's Thrush suggest that it only benefits from the selection harvest treatment when the density of poles (1-8 cm dbh; ~ 6-10 m high) exceeds a certain threshold. However, contrary to our prediction, a positive response to the treatment was not observed in the American Redstart, suggesting that postharvest regeneration did not reach the height required by this species (Holmes and Pitt 2007).

There is considerable concern over the disappearance of primary forests worldwide (Gibson et al. 2011), but old second or third growth forests are also being managed at a fast rate (Betts et al. 2006). Loss or alteration of older forests may negatively affect certain species (Vanderwel et al. 2007, 2009, Roberge et al. 2008) and benefit others (King et al. 2001, Gram et al. 2003). Given these species-specific responses to a given management regime, conservation goals and corresponding targets must be carefully defined (Villard and Jonsson 2009) to ensure that species most in need of habitat protection receive appropriate attention. In this context, the concept of ecosystem management, whereby biodiversity conservation targets are inspired from natural disturbance regimes typical of an ecoregion, may assist in the development of valid benchmarks (Perera et al. 2004, Drapeau et al. 2009). Ecoregions characterized by relatively infrequent, fine-scale disturbances such as the northern hardwood forests should be managed to conserve species associated with relatively large blocks of older forest. This statement applies to portions of the northern hardwood forest under active forest management, such as in northwestern New Brunswick and central Ontario (Betts et al. 2006, Holmes et al. 2012), whereas in certain regions of New England, massive reforestation has now caused a shortage of habitat for early-seral species that may require active management (Askins 2001, Schlossberg et al. 2010).

Other studies have reported negative effects of partial harvest treatments on old forest associates such as the Black-throated Green Warbler (Germaine et al. 1997, Flaspohler et al. 2002,

Doyon et al. 2005, Vanderwel et al. 2009, Kardynal et al. 2011; but see Tozer et al. 2010). However, the mechanisms underlying this pattern remain unclear. A possible explanation could be the reduction in the amount of canopy foliage and associated food. In the boreal mixedwood forest of Alberta, this species seems to require the presence of scattered mature conifers in deciduous-dominated stands (Robichaud and Villard 1999, Morse and Poole 2005). However, in this study, there was no significant reduction in density or basal area of conifers following the treatment. Other bird species associated with mature hardwood stands have been shown to respond negatively to partial harvest treatments. In the same study sites, selection harvesting had a negative effect on territory densities of Ovenbirds (*Seiurus aurocapilla*) and nest densities of Brown Creepers (*Certhia americana*; Haché and Villard 2010, Poulin et al. 2010). The Ovenbird (Pérot and Villard 2009) and many other species responded negatively to harvesting intensity in the same study region (Guénette and Villard 2005). However, most species were relatively tolerant to treatments of moderate intensity such as selection harvesting (Vanderwel et al. 2007). Nonetheless, it will be critical to determine whether future harvest entries have a similar, relatively moderate, effect on these bird species as simplification of the vertical structure and loss of old-growth characteristics are anticipated (Angers et al. 2005).

Larger birds, such as raptors and many woodpeckers, are difficult to monitor owing to their extensive area requirements and correspondingly low densities. In agricultural and suburban landscapes of southwestern Ontario, four species of woodpeckers, including the Yellow-bellied Sapsucker, showed a negative short-term response to selection harvesting (Straus et al. 2011), whereas no treatment effects were reported on the same species in a managed forest landscape located further northeast (Tozer et al. 2010). Finally, a literature review revealed no negative effects of partial harvesting on Yellow-bellied Sapsuckers (Vanderwel et al. 2009). That we found no negative effect of selection harvesting in the present study may reflect the fact that mean snag density remained similar between treated plots and controls over the five years postharvest (Fig. 1E). The wide variation in snag density among treated plots resulted from variation in mechanical disturbance and proportion of trees attacked by beech bark disease (Kasson and Livingston 2012; S. Haché, T. Pétry, M.-A. Villard, *personal observations*). With respect to raptors, Vanderwel et al. (2009) reported that the abundance of six out of the seven species would be expected to respond negatively to treatments removing more than 50% of the basal area. However, only the Barred Owl (*Strix varia*) was expected to show a decrease in response to treatments removing 25% of the basal area, a level comparable to the experimental disturbance applied in this study. Although low sample size prevents us from making strong inferences, active nests of Northern Goshawks (*Accipiter gentilis*), Red-tailed Hawks (*Buteo jamaicensis*), and Broad-winged Hawks (*Buteo*

platypterus) were only found in controls. Similarly, Barred Owls were only detected in controls, whereas Pileated Woodpeckers (*Dryocopus pileatus*) nested in both treated plots and controls.

In this study, we showed that selection harvesting creates habitat that can support high densities of early successional songbirds, at least during the first few years postharvest. In addition, there was no evidence for local extinction or a dramatic decline in mature forest associates. In the same study plots, Haché et al. (2013) found no effect of selection harvesting on per capita productivity and daily nest survival rate of Ovenbirds, suggesting that individuals can nest successfully in selection cut stands (see also Leblanc et al. 2011) by increasing the size of their territories to account for lower food abundance. There is also growing evidence that early-seral stands can be important for mature forest associates during the postfledging period (Vitz and Rodewald 2006, Chandler et al. 2012). Nonetheless, it would be prudent to maintain untreated blocks of mature forest across the landscape because it represents optimal habitat from the perspective of productivity per unit area for species such as the Ovenbird, the Brown Creeper, and possibly the Black-throated Green Warbler. Similar research should be conducted on other species, including raptors, to provide a more complete assessment of the effects of habitat alteration on avian assemblages. Compared to point-count surveys that are usually based on three visits to each station (but see Sólýmos et al. 2012), spot mapping is more labor intensive but it provides more accurate estimates of density (Hunt et al. 2012). For broad-scale monitoring, an index of abundance is clearly the most efficient approach, e.g., Boreal Avian Modelling Project. However, spot mapping combined with detailed demographic data are needed to investigate causal relationships between human land use and avian population trends. Such intensive studies are required to inform conservation planning.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/584>

Acknowledgments:

This study was supported by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and from the New Brunswick Wildlife Trust Fund to M.-A. Villard, by an NSERC-J.D. Irving Ltd. Industrial Postgraduate Scholarship, an NSERC Postgraduate Scholarship, Queen Elizabeth II Graduate Scholarships, and a Dissertation Fellowship (University of Alberta) to S.Haché. J.-F. Poulin, A. Pérot, S. Thériault, E. D'Astous, and A. Vernouillet helped with fieldwork planning and data collection whereas M.-C. Bélair, P. Bertrand, G. D'Anjou, I. Devost, V. Drolet, J.

Frenette, S. Frigon, P. Goulet, H. Laforge, J.-A. Otis, E. Ouellette, and M. Ricard provided valuable help in data collection. We also thank Gaetan Pelletier and Greg Adams, from J.D. Irving Ltd., for logistical support and advice on study design.

LITERATURE CITED

- Askins, R. A. 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. *Wildlife Society Bulletin* 29:407-412. [online] URL: http://www.ctenvirothon.org/studyguides/wildlife_docs/ConservationofWoody/Ch1.pdf
- Betts, M. G., A. W. Diamond, G. J. Forbes, M.-A. Villard, and J. S. Gunn. 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecological Modelling* 191:197-224. <http://dx.doi.org/10.1016/j.ecolmodel.2005.04.027>
- Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. *Bird census techniques*. Second edition. Academic Press, San Diego, California, USA.
- Bourque, J., and M.-A. Villard. 2001. Effects of selection cutting and landscape-scale harvesting on the reproductive success of two neotropical migrant bird species. *Conservation Biology* 15:184-195. <http://dx.doi.org/10.1111/j.1523-1739.2001.99436.x>
- Campbell, S. P., J. W. Witham, and M. L. Hunter, Jr. 2007. Long-term effects of group-selection timber harvesting on abundance of forest birds. *Conservation Biology* 21:1218-1229. <http://dx.doi.org/10.1111/j.1523-1739.2007.00768.x>
- Chandler, C. C., D. I. King, and R. B. Chandler. 2012. Do mature forest birds prefer early-successional habitat during the post-fledging period? *Forest Ecology and Management* 264:1-9. <http://dx.doi.org/10.1016/j.foreco.2011.09.018>
- Chandler, R. B., D. I. King, and C. C. Chandler. 2009. Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA. *Forest Ecology and Management* 258:1669-1676. <http://dx.doi.org/10.1016/j.foreco.2009.07.025>
- Cox, G. W. 1960. A life history of the Mourning Warbler. *Wilson Bulletin* 72:5-28
- Craig, M. D. 2002. Comparative ecology of four passerine species in Jarrah forests used for timber production in southwestern Western Australia. *Conservation Biology* 16:1609-1619. <http://dx.doi.org/10.1046/j.1523-1739.2002.00567.x>
- Doyon, F., D. Gagnon, and J.-F. Giroux. 2005. Effects of strip and single-tree selection cutting on birds and their habitat in southwestern Quebec northern hardwood forest. *Forest*

Ecology and Management 209:101-116. <http://dx.doi.org/10.1016/j.foreco.2005.01.005>

Drapeau, P., A. Leduc, and Y. Bergeron. 2009. Bridging ecosystem and multiple species approaches for setting conservation targets in managed landscapes. Pages 129-160 in M.-A. Villard and B. G. Jonsson, editors. *Setting conservation targets for managed forest landscapes*. Cambridge University Press, Cambridge, UK.

Edman, M., A.-M. Eriksson, and M.-A. Villard. 2008. Effects of selection cutting on the abundance and fertility of indicator lichens *Lobaria pulmonaria* and *Lobaria quercizans*. *Journal of Applied Ecology* 45:26-33. <http://dx.doi.org/10.1111/j.1365-2664.2007.01354.x>

Edman, M., M. Gustafsson, J. Stenlid, and L. Ericson. 2004. Abundance and viability of fungal spores along a forestry gradient – response to habitat loss and isolation? *Oikos* 104:35-42. <http://dx.doi.org/10.1111/j.0030-1299.2004.12454.x>

Eng, M. L., B. J. M. Stutchbury, D. M. Burke, and K. A. Elliott. 2011. Influence of forest management on pre- and post-fledging productivity of a neotropical migratory songbird in a highly fragmented landscape. *Canadian Journal of Forest Research* 41:2009-2019. <http://dx.doi.org/10.1139/x11-119>

Flaspohler, D. J., C. J. F. Huckins, B. R. Bub, and P. J. van Dusen. 2002. Temporal patterns in aquatic and avian communities following selective logging in the upper Great Lakes region. *Forest Science* 48:339- 349.

Germaine, S. S., S. H. Vessey, and D. E. Capen. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. *Condor* 99:708-718. <http://dx.doi.org/10.2307/1370482>

Gibson, L., T. M. Lee, L. P. Koh, B. W. Brook, T. A. Gardner, J. Barlow, C. A. Peres, C. J. A. Bradshaw, W. F. Laurance, T. E. Lovejoy, and N. S. Sodhi. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378-381. <http://dx.doi.org/10.1038/nature10425>

Gitzen, R. A., S. D. West, C. C. Maguire, T. Manning, and C. B. Halpern. 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests. *Forest Ecology and Management* 251:142-155. <http://dx.doi.org/10.1016/j.foreco.2007.05.028>

Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter. 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conservation Biology* 17:1324-1337. <http://dx.doi.org/10.1046/j.1523-1739.2003.02171.x>

Guénette, J.-S., and M.-A. Villard. 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. *Conservation Biology* 19:1168-1180. <http://dx.doi.org/10.1111/j.1523-1739.2005.00085.x>

Haché, S., and M.-A. Villard. 2010. Age-specific response of a migratory bird to an experimental alteration of its habitat. *Journal of Animal Ecology* 79:897-905. <http://dx.doi.org/10.1111/j.1365-2656.2010.01694.x>

Haché, S., M.-A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology, in press*. <http://dx.doi.org/10.1890/12-1025.1>

Heltzel, J. M., and P. L. Leberg. 2006. Effects of selective logging on breeding bird communities in bottomland hardwood forests in Louisiana. *Journal of Wildlife Management* 70:1416-1424. [http://dx.doi.org/10.2193/0022-541X\(2006\)70\[1416:EOSLOB\]2.0.CO;2](http://dx.doi.org/10.2193/0022-541X(2006)70[1416:EOSLOB]2.0.CO;2)

Holmes, S. B., and D. G. Pitt. 2007. Response of bird communities to selection harvesting in a northern tolerant hardwood forest. *Forest Ecology and Management* 238:280-292. <http://dx.doi.org/10.1016/j.foreco.2006.10.022>

Holmes, S. B., D. G. Pitt, K. A. McIlwrick, and M. K. Hoepting. 2012. Response of bird communities to single-tree selection system harvesting in northern hardwoods: 10-12 years post-harvest. *Forest Ecology and Management* 271:132-139. <http://dx.doi.org/10.1016/j.foreco.2012.02.001>

Holmes, R. T., N. L. Rodenhouse, and T. S. Sillett. 2005. Black-throated Blue Warbler (*Setophaga caerulescens*). In A. Poole, editor. *Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.

Homyack, J. A., and C. A. Haas. 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. *Biological Conservation* 142:110-121. <http://dx.doi.org/10.1016/j.biocon.2008.10.003>

Hunt, P. D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. *Auk* 113:875-888. <http://dx.doi.org/10.2307/4088865>

Hunt, J. W., F. W. Weckerly, and J. R. Ott. 2012. Reliability of occupancy and binomial mixture models for estimating abundance of Golden-cheeked Warblers (*Setophaga chrysoparia*). *Auk* 129:105-114. <http://dx.doi.org/10.1525/auk.2012.11093>

Jobes, A. P., E. Nol, and D. R. Voigt. 2004. Effects of selection cutting on bird communities in contiguous eastern hardwood forests. *Journal of Wildlife Management* 68:51-60. [http://dx.doi.org/10.2193/0022-541X\(2004\)068\[0051:EOSCOB\]2.0.CO;2](http://dx.doi.org/10.2193/0022-541X(2004)068[0051:EOSCOB]2.0.CO;2)

Kardynal, K. J., J. L. Morissette, S. L. Van Wilgenburg, E. M. Bayne, and K. A. Hobson. 2011. Avian responses to experimental harvest in southern boreal mixedwood shoreline forests: implications for riparian buffer management. *Canadian Journal of Forest Research* 41:2375-2388. <http://dx.doi.org/10.1139/x11-145>

- Kasson, M. T., and W. H. Livingston. 2012. Relationships among beech bark disease, climate, radial growth response and mortality of American beech in northern Maine, USA. *Forest Pathology* 42:199-212. <http://dx.doi.org/10.1111/j.1439-0329.2011.00742.x>
- Kendeigh, S. C. 1945. Nesting behavior of wood-warblers. *Wilson Bulletin* 57:145-164.
- King, D. I., R. M. Degraaf, and C. R. Griffin. 2001 Productivity of early successional shrubland birds in clearcuts and groupcuts in an eastern deciduous forest. *Journal of Wildlife Management* 65:345-350. <http://dx.doi.org/10.2307/3802914>
- Leblanc, J. P., D. M. Burke, and E. Nol. 2011. Ovenbird (*Seiurus aurocapilla*) demography and nest-site selection in response to single-tree selection silviculture in a northern hardwood managed forest landscape. *Ecoscience* 18:26-36. <http://dx.doi.org/10.2980/18-1-3381>
- Lindenmayer, D. B., and J. F. Franklin. 1997. Managing stand structure as part of ecologically sustainable forest management in Australian mountain ash forests. *Conservation Biology* 11:1053-1068. <http://dx.doi.org/10.1046/j.1523-1739.1997.96150.x>
- Löhmus, A., and P. Löhmus. 2010. Epiphyte communities on the trunks of retention trees stabilise in five years after timber harvesting, but remain threatened due to tree loss. *Biological Conservation* 143:891-898. <http://dx.doi.org/10.1016/j.biocon.2009.12.036>
- Mack, D. E., and W. Yong. 2000. Swainson's Thrush (*Catharus ustulatus*). In A. Poole, editor. *Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Martikainen, P., J. Kouki, and O. Heikkala. 2006. The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests. *Ecography* 29:659-670. <http://dx.doi.org/10.1111/j.2006.0906-7590.04562.x>
- Moldenhauer, R. R., and D. J. Regelski. 2012. Northern Parula (*Setophaga americana*). In A. Poole, editor. *Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA..
- Morse, D. H., and A. F. Poole. 2005. Black-throated Green Warbler (*Setophaga virens*). In A. Poole, editor. *Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Norton, M. R., and S. J. Hannon. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Canadian Journal of Forest Research* 27:44-53. <http://dx.doi.org/10.1139/x96-149>
- Nyland, R. D. 1998. Selection system in northern hardwoods. *Journal of Forestry* 96:18-21.
- Nyland, R. D. 2003. Even- to uneven-aged: the challenges of conversion. *Forest Ecology and Management* 172:291-300. [http://dx.doi.org/10.1016/S0378-1127\(01\)00797-6](http://dx.doi.org/10.1016/S0378-1127(01)00797-6)
- Perera, A. H., L. J. Buse, and M. G. Weber. 2004. Emulating natural forest landscape disturbances: concepts and applications. Columbia University Press, New York, New York, USA.
- Pérot, A., and M.-A. Villard. 2009. Putting density back into the habitat-quality equation: case study of an open-nesting forest bird. *Conservation Biology* 23:1550-1557. <http://dx.doi.org/10.1111/j.1523-1739.2009.01272.x>
- Pitocchelli, J. 2011. Mourning Warbler (*Geothlypis philadelphia*). In A. Poole, editor. *Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Poulin, J.-F., M.-A. Villard, and S. Haché. 2010. Short-term demographic response of an old forest specialist to experimental selection harvesting. *Ecoscience* 17:20-27. <http://dx.doi.org/10.2980/17-1-3297>
- Richardson, M., and D. W. Brauning. 1995. Chestnut-sided Warbler (*Setophaga pensylvanica*). In A. Poole, editor. *Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Roberge, J.-M., P. Angelstam, and M.-A. Villard. 2008. Specialised woodpeckers and naturalness in hemiboreal forests - deriving quantitative targets for conservation planning. *Biological Conservation* 141:997-1012. <http://dx.doi.org/10.1016/j.biocon.2008.01.010>
- Robichaud, I., and M.-A. Villard. 1999. Do Black-throated Green Warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. *Condor* 101:262-271. <http://dx.doi.org/10.2307/1369989>
- Sabo, S. R. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. *Ecological Monographs* 50:241-259. <http://dx.doi.org/10.2307/1942481>
- Schlossberg, S., D. I. King, R. B. Chandler, and B. A. Mazzei. 2010. Regional synthesis of habitat relationships in shrubland birds. *Journal of Wildlife Management* 74:1513-1522. <http://dx.doi.org/10.2193/2008-601>
- Sherry, T. W., and R. T. Holmes. 1989. Age-specific social dominance affects habitat use by breeding american redstarts (*Setophaga ruticilla*): a removal experiment. *Behavioral Ecology and Sociobiology* 25:327-333.
- Sherry, T. W., and R. T. Holmes. 1997. American Redstart (*Setophaga ruticilla*). In A. Poole, editor. *Birds of North*

America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Sólymos, P., S. Lele, and E. Bayne. 2012. Conditional likelihood approach for analyzing single visit abundance survey data in the presence of zero inflation and detection error. *Environmetrics* 23:197-205. <http://dx.doi.org/10.1002/env.1149>

Steele, B. B. 1992. Habitat selection by breeding Black-throated Blue Warblers at two spatial scales. *Ornis Scandinavica* 23:33-42. <http://dx.doi.org/10.2307/3676425>

Straus, M. A., K. Bavrlic, E. Nol, D. M. Burke, and K. A. Elliott. 2011. Reproductive success of cavity-nesting birds in partially harvested woodlots. *Canadian Journal of Forest Research* 41:1004-1017. <http://dx.doi.org/10.1139/x11-012>

Thorpe, H. C., S. C. Thomas, and J. P. Caspersen. 2008. Tree mortality following partial harvests is determined by skidding proximity. *Ecological Applications* 18:1652-1663. <http://dx.doi.org/10.1890/07-1697.1>

Tittler, R., S. J. Hannon, and M. R. Norton. 2001. Residual tree retention ameliorates short-term effects of clear-cutting on some boreal songbirds. *Ecological Applications* 11:1656-1666. [http://dx.doi.org/10.1890/1051-0761\(2001\)011\[1656:RTRAST\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2001)011[1656:RTRAST]2.0.CO;2)

Toms, J. D., F. K. A. Schmiegelow, S. J. Hannon, and M.-A. Villard. 2006. Are point counts of boreal songbirds reliable proxies for more intensive abundance estimators? *Auk* 123:438-454. [http://dx.doi.org/10.1642/0004-8038\(2006\)123\[438:APCOBS\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2006)123[438:APCOBS]2.0.CO;2)

Tozer, D. C., D. M. Burke, E. Nol, and K. A. Elliott. 2010. Short-term effects of group-selection harvesting on breeding birds in a northern hardwood forest. *Forest Ecology and Management* 259:1522-1529. <http://dx.doi.org/10.1016/j.foreco.2010.01.028>

Vanderwel, M. C., J. R. Malcolm, and S. C. Mills. 2007. A meta-analysis of bird responses to uniform partial harvesting across North America. *Conservation Biology* 21:1230-1240. <http://dx.doi.org/10.1111/j.1523-1739.2007.00756.x>

Vanderwel, M. C., S. C. Mills, and J. R. Malcolm. 2009. Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. *Forestry Chronicle* 85:91-104. [online] URL: http://www.clas.ufl.edu/users/mark.vanderwel/pdfs/vanderwel_et_al_20-09_ForestryChronicle.pdf

Villard, M.-A., and B. G. Jonsson. 2009. *Setting conservation targets for managed forest landscapes*. Cambridge University Press, Cambridge, UK.

Vitz, A. C., and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biological Conservation* 127:477-486. <http://dx.doi.org/10.1016/j.biocon.2005.09.011>

Walters, E. L., E. H. Miller, and P. E. Lowther. 2002. Yellow-bellied Sapsucker (*Sphyrapicus varius*). In A. Poole, editor. *Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.

Work, T. T., J. M. Jacobs, J. R. Spence, and W. J. Volney. 2010. High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests. *Ecological Applications* 20:741-751. <http://dx.doi.org/10.1890/08-1463.1>

Appendix 1.

Table A1.1. Year-specific treatment effects on density of Black-throated Green Warbler, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	1.06	0.295
Post-harvest (1) controls vs. treated plots	1.22	0.229
Post-harvest (2) controls vs. treated plots	2.76	0.009
Post-harvest (3) controls vs. treated plots	1.80	0.080
Post-harvest (4) controls vs. treated plots	1.95	0.059
Post-harvest (5) controls vs. treated plots	2.46	0.019

Table A1.2. Year-specific treatment effects on density of Northern Parula, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	-0.46	0.650
Post-harvest (1) controls vs. treated plots	-0.81	0.424
Post-harvest (2) controls vs. treated plots	-1.47	0.150
Post-harvest (3) controls vs. treated plots	0.52	0.609
Post-harvest (4) controls vs. treated plots	-0.16	0.877
Post-harvest (5) controls vs. treated plots	-1.17	0.250

Table A1.3. Year-specific treatment effects on density of Yellow-bellied Sapsucker, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	0.33	0.747
Post-harvest (1) controls vs. treated plots	1.08	0.288
Post-harvest (2) controls vs. treated plots	0.20	0.842
Post-harvest (3) controls vs. treated plots	-0.08	0.941
Post-harvest (4) controls vs. treated plots	0.50	0.619
Post-harvest (5) controls vs. treated plots	-0.53	0.602

Table A1.4. Year-specific treatment effects on density of Swainson's Thrush, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	0.76	0.454
Post-harvest (1) controls vs. treated plots	1.42	0.163
Post-harvest (2) controls vs. treated plots	0.24	0.810
Post-harvest (3) controls vs. treated plots	1.48	0.146
Post-harvest (4) controls vs. treated plots	0.30	0.764
Post-harvest (5) controls vs. treated plots	-2.54	0.015

Table A1.5. Year-specific treatment effects on density of Mourning Warbler, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	0.00	1.000
Post-harvest (1) controls vs. treated plots	1.62	0.112
Post-harvest (2) controls vs. treated plots	0.00	1.000
Post-harvest (3) controls vs. treated plots	-9.22	<0.001
Post-harvest (4) controls vs. treated plots	-6.52	<0.001
Post-harvest (5) controls vs. treated plots	-9.03	<0.001

Table A1.6. Year-specific treatment effects on density of Chestnut-sided Warbler, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	0.00	1.000
Post-harvest (1) controls vs. treated plots	-0.85	0.402
Post-harvest (2) controls vs. treated plots	-0.36	0.722
Post-harvest (3) controls vs. treated plots	-3.10	0.004
Post-harvest (4) controls vs. treated plots	-2.49	0.017
Post-harvest (5) controls vs. treated plots	-4.31	<0.001

Table A1.7. Year-specific treatment effects on density of Black-throated Blue Warbler, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	-1.35	0.184
Post-harvest (1) controls vs. treated plots	0.07	0.943
Post-harvest (2) controls vs. treated plots	-0.92	0.362
Post-harvest (3) controls vs. treated plots	-1.39	0.173
Post-harvest (4) controls vs. treated plots	-2.11	0.041
Post-harvest (5) controls vs. treated plots	-2.33	0.025

Table A1.8. Year-specific treatment effects on density of American Redstart, according to multiple comparison analyses (DF = 40).

Test	<i>t</i> -value	<i>P</i> -value
Pre-harvest controls vs. treated plots	0.65	0.518
Post-harvest (1) controls vs. treated plots	-1.56	0.127
Post-harvest (2) controls vs. treated plots	-0.82	0.420
Post-harvest (3) controls vs. treated plots	-1.55	0.129
Post-harvest (4) controls vs. treated plots	-1.63	0.111
Post-harvest (5) controls vs. treated plots	-1.14	0.261