Canadian Journal of Forest Research
Revue canadienne de recherche forestière

**Resident and cavity-nesting avian community is affected by
amount but not age of white pine in central Ontario mature
mixedwood forests**

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2015-0477.R1
Manuscript Type:	Article
Date Submitted by the Author:	29-Feb-2016
Complete List of Authors:	Thompson, Ian; Canadian Forest Service Wiebe, Philip; Canadian Forest Service Kirk, David; Aquila Applied Ecologists
Keyword:	old growth, cavity nesters, resident birds, white pine, selection harvesting

**Resident and cavity-nesting avian community is affected by amount but not age of white pine
in central Ontario mature mixedwood forests**

Ian D. Thompson, Canadian Forest Service, 1219 Queen St. east, Sault Ste. Marie, Ontario,
Canada P6A 2E5 (ian.thompson@canada.ca)

Philip Wiebe, Canadian Forest Service, 1219 Queen St. east, Sault Ste. Marie, Ontario, Canada
P6A 2E5 (philip.wiebe@canada.ca)

and

David. A. Kirk, Aquila Conservation and Environmental Consulting, Ottawa, Ontario, Canada
(david.kirk1@sympatico.ca)

Corresponding author:

Ian Thompson

Canadian Forest Service,

1219 Queen St. east, Sault Ste. Marie, Ontario, Canada P6A 2E5

Email: ian.thompson@canada.ca

Tel: 705 541 5644

Fax: 705 541 5700

Abstract

Forests with old growth white pines have been severely reduced compared to historical levels. We examined resident and cavity-nesting bird species abundances in winter and the breeding season because some of these species may prefer old forest habitats for breeding. We counted birds over 10 years in four mixedwood types: old pine, mature pine, mature non-pine, and selection-harvested stands. We expected that old pine stands would be selected by some species because of abundant snags and large trees for foraging. We assessed habitat use among years, and changes following harvesting. Counts of nomadic species varied across years but counts for others did not. Species used old and mature pine mixedwoods equally and more than non-pine or harvested stands in winter and for breeding, but old stands were not preferred. Important variables included percent pine and large tree density. Selection harvesting benefitted yellow-bellied sapsuckers but reduced counts of black-capped chickadees and brown creepers. Black-capped chickadees changed habitats between seasons and in some years. Black-backed woodpeckers were most common in pine stands but abundant in harvested stands for 2 years following cutting. Regardless of stand age, large (>40 cm) pines provide important habitat for residents and cavity-nesters.

Keywords: old growth, cavity nesters, resident birds, white pine, selection harvesting.

Introduction

Loss of primary forests is a global concern as a result of unsustainable use in many areas, because of the long time period for forest recovery, stand degradation, and uncertainty

over the quality of second-growth forests to sustain the original biodiversity (Thomas et al. 1988, Mosseler et al. 2003, Blaser et al. 2012). In eastern Canada, long-lived tree species, including white pine (*Pinus strobus*) and red pine (*P. resinosa*), occur in the Great Lakes-St. Lawrence forest type and the most southern parts of the boreal forest (Rowe 1972). These pine forests, in pure or mixedwoods with 30 to 80% pine by basal area, have been logged for centuries, starting early in the 1600s for wooden ships and continuing until the present for sawn wood (Aird 1985, Wray 1986). This long history of pine logging, coupled with fire suppression, which reduces the rate of natural regeneration (Carleton 2003), has resulted in only a few remaining fragmented primary old-growth pine forest stands and the loss of this forest type over much of the region (Thompson et al. 2006, Venier et al. 2014).

The vast reductions of old growth pines, from pure and mixedwood stands in Ontario has led to concerns about the distinct biodiversity that might be supported in these forests (Welsh et al. 1992, Venier et al. 2014). In an earlier study, Kirk et al. (2012) assessed the value of mature and old red pine and white pine mixedwood forests in Ontario as avian habitats and found that age and size (diameter) of pine in these stands contributed to breeding habitat selection by several species. They derived models implicating old growth conditions as important for some resident and cavity-nesting species including brown creeper, red-breasted nuthatch, and pileated woodpecker (see Appendix 1 for scientific names). These species use cavities or dead trees to nest, and the pileated woodpecker is a management indicator species in Great Lakes-St. Lawrence Forest type in Ontario (Ontario MNRF 2015). Brown creeper and boreal chickadee are species that have been suggested as old forest specialists in several studies, both in mixed transition forests (Poulin et al. 2008) and in the boreal forest to the north

(Drapeau et al. 2000, Thompson et al. 2014). Hence, these species may be declining with the loss of old-growth forest habitats (Venier et al. 2014). An important structure that is usually more abundant in old growth than mature forests is snags (Smirnova et al. 2008, Vaillancourt et al. 2008), which are important for roosting, feeding, and breeding by cavity nesters and many resident species (Hejl et al. 2002, Lemaitre and Villard 2003, Poulin et al. 2008, Straus et al. 2011). Similarly, very large live trees, such as white pine and red pine, in old growth forests provide a foraging resource for many avian species (Connor 1981, Weikel and Hayes 1999).

Here, we build on the earlier work of Kirk et al. (2012), with a study during an 11-year period, to assess the importance of old pine mixedwood stands specifically for resident birds and the non-resident cavity-nesters on an annual basis, in spring for breeding and over winter for food and shelter. For the resident birds, individual fitness is affected by the quality of overwintering habitats where they have to survive harsh winter conditions, as well as by the quality of spring breeding habitats (Desrochers et al. 1988, Straus et al. 2011). We asked the following five questions: 1.) does age of pine and amount of pine in a stand affect resident and cavity-nesting species habitat selection in spring and in winter for residents? We asked this question because of the preference of forest managers to cut white and red pines before the old growth stage. Our hypothesis was that old growth stands would have more snags and more large trees than mature stands, and so should be more important to breeding birds and winter foraging than stands without large pines (Flemming et al. 1999, Harestad and Keisker 1999, Nappi et al. 2015). 2.) Are winter densities equivalent among years, or are there some years in which old growth pine or other stands are especially important to some species? For the latter question, we expected that nomadic (irruptive) species that feed on mast, such as pine siskins, crossbills,

and pine grosbeaks, might invade stands with a high density of pines during years with abundant mast (Koenig and Knops 2001). 3.) Based on differing responses of bird species to selection harvesting (Gram et al. 2003, Poulin et al. 2010), we assessed whether or not selection harvesting for large pines would reduce the nesting density of cavity-nesting species. Finally, with respect to inter-annual bird abundances and species composition, we asked two questions. First, 4.) does winter abundance predict spring breeding density of resident species? This question is of interest because of the potential for censusing indicator species in winter, rather than during spring breeding. Several authors have noted differences in foraging behaviours and habitat preferences between summer and winter for various resident species (Kilham 1965, Connor 1981, Gow et al. 2013) and dissimilarity in seasonal habitat use has management implications. Our last question was 5.) does habitat selection vary within species across years? Most avian studies are conducted over a much shorter term and so cannot address this question of change in habitat use that may occur as a result of changes in resources (e.g., food) among years.

Methods

Study area

Our study area was located in the Lower Spanish Forest Management Unit, north of Espanola and west of Sudbury, Ontario, in an area of transition between southern temperate mixedwood forests and the northern boreal zone. We selected the area because it still maintained large stands of old growth (>120 yrs) and mature (90-120 yrs) white pine and red

pine mixedwoods in forest reserves. The topography was hilly and rough with frequent rock outcrops and cliffs, surrounding numerous large lakes, and underlain by coarse glacial tills. Winter temperatures were below -40 C for extended periods and summer temperatures rose to near 35 C. Colder winters were common when the study began in 1995 but less cold winters generally prevailed after 1998. We conducted our winter study from spring 1995 to 2005, with no data collection in winter 1999-2000 because the main access road was not ploughed. We sampled breeding birds in spring from 1999-2007.

We sampled forest stands in four types of mixedwoods, where pine ranged from 30 to 80% of the basal area: old growth pine (n = 6), mature pine (n = 7, n = 6 after 2003), mature non-pine (80-120 yrs, with <20% basal area in pine) (n = 4), and selection-logged former pine dominated stands (n = 4, n = 5 after 2003). Of the latter stands, we could only sample two in winter (3 after 2003) and so these data were not used in analyses. Dominant deciduous species were trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and sugar maple (*Acer saccharum*), with some yellow birch (*B. alleghaniensis*). Dominant conifers, other than pines, were black spruce (*Picea mariana*), white spruce (*P. glauca*), and balsam fir (*Abies balsamea*). The selection-harvested stands were logged primarily for large pines in the first year of the study, with one or two pines/ha left as seed trees. These four stands were the only ones available on the study area. A mature pine stand was selection-logged in 2003 and so changed type, and increased our sample of harvested stands to 5 for the last 4 years of summer study.

Data collection

111 Avian sampling

112 We censused birds in winter (January or February) and in spring (May to late June).

113 Most of the same stands/plots were used in many years but some could not be censused in all
114 years owing to impassible winter access. Regardless, our sample was a minimum of five plots
115 for all unmanaged stand types. For winter surveys, one fixed square 0.49 km² plot (700 x 700
116 m) was established in each stand, located 100 m from an edge or other stand type on all sides.
117 In summer, we used a smaller 0.25 km plot (500 x 500 m) that was centred within the winter
118 plot.

119 In winter, we sampled birds on four parallel transects 175 m apart and along the joining
120 lines between the long transects, which covered the entire plot such that no part of the plot
121 was more than 87 m from an observer. A single observer walked slowly along the transects,
122 stopping frequently and recording all birds seen or heard, including those flying over the plot.
123 Quiet 'pishing' was used in winter, if necessary, to draw already-detected birds to the observer
124 for identification. Time on plot varied among observers and plots, ranging from 2.5 to 3.5 hrs,
125 mostly owing to terrain differences on the plots. We censused two plots per day, after testing
126 results from six plots showed that the number and species of birds detected in the morning and
127 afternoon did not differ. Winter surveys were done during late January and early February, and
128 late February to early March. In the last several years of the study, we could only make one
129 winter trip and the late period was selected for the census.

130 In spring, surveys were done from mid-May until late June. We used call playbacks to
131 census woodpeckers (e.g., Hoyt and Hannon 2002) with a mixture of calls and drumming of
132 each species was played, individually in a sequence of 1 minute followed by 3 minutes of

silence, three times at each station. There were nine stations on each plot, such that no point on the plot was located more than 50 m from a playback station. We adjusted the volume of all playback cassette player and speaker combinations so that we could hear the calls faintly at 50 m. Resident species (other than woodpeckers) were recorded when seen or heard singing/calling at each listening station during the playback period and during an additional 5-min listening period after the playbacks, for an unlimited distance (Welsh 1995). Spring plots were only censused in mornings until 10:30 hrs.

In spring and winter, we used plot maps to aid in determining if a bird may have been detected more than once, by mapping the approximate location when first heard and any subsequent movements by the bird, and all obvious duplicates were only counted once. Plots were not censused if the wind exceeded 20 kmh, or on days when it was snowing heavily or raining. Plot surveys were discontinued if winds came up during the census and the plot was re-started on another day.

Vegetation sampling

Stands were surveyed for tree (>10 cm dbh), small tree (<10 cm dbh, >3 m tall), snag (dead tree), and shrub (<3 m tall) densities, heights, diameters, and species composition. Woody vegetation data were collected systematically at 50 or 100 points per stand, depending on variance after 50 points, 20 to 30 m apart along random transects across the entire stand, using the point-distance technique of Batcheler (1975). Stand basal area was determined by multiplying stem density by the average diameter for each species and then summed. The point-distance method corresponds well to values for basal area determined using standard

forest inventory prism plots (Thompson et al. 2006). The age of each stand and species was taken from government forest resource inventory maps.

Cavity searches

In spring of each year, we searched two to four plots of each forest type to determine the number of cavities present and to attempt to locate nests. Four observers walked parallel lines a few metres apart, examining all trees on the plots for possible cavities. Cavities accessible either by climbing or using a 4 m ladder were all examined. Cavities larger than 2 cm and lower than 16 m were examined with a remote camera mounted on a telescoping pole. Cavities located above 16 m could only be estimated, by using binoculars, as either nesting or feeding, unless birds were seen using the hole. We recognize the inherent difficulties with finding cavities (Harper et al. 2004, Ouellet-Lapointe et al. 2012) and that cavities above 16 m were likely overestimated as useable, although few cavities were above that height.

Treatment and analysis of data

Avian detections were linearly related to time on winter plots ($r^2 = 0.55$, $P < 0.01$), so we first standardized census data by using the catch-per-unit-effort (CPUE) method to adjust each plot count of birds to 3 hours sampling duration. For the years 1995-1998, two visits were made in winter to sites, whereas for other years (1999-2005) only one visit was made in February. To rectify this uneven sampling effort, we randomly selected one of the two visits from 1995-1998. (Taking the maximum or mean count of the two visits could have biased the counts for the sites that were visited twice.)

We created separate data matrices for the winter and spring bird data, and a separate dataset with matched winter and spring plots for those species that occurred in both seasons. The spring data were the number of birds of each species, with territorial individuals counted as two and possibly unmated birds counted as an individual. We combined these counts to make them equivalent to counts of birds done during the winter period, adjusted to plot size. We pooled bird species into functional groups based on their cavity-use and residency status (see Appendix 1). We calculated Simpson's diversity index individually for all sites.

Statistical analyses

Winter and spring data were analysed separately. For single species, functional groups, nomads, and the Simpson's diversity index, we used generalized linear mixed models (GLMM) to determine the importance of habitat characteristics on abundance and diversity. Abundance of single species, pooled abundance for functional groups and Simpson's Diversity Index were used separately as response variables and stand structural variables and year as predictors. For Simpson's index, we used Box-Cox normality plots to determine the best power transformations based on a Gaussian error family. For all of the other response variables, which were count data, we used a Poisson error family with log-link. For all models, we included year as a random factor to account for repeated measures because of possible temporal autocorrelation, as our surveys were conducted at the same sites for 10 years.

Small sample sizes of each forest type limited the number of variables that could be included in each regression model, so we chose to use model averaging for parameter estimation according to methods recommended by Burnham and Anderson (2002), and AICc

(Akaike's Information Criteria, corrected for small sample size) as the selection criterion. From global models that included stand type, percent pine in the stand, basal area of the stand, and density of snags in the stand as fixed effects, we compared all subsets that included three or fewer variables. Parameter estimates were averaged over all models included in the 95% confidence set that included each variable. Conditional averages were reported instead of full-model averages because not all variables had the opportunity to be included in all models. The importance of each variable was calculated by summing the AICc weights of all of the models in the 95% confidence set that included that variable.

For each instance where the model-averaged stand type parameter estimates indicated that there were significant differences among levels, post-hoc multiple comparison tests were conducted on a GLMM model that included each of the variables that had 95% confidence intervals that did not include 0 to determine where differences existed. Tukey's method was used to adjust the confidence limits based on the number of tests conducted.

We used GLMMs to test for differences in the proportion of birds in particular stand types between winter and spring census periods. Odds ratios were used as response variables consisting of counts of each bird species within plots compared with the total number of birds of the same species in all other plots from the same census season. A binomial family of errors was used with a logit link. Stand type nested within year were designated as random factors to pair similar stands within years and account for the repeated measures. We designated year as a random effect and where season and stand type plus an interaction term were fixed effects. A significant interaction or difference by season would indicate differences in proportion of species within a particular stand type between seasons. To test for differences between winter

219 and spring counts, we used counts for the 6 years for which we able to sample in both winter
220 and spring in the same year.

221 For species that were known to nest in snags, we used general additive model (GAM)
222 plots and GLMM models to test for non-linear relationships with snag density that might
223 indicate thresholds up to which snag density might be a limiting resource. If snag density was
224 limiting, but only up to a certain level, then we expected to observe significant curve
225 parameters using quadratic terms for snag density that indicated a hump-shaped relationship
226 peaking at intermediate snag densities, but not decreasing substantially at the high end of
227 values measured. Snag densities within stands were positively skewed and were transformed
228 to improve model performance. Box-Cox normality plots indicated the best power
229 transformation was -1 (inversion). Nesting season counts were used with weak cavity nesters,
230 black-capped chickadees, red-breasted nuthatches, and brown creepers.

231 To test for differences in habitat selection among years, we constructed GLM or GLMM
232 models that included species counts as the response, stand type as an explanatory variable, and
233 three different forms of year as explanatory variables. For each species that contained at least
234 100 observations across all years for a season, plus brown creepers, we compared three models
235 using AICc and calculated the Akaike weight for each: year as a random intercept, year as a
236 fixed intercept, and year as a fixed intercept plus an interaction with stand type. If the AICc
237 comparison indicated that the latter model was the most parsimonious, then we accepted this
238 as evidence for differences in habitat selection among years.

239 We examined generalized linear mixed models (GLMM) in the R-statistical package
240 (version 3.2.0; R Core Team 2015), using package lme4 (version 1.1-8; Bates et al. 2015). Multi-

model inference and parameter estimation was conducted using package MuMIn (version 1.15.1; Barton 2015). Multiple comparison tests were conducted using the multcomp package (version 1.4-0; Hothorn, Bretz and Westfall 2008). For GAM model plotting, we used the mgcv package (Wood 2011).

Results

Avian species composition and abundance

The most common resident birds recorded in winter, totalled for the 11 years, in rank order were: black-capped chickadee, red-breasted nuthatch, downy woodpecker, common redpoll, and white-winged crossbill (Figures 1 and 2, Appendix 2). In spring, the rank order of the most common resident and/or cavity-nesting species was black-capped chickadee, red-breasted nuthatch, and downy woodpecker (Figures 3 and 4, Appendix 3). White-winged crossbills and pine siskins, while common in winter, were irruptive and rarely present in the spring. We recorded 17 other resident species (total resident species = 22) although some, such as three-toed woodpecker, were seldom seen. Among the migrant cavity-nesting species, yellow-bellied sapsucker was the most abundant species (total cavity-nesting species = 9), surpassing all other species in abundance for all stand types in most years.

There were no differences in the abundances of common species among years for either season ($P_s > 0.05$), although numbers fluctuated considerably (Figures 1 to 4). Among the winter nomadic bird species, white-winged crossbills were only abundant from 2003 to 2005, occurring mostly in old and mature pine stands, compared to a very few individuals in most

other years or stand types (Figure 2). Other irruptive species included pine siskins that were common in 2003, common redpolls that were abundant only in 2001, red crossbills that were most common in 1997 but absent after that, and pine grosbeaks that were relatively abundant in 2003 but with few individuals recorded in only two other years.

Stand variables

We found no difference in the mean number of snags/ha among the four stand types, which within stand types ranged from 16.2 ± 3.2 to 48.1 ± 3.1 /ha. There was a significantly lower tree basal area in the selection logged stands (9.4 ± 1.8 m²/ha) than in the other stand types ($P < 0.001$), where the basal areas did not differ (stand range 17.0 ± 0.9 to 20.0 ± 1.2 m²/ha). The basal area of large trees (>40 cm) was the same in old and mature pine types (10.4 and 8.9 m²/ha, respectively) but significantly higher than in the non-pine mixedwoods (1.0 m²/ha) and the selection harvested stands (2.2 m²/ha) ($P < 0.001$). Large tree density was correlated to total tree basal area in the stand. Our pine stands varied in amount of pine from 30 to 84% of the tree basal area, with significantly more pine in the two pine types than the other two stand types ($P < 0.001$).

Stand variables influencing winter bird species abundance and composition

In winter, stand type was important for weak cavity excavators, residents, and for six among 14 species, excluding ravens (Table 1). Species richness was the same for all three stand types. For those species with models implicating stand type as significant, mature and old growth pine was used most by weak cavity excavators, residents, back-capped chickadee, red-

breasted nuthatch, and pine siskin (Table 2). Old growth pine was not the most used type for any group or species. Percent pine was a significant variable for residents, nomads, and four species (but negative for boreal chickadee). Tree basal area was significant for weak cavity excavators, residents, and six species (negative for pine siskin, black-backed woodpecker, and pine grosbeak). Number of snags/ha had a negative effect for overall species richness, weak cavity excavators, residents, and black-capped chickadee, and was positive for pine siskin, an irruptive species in our area.

Stand variables influencing breeding cavity-nesting bird species composition and abundance

In the breeding season, stand type influenced the strong excavator guild, non-residents, and six of the nine common breeding species (Table 3), but none of those species preferred old growth pine stands (Table 2). Species composition did not differ among the four stand types. Black-capped chickadee and brown creeper used harvested stands least and brown creepers were most common in old and mature pine mixedwoods (Table 2). Strong cavity excavators preferred selection harvested stands, where we recorded the highest counts of yellow-bellied sapsuckers (Figure 3). Percent pine was positively related to abundance in models for black-backed woodpecker and brown creeper and was negative for yellow-bellied sapsuckers. Selection harvesting reduced stand use significantly by black-capped chickadee and brown creeper. Stand basal area (or its correlate large trees) was important for weak cavity excavators. Snags was positive for yellow-bellied sapsuckers, slightly negative for pileated woodpeckers, but had no effect in models for any of the weak cavity excavators (Table 3). We

also tested subsets of snags in small (10-19 cm dbh) and large size (≥ 20 cm dbh) classes in our models but found the same non-effect.

In a post-hoc fashion, we tested the relationship between numbers of snags and numbers of breeding birds of each species to determine if the number of snags might be so numerous as not to limit breeding sites. We saw no relationship between the number of snags and bird abundance for red-breasted nuthatches, from the GAM plots and polynomial GLMM models. For brown creeper, we observed an inflection point at 20 snags/ha ($P < 0.06$) and for black-capped chickadee there was a clear inflection point at 14 snags/ha ($P < 0.04$).

Selection harvesting had no effect on species richness and six of our nine breeding species, a positive effect for two woodpeckers, and a negative effect on brown creeper and black-capped chickadee (Table 2). Although we observed low variance among years for breeding cavity-nesting species, we noted a significant decline in the number of black-backed woodpeckers breeding in our selection harvested stands in the third year after the stands had been harvested (Figure 3, $z = 2.61$, $P < 0.01$). Further, the number of black-backed woodpeckers breeding in harvested stands was significantly higher than in all other stand types for the first 2 years post-harvest, after which counts then declined to levels similar to those in the other stands ($z = 2.76$, $P < 0.01$).

Nest sites

We documented 47 nest sites of eight cavity-nesting species on or near our plots. Of these nests, 68% were in trembling aspen, and 62% were in live trees and 38% were in snags. Most nests that we located were of red-breasted nuthatch (11; 9 in snags) and yellow-bellied

sapsucker (18; 15 in live trees). Aspen used by small woodpeckers ($n = 21$) had a mean dbh of 33.5 cm, while pileated woodpeckers ($n = 3$) used larger aspen with a mean diameter of 53 cm, all of which were in old growth stands. We found four nests in large diameter declining old white pine, three of which were common flickers. For the weak cavity excavators, 10 of 12 nests were in snags (9 red-breasted nuthatch and 1 black-capped chickadee).

Abundance of resident birds in winter relative to spring

With the exception of black-capped chickadees and black-backed woodpeckers in mature pine, abundances in winter did not differ from breeding counts in spring ($P_s > 0.05$). Numbers of black-capped chickadees did not differ in old pine or non-pine mixedwoods, but counts in mature pine were significantly higher in winter than in spring ($P < 0.01$). Therefore, for most species, winter counts predicted the numbers of spring breeders. Counts in selection harvested stands in winter were high by inspection, but the sample was insufficient to test.

Relative abundances of bird species within habitat types over 10 years

For spring breeding birds, no models with an interaction between stand type and year were more parsimonious than models without an interaction, indicating that the relative abundances among stand types did not change for any species over the 10 years of study (Table 4). The result was the same for all species in winter, except for black-capped chickadees that differed in relative abundances among stand types in some winters (Table 4).

Discussion

Contrary to our expectation, old growth pine mixedwoods was not a preferred habitat for any resident or cavity-nesting species, for breeding or over-wintering. No species selected white pine/red pine mixedwood stands more than the non-pine mixedwood types for breeding and old growth pine and mature pine mixedwoods had similar importance levels in all cases, in either spring or winter. In winter, old pine stands were not used more by resident birds than either mature pine or non-pine, depending on the species or group. Part of the reason for that result may have been that old growth and the other forest types maintained similar numbers of snags, and that the numbers of large trees in both pine age classes was also similar. The amount of pine in the stands, however, was a significant positive variable for several species and guilds, both for breeding and over-wintering, as also found by Kirk et al. (2012).

Amount of pine, and large pines in particular, may have provided good foraging substrates for many wintering birds, especially for residents as a guild, and white-winged crossbills that were a common nomadic species. Connor (1981) observed an increase in foraging on pines in winter by downy and hairy woodpeckers, and pileated woodpeckers are well-known to seek carpenter ant galleries in old and mature pine trees (Lemaitre and Villard 2005). Brown creepers forage on large trees with deeply furrowed bark and red-breasted nuthatches also prefer large trees for foraging (Weikel and Hayes 1999, Farris et al. 2010). Large trees support more arthropods, including eggs and larvae than smaller trees (Mariani and Manuwal 1990, Farris et al. 2010) and mature and older white and red pines, with their deeply furrowed bark, likely provided this resource in our area. Percent pine in a stand was also important to white-winged crossbills although they did not favour pine stands and to pine siskins that used pine stands more than non-pine stands; both latter species are well-known to

forage on pine seeds (Koenig and Knops 2001). Total abundance of nomads did not, however, vary among stand types and this may have been because the other abundant nomadic species, common redpolls, feed mostly on seeds of deciduous species (Martin et al. 1951, Kennard 1976). Black-capped chickadees forage for insects on many tree and shrub species, often favouring deciduous trees (Holmes and Robinson 1981, Hill and Lien 1988, Gayk and Lindsay 2012), but also feed on mast. Black-capped chickadees preferred pine mixedwoods in the winter possibly for both mast from pines and foraging resources on the deciduous component. Our data indicated that resident birds do not distinguish between old growth and mature pine stands but the presence of large pine trees (correlated to basal area in our models) was likely a key foraging habitat for many resident species.

Pine was important for two species during the breeding season. For breeding black-backed woodpeckers, the importance of pine was probably related to foraging opportunities on the several species of bark beetles (Scolytidae) that are associated with both red and white pines in eastern North America (Rose and Lindquist 1984). Black-backed woodpeckers forage preferentially on large conifer trees in old forests (Villard 1994, Tremblay et al. 2009, Nappi et al. 2015). Similarly, brown creepers forage for arthropods preferentially on large conifer trees with rough bark, such as old pines, at all times of the year (Franzreb 1985, Adams and Morrison 1993, Poulin et al. 2008). Poulin et al. (2008) suggested a threshold of 127 large trees/ha (>30 cm), above which brown creepers were likely to nest in old forests in New Brunswick. On our area, mature and old pine stands had an average of more than 228 trees/ha >30 cm, but our non-pine mixedwoods that were used equally by brown creepers had a mean of 94 large trees/ha. On the other hand, selection harvested stands, with significantly fewer brown

394 creepers, had only 64 large trees/ha. This would suggest that brown creepers in eastern
395 transition mixedwoods may need as few as 94 large trees/ha for breeding, somewhat less than
396 was required in New Brunswick. In our mixedwood forests, brown creepers may have required
397 fewer large trees than was suggested in New Brunswick because many of largest trees on our
398 study area exceeded 40 cm dbh providing a much greater foraging surface than a 30 cm tree.
399 Kirk et al. (2012) showed a 33% probability of occurrence of brown creepers with 62 stems/ha
400 of medium and large pines. Thresholds are of direct management interest because they enable
401 direction for key variables for planning.

402 Snags provide another important foraging and nesting substrate for residents and
403 woodpeckers (e.g., Kisiel 1972, Lemaître and Villard 2005, Nappi et al. 2015) and so the lack of a
404 difference in snag density among our stand types could partly explain the similar use that we
405 observed for many species. Although less use is made of snags for nesting by woodpeckers
406 than live trees in general (Peck and James 1983, Tozer et al. 2011), snags are used by some
407 woodpeckers to nest and by weak-cavity excavators (Harestad and Keisker 1988, Hejl et al.
408 2002). For weak cavity excavators, the lack of a relationship between numbers of snags and
409 breeding pairs was unexpected because these species usually nest in dead trees, or under the
410 bark of dead trees in the case of brown creepers (Davis 1978). Our data for red-breasted
411 nuthatch also indicated a preference for nesting in snags and the lone black-capped chickadee
412 nest that we found was in a small broken dead white birch stem. Some authors have also found
413 no correlation between breeding cavity nesters and snag or hole density (Waters et al. 1990,
414 Carleson et al. 1998, Spiering and Knight 2005), while others have reported nest site limitation
415 for cavity nesters (Brush 1983, Miller 2010). We found no relationship in our models between

breeding density and snags for any species but we did find evidence of a threshold for snags for two of the three weak cavity excavator species tested. Elsewhere, Guenette and Villard (2005) and Poulin et al. (2008) suggested that a threshold for occurrence and breeding of brown creepers was about 56 snags/ha in New Brunswick substantially higher the value of 20/ha that our data suggested. Their Atlantic forests were largely balsam fir and black spruce that we suspect provided much lower quality nesting snags than pine mixedwoods. The characteristic thick bark of pines hangs in sheets on dead trees for several years providing nesting cover unlike the thin bark of balsam fir that provides little cover. As a result, more snags are likely necessary in New Brunswick spruce-fir forests, than in our mixedwoods, to ensure sufficient snag quality for nesting brown creepers. Tremblay et al. (2015) suggested that black-backed woodpeckers would use stands with 200 snags/ha in boreal forests, which was about four to five times more than occurred in any of our stands and yet this species nested in comparable density in our forests. The latter comparisons for a snag thresholds between regional forest types, similar to the comparison above for large trees, clearly shows that thresholds for specific variables influencing species' life histories need to be developed independently for different forest ecosystems.

From the few published records, woodpeckers use larger trees than the stand mean dbh for nesting, although the reported required sizes vary among those few studies. In boreal and transition forests of eastern North America, trees with a dbh >20-33 are common for nesting by small woodpeckers (Peck and James 1983, Ouellet-Lapointe et al. 2012, Tremblay et al. 2015), while pileated woodpeckers nest in trees with a dbh >35 cm (Peck and James 1983, Towers et al. 1992). Our nest tree diameter data were similar to these values. Regardless,

there is surprisingly little available information on tree sizes selected for most nesting by cavity-nesting bird species in eastern temperate and transition forests.

Selection harvesting has previously been found to have negative effects on some cavity-nesting species through the removal of large trees and the loss of snags (Poulin et al. 2010, Tozer et al. 2010, Straus et al. 2011), and positive or neutral effects for other species (Mancuzzo et al. 2008, Tozer et al. 2010, Straus et al. 2011). Our results also indicated positive, neutral, and negative effects depending on the species. For brown creepers, loss of large foraging trees and appropriate nesting snags was likely responsible for the observed decline in logged stands. Poulin et al. (2010) attributed a decline of brown creepers in partially harvested New Brunswick forests to foraging opportunity limitation as well. Yellow-bellied sapsuckers responded positively to selection harvesting, where they nested almost exclusively in large remaining aspens. Impacts of selection harvesting on sapsuckers has had different effects: in southwestern Ontario, lower densities of this species occurred following partial harvesting, while Mancuso et al. (2014) found little effect on breeding density in eastern Ontario. We did not follow the success of individual nests but Tozer et al. (2009) reported lower nesting success by sapsuckers in open stands following partial harvesting, suggesting that density alone may not be a good indicator of fitness.

Black-backed woodpeckers generally occur in old forests in low densities but are attracted to burned areas with their short-term abundant food resources (Hannon and Drapeau 2005). We found that black-backed woodpeckers increased their use of selection harvested stands for at least 2 years following harvesting to densities exceeding those in our uncut forests and equivalent to counts reported in some burned forests, where numbers also decline after 2-

3 years (Murphy and Lenhhausen 1998, Hobson and Schieck 1999). In burned areas, increased density of these woodpeckers is attributed to increased food resources of insects on and in fire-killed trees (Rota et al. 2015, Hannon and Drapeau 2005). We suspect that selection logging, which produces large amounts of residual wood left on the forest floor, piles of untransported logs, and trees damaged from the logging operations, results in an increase in boring insects similar to burning, and attracts black-backed woodpeckers from surrounding forests. Nevertheless, burned and selection logged forests are only a temporary supply of high value food patches that do not last much longer than 3 years (Hannon and Drapeau 2005, Nappi et al. 2009). Therefore, while burned and partly-logged forests may act as sources (Nappi et al. 2009), old and mature forests must act as reservoirs for this species, where although breeding densities are low, large numbers of birds exist across large landscapes making it important to maintain large blocks of mature and older forests for black-backed woodpecker populations.

We were surprised that winter occurrence predicted spring breeding counts for five of seven resident species because a winter population includes non-breeding birds and juveniles, as well as adults from the previous spring. We are aware of only of two other studies that compared winter to breeding densities of resident birds from an area with snow and cold temperatures. Desrochers et al. (1999) found lower breeding densities of black-capped chickadees than occurred in winter. In our area, black-capped chickadees appeared to use mature pine in winter at higher densities than in summer, suggesting that these stands may be important wintering habitats. Koivula and Schmiegelow (2007) found no correlation between winter abundance and breeding season abundance of black-backed woodpeckers in unlogged stands but comparable numbers in various logged stands, in Alberta. Our results were similar

but only for the unmanaged mature pine stands, with no differences in either other stand types from winter to summer. Similar to chickadees, this woodpecker species used mature pine mixedwood stands in these transition forests as important wintering habitat.

Short-term data does not enable assessment of how communities may change over time and most studies of breeding birds are conducted only over a short time of 2 or 3 seasons. Our longer term data enabled us to assess inter-year variance of relative abundance by species among habitats. The general lack of difference in abundances across years among our unharvested stand types suggested stable community structure and habitat selection by all of our resident and woodpecker breeding species, and for all residents except black-capped chickadees. Kampichler et al. (2014) also detected long-term stable community structure among most breeding birds using datasets from several different ecosystems that had little or no anthropogenic disturbance. Our black-capped chickadees were likely responding to availability of winter foods, similar to a few species in the Kampichler et al. (2014) study that responded numerically to irruptive insect larvae.

Somewhat contrary to the results of Kirk et al. (2012), our data suggested that old growth pine did not support a particular resident or cavity-nesting community. Nevertheless, it was clear from our results that large pine trees are an important resource for many species both as foraging and nesting substrates. Unfortunately, in many areas of eastern Canada, these trees were harvested without replacement decades ago (Thompson et al. 2006, Kirk et al. 2012). We suggest that, regardless of age, stands with a large proportion of pine trees of dbh >40 cm provide important habitats for resident and cavity-nesting birds in mixedwood forests

and that maintaining landscapes with a high proportion of large conifer trees may be essential for black-backed woodpecker populations.

Acknowledgements

This study was initiated and funded for the first 2 years under the Ontario Ministry of Natural Resources, Landscape Ecology Program through A. Perera of the Ontario Forest Research Institute. We thank J.A. Baker and D.A. Welsh who assisted with the study design and also thank the several observers who participated over the 11 years, including: D. Ortiz, D. Oliver, K. McIlwrick, M. O'Connor, C. Jastrebski, S. Dobbyn, R. Russell, E. Wianko, K. Falk, R. Knudsen, D. Wiese, P. Mikoda, and C. Sanders. In particular, D. Ortiz, D. Oliver and C. Jastrebski observed in most years. L. Nituch assisted with some analyses.

References

Adams, E.M., and Morrison, M.L. 1993. Effects of forest stand structure and composition on red-breasted nuthatches and brown creepers. *J. Wildl. Manage.* **57**: 616-629.

Aird, P.L. 1985. In praise of pine: the eastern white pine and red pine timber harvest from Ontario's Crown forest. Canadian Forest Service Report No. PI-X-52, Petawawa, ON.

Anderson, M.J., Clarke, K.R., and Gorley, R.N. 2008. PERMANOVA + for Primer v6: User manual/tutorial. Primer-E, Plymouth, UK.

Barton, K. 2015. MuMIn: Multi-Model Inference. R package version 1.15.1. <http://CRAN.R-project.org/package=MuMIn>

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-8, <http://CRAN.R-project.org/package=lme4>.

Blaser, J., Sarre, A., Poore, D., and Johnson, S. 2011. Status of Tropical Forest Management 2011. ITTO Technical Series No 38. International Tropical Timber Organization, Yokohama, Japan.

Brush, T. 1983. Cavity use by secondary cavity-nesting birds and response to manipulations. *Condor* **85**: 461-466.

Carleton, T. J. 2003. Old growth in the Great Lakes forest. *Environ. Rev.* **11**: S115-S134.

Clarke, K.R., and Gorley, R.N. 2001. Primer v5: User manual/tutorial. Primer-E, Plymouth, UK.

Davis, C.M. 1978. A nesting study of the brown creeper. *Living Bird* **17**: 237-263.

Desrochers, A., Hannon, S.J., and Nordin, K.E. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. *The Auk* **105**: 727-736.

Drapeau, P., A. Leduc, J.-F. Giroux, J.-P. Savard, Y. Bergeron, and W.L. Vickery. 2000. Landscape scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecol. Monogr.* **70**: 423-444.

Franzreb, K.E. 1985. Foraging ecology of brown creepers in a mixed-coniferous forest. *Journal of Field Ornithology* **56**: 9-16.

Godfrey, W.E. 1990. The birds of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa.

Hejl, S.J., Newlon, K.R., McFadzen, M.E., Young, J.S., and Ghalambor, C.K. 2002. Brown creeper (*Certhia americana*) In The birds of North America online. Edited by A. Poole. Cornell

Laboratory of Ornithology, Ithaca, NY. Available online at:

<http://bna.birds.cornell.edu/bna/species/669/articles/introduction> (accessed Nov. 23, 2015)

Holmes, R.T., and Robinson, S.K. 1988. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* **48**: 31-35.

Hothorn, T., F. Bretz and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometr. J.* **50**: 346--363.

Hout, J.S., and Hannon, S.J. 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. *Can. J. For. Res.* **32**: 1881-1888.

Kampichler, C., Angeler, D.G., Holmes, R.T., Leito, A., Svensson, S., van der Jeugd, H.P., and Wesołowski, T. 2014. Temporal dynamics of bird community composition: an analysis of baseline conditions from long-term data. *Oecologia* **175**: 1301–1313.

Kennard, J.H. 1976. A biennial rhythm in the winter distribution of the Common Redpoll. *Bird-Banding* **47**: 231-237.

Kirk, D.A., Welsh, D.A., Baker, J.A., Thompson, I.D., and Csizy, M. 2012. Avian assemblages differ between old-growth and mature white pine forests of Ontario: a role for super-canopy pine? *Avian Conserv. Ecol.* **7**: art. 4 <http://www.ace-eco.org/vol7/iss1/>.

Koenig, W.D., and Knops, J.M.H. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. *J. Anim. Ecol.* **70**: 609–620.

Mariani, J.M., and Manuwal, D.A. 1990. Factors influencing brown creeper abundance patterns in the southern Washington cascade range. *Stud. Avian Biol.* **13**: 53-57.

Martin, A.C., Zim, H.S., and Nelson, A.L. 1951. American wildlife and plants: A guide to wildlife food habits. Dover, New York.

Mosseler, A., Thompson, I., and B.A. Pendrel, B.A. 2003. Overview of old-growth forests in Canada from a science perspective. *Environ. Rev.* **11**: S1-S7.

Murphy, E.C., and Lenhhausen, W.A. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *J. Wildl. Manage.* **62**: 1359-1372.

Nappi, A., and Drapeau, P. 2009. Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: Are burns source habitats? *Biol. Conserv.* **142**: 1381-1391.

Ontario MNRF (Ministry of natural Resources and Forests). 2015. State of Ontario's forests. <http://www.ontario.ca/document/state-ontarios-forests> accessed: 5 October 2015.

Poulin, J.F., Villard, M.-A., Edman, M., Goulet, P.J., and Eriksson, A.M. 2008. Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper (*Certhia americana*), as conservation targets. *Biol. Conserv.* **141**: 1129-1137.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

Rowe, J.S. 1972. The forest regions of Canada. Canadian Forest Service Publication No. 1300. Ottawa.

Smirnova, E., Bergeron, Y., and Brais, S. 2008. Influence of fire intensity on structure and composition of jack pine stands in the boreal forest of Quebec: live trees, understory vegetation and dead wood dynamics. *For. Ecol. Manage.* **255**: 2916-2927.

Thomas, J.W., Ruggiero, L.F., Mannan, R.W., Schoen, J.W., and Lancia, R.A. 1988. Management and conservation of old-growth forests in the United States. *Wildl. Soc. Bull.* **16**: 252-262.

Thompson, F.R., and Capen, D.E. 1988. Avian assemblages in seral stages of a Vermont forest. *J. Wildl. Manage.* **52**: 771-777.

Thompson, I.D., Kirk, D.A., and Jastrebski, C. 2013. Does post-harvest silviculture improve convergence of avian communities in managed forests with those using old growth boreal forests? *Can. J. For. Res.* **43**: 1050–1062.

Thompson, I.D., Simard, J., and Titman, R. 2006. Historical changes in the density of white pine in Algonquin Park, Ontario, Canada in the 19th century. *Natur. Areas J.* **26**: 61-71.

Vaillancourt, M.-A., Drapeau, P., Gauthier, S., and Robert, M. 2008. Availability of standing trees for large cavity-nesting birds in the eastern boreal forest of Quebec, Canada. *For. Ecol. Manage.* **255**: 2272-2285.

Venier, L.A., Thompson, I.D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J.A., Langor, D., Sturrock, R., Patry, C., Outerbridge, R.O., Holmes, S.B., Haeussler, S., De Grandpré, L., Bayne, E., Arsenault, A., and Brandt, J.P. 2014. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Envir. Rev.* **22**: 457-490.

Welsh, D.A., Clark, T., and Clark, K. 1992. Fauna of red and white pine old-growth forests in Ontario: issues and recommendations for research. *Ont. Min. Nat. Res., Ont. For. Res. Inst. Forest Fragmentation and Biodiversity Proj., Rept. No. 3. Sault Ste. Marie, Ont.*

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)* **73**:3-36.

Wray, D. 1986. Managing white pine in Ontario. *In* Eastern white pine: today and tomorrow.

Edited by D.T. Funk. Gen. Tech. Rept. WO-51, U.S. Dept. Agric., For. Serv., Durham, New Hampshire, USA. pp. 67-69.

Draft

Figure captions:

Figure 1. Mean abundance (SE) of the five most common resident birds in winter in the Spanish Forest on 0.5 km² plots by stand types, from 1995 to 2005.

Figure 2. Mean annual winter counts of five nomadic species in winter in the Spanish Forest on 0.5 km² plots by stand types, from 1995 to 2005.

Figure 3. Number of breeding woodpecker pairs by species among years and stand types on 0.25 km² plots in the Spanish forest by stand types, from 1999 to 2007.

Figure 4. Number of breeding pairs of secondary cavity-nesters in the Spanish forest on 0.25 km² plots by stand types, from 1999 to 2007.

Draft

Table 1. Model averaging results for resident birds in winter in the Lower Spanish Forest, Ontario, from 1995 to 2005. Mixedwood stand types were: old growth pine (>150 yrs), mature pine, and mature non-pine. Importance value is the sum of AIC_c weight scores for the models in the 95% confidence set that included the row variable.

Response	Stand type	Stand type importance	% Pine	% Pine importance	Basal area m ² ha ⁻¹	Basal area importance	Snags	Snags importance
Species Richness	NS	0.19	NS	0.25	NS	0.22	*, -	0.85
Simpson's index	NS	0.53	NS	0.39	NS	0.26	*, -	0.78
Strong cavity excavators	NS	0.17	NS	0.29	NS	0.31	NS	0.35
Weak cavity excavators	***	1.00	NS	0.10	*, +	0.70	**, -	1.00
Secondary cavity users	NS	0.27	NS	0.50	NS	0.27	NS	0.24
Residents	***	0.86	***, +	0.14	**, +	1.00	***, -	1.00
Nomads	NS	0.13	*, +	0.95	NS	0.29	NS	0.24
Downy woodpecker	NS	0.05	NS	0.27	NS	0.41	NS	0.58
Hairy woodpecker	NS	0.26	NS	0.22	NS	0.24	NS	0.43
Pileated woodpecker	NS	0.22	NS	0.24	NS	0.28	NS	0.24
Black-backed woodpecker	NS	0.15	*, +	0.82	*, -	0.93	NS	0.22
Red-breasted nuthatch	***	1.00	NS	0.29	*, +	0.90	NS	0.17
Black-capped chickadee	***	0.84	NS	0.35	NS	0.27	**, -	1.00
Boreal chickadee	NS	0.12	*, -	0.84	NS	0.31	NS	0.53
Gray jay	**	0.97	NS	0.28	NS	0.31	NS	0.36
Blue jay	*	0.85	NS	0.31	NS	0.28	NS	0.36
White-winged crossbill	**	0.96	***, +	1.00	*, +	0.70	NS	0.14
Common redpoll	NS	0.17	., -	0.77	NS	0.47	NS	0.54
Pine siskin	**	0.96	NS	0.15	*, -	0.67	**, +	0.97
Pine grosbeak	NS	0.19	NS	0.32	*, -	0.89	NS	0.31
Ruffed grouse	NS	0.11	NS	0.24	*, +	0.87	NS	0.44

¹ Significance levels: *** = < 0.0001, ** < 0.001, * = < 0.05, . = < 0.1, NS = not significant;

² + or - = direction of effect

Table 2. Significant differences among stand types used in winter and spring by resident and cavity-nesting birds in the Spanish Forest. Stand rankings were determined by Tukey tests for groups or species where the GLMM indicated a 'stand type' effect. Stands are ranked from 'a' most used, to 'c' least used and stands with the same letter were used equally ($P < 0.05$). (Harvested stands were not surveyed in winter.)

Season/ Species or guild	Old growth pine	Mature pine	Non-pine mixedwood	Selection harvested
Winter				
Species Richness	a	a	a	
Simpson's index	a	a	a	
Strong cavity excavators	a	a	a	
Weak cavity excavators	a	a	b	
Residents	a	a	b	
Nomads	a	a	a	
Downy woodpecker	a	a	a	
Hairy woodpecker	a	a	a	
Pileated woodpecker	a	a	a	
Black-backed woodpecker	a	a	a	
Red-breasted nuthatch	a	a	b	
Black-capped chickadee	a	a	b	
Boreal chickadee	a	a	a	
Gray jay	b	ab	a	
Blue jay	a	a	a	
White-winged crossbill	a	a	a	
Common redpoll	a	a	a	
Pine siskin	a	a	b	
Pine grosbeak	a	a	a	
Ruffed grouse	a	a	a	
Spring				
Species Richness	a	a	a	a
Simpson's index	a	a	a	a
Strong cavity excavators	b	b	b	a
Weak cavity excavators	a	a	a	a
Residents	a	a	a	a
Non-residents	b	ab	ab	a
Downy woodpecker	a	a	a	a
Hairy woodpeckers	b	ab	ab	a
Pileated woodpecker	a	a	a	a
Yellow-bellied sapsucker	b	bc	c	a
Common flicker	b	ab	ab	a
Black-backed woodpecker	a	a	a	a
Red-breasted nuthatch	a	a	a	a
Black-capped chickadee	ab	a	ab	b
Brown creeper	a	a	a	b

Table 3. Model averaging results for breeding cavity-nesting bird species in the Lower Spanish Forest, Ontario from 1999 to 2007. Mixedwood stand types were: old growth pine (>150 yrs), mature pine, and mature non-pine. Importance value is the sum of AIC_c weight scores for the models in the 95% confidence set that included the row variable.

Response	Stand type	Stand type importance	% Pine	% Pine importance	Basal area m ² ha ⁻¹	Basal area importance	Snags	Snag importance
Species Richness	NS	0.02	NS	0.26	NS	0.25	NS	0.24
Simpson's index	NS	0.05	NS	0.28	NS	0.37	NS	0.29
Strong cavity excavators	**	1.00	*, -	0.81	NS	0.17	NS	0.22
Weak cavity excavators	NS	0.22	NS	0.25	., +	0.69	NS	0.27
Residents	NS	0.11	NS	0.60	NS	0.53	NS	0.24
Non-residents	*	0.75	NS	0.49	NS	0.40	NS	0.46
Downy woodpecker	NS	0.30	NS	0.33	NS	0.78	NS	0.31
Hairy woodpecker	.	1.00	NS	0.32	NS	0.40	NS	0.25
Yellow-bellied sapsucker	***	1.00	**, -	0.98	NS	0.06	*, +	0.75
Pileated woodpecker	NS	0.00	NS	0.26	NS	0.25	., -	0.60
Common flicker	*	0.47	NS	0.51	NS	0.29	NS	0.48
Black-backed woodpecker	*	0.68	., +	1.00	NS	0.34	NS	0.21
Red-breasted Nuthatch	NS	0.33	NS	0.32	NS	0.29	NS	0.35
Black-capped Chickadee	.	0.63	NS	0.53	NS	0.29	NS	0.41
Brown creeper	***	1.00	***, +	1.00	NS	0.56	NS	0.00

Significance levels: *** = < 0.0001, ** < 0.001, * = < 0.05, . = < 0.1, NS = not significant; + or - = direction of effect

Table 4. AIC values for a year x habitat interaction, in a model of species counts in habitat by year. For species acronyms see Appendix 1.

								Species							
Season	Year treatment	BCCH	RBNU	DOWO	WWCR	CORE	PISI	GRJA	CORA	BOCH	HAWO	BRCR	YBSS	COFL	PIWO
Winter	random	0.000	0.000	0.001	0.000	0.000	0.000	0.977	0.270	0.670	0.998	0.998	NA	NA	NA
	fixed intercept	0.000	1.000	0.999	1.000	0.972	1.000	0.024	0.730	0.330	0.002	0.002	NA	NA	NA
	interaction	1.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000	NA	NA	NA
Spring	random	0.000	0.021	0.181	NA	NA	NA	NA	NA	NA	0.927	0.006	0.382	0.371	0.200
	fixed intercept	0.999	0.976	0.819	NA	NA	NA	NA	NA	NA	0.073	0.994	0.618	0.629	0.801
	interaction	0.001	0.003	0.000	NA	NA	NA	NA	NA	NA	0.000	0.000	0.000	0.000	0.000

Draft

Figure 1

Figure 2

Figure 3

Figure 4

Appendix 1. Common and scientific names of birds recorded in winter or spring and their guild assignments.

Acronym	Common Name (Scientific name)	Cavity guild	Migratory Status
AMGO	American Goldfinch <i>Spinus tristis</i>		Short-distance migrant
BBWO	Black-backed Woodpecker <i>Picoides arcticus</i>	Strong primary	Resident
BCCH	Black-capped Chickadee <i>Poecile atricapillus</i>	Weak primary	Resident
BLJA	Blue Jay <i>Cyanocitta cristata</i>		Short-distance (resident)
BOCH	Boreal Chickadee <i>Poecile hudsonicus</i>	Weak primary	Resident
BOOW	Boreal Owl <i>Aegolius funereus</i>	Secondary	Resident
BRCR	Brown Creeper <i>Certhia americana</i>	Secondary	Short-distance
CORA	Common Raven <i>Corvus corax</i>		Resident
CORE	Common Redpoll <i>Acanthis flammea</i>		Nomad (resident)
DOWO	Downy Woodpecker <i>Picoides pubescens</i>	Weak primary	Resident
GCKI	Golden-crowned Kinglet <i>Regulus satrapa</i>		Short-distance (resident)
GRAJ	Gray Jay <i>Perisoreus canadensis</i>		Resident
HAWO	Hairy Woodpecker <i>Picoides villosus</i>	Strong primary	Resident
NOFL	Northern Flicker <i>Colaptes auratus</i>	Strong primary	Short-distance migrant
PIGR	Pine Grosbeak <i>Pinicola enucleator</i>		Nomad (resident)
PISI	Pine Siskin <i>Spinus pinus</i>		Nomad (short-distance)
PIWO	Pileated Woodpecker <i>Dryocopus pileatus</i>	Strong primary	Resident
PUFI	Purple Finch <i>Carpodacus purpureus</i>		Short-distance (resident)
RBNU	Red-breasted Nuthatch <i>Sitta canadensis</i>	Weak primary	Resident (nomadic)
RECR	Red Crossbill <i>Loxia curvirostra</i>		Nomad
RUGR	Ruffed Grouse <i>Bonasa umbellus</i>		Resident

SPGR	Spruce Grouse <i>Falcipennis canadensis</i>		Resident
TTWO	American Three-toed Woodpecker <i>Picoides dorsalis</i>	Strong primary	Resident
WBNU	White-breasted Nuthatch <i>Sitta carolinensis</i>	Weak primary	Resident
WWCR	White-winged Crossbill <i>Loxia leucoptera</i>		Nomad (resident)
YBSS	Yellow-bellied Sapsucker <i>Sphyrapicus varius</i>	Strong primary	Short-distance migrant

Draft

Appendix 2. Mean counts of bird species in winter by stand types from 1995-2005. (One mature pine stand was converted to a selection harvested stand in 2003.)

Species	Non-pine mixed wood (n = 4)		Mature pine (n = 7, 6)		Old-growth pine (n = 6)		Selection harvested (n = 2, 3)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Downy woodpecker	2.10	0.29	2.22	0.2359 03	2.13	0.20	1.33	0.88
Hairy woodpecker	0.46	0.12	0.56	0.08	0.52	0.09	0	0
Pileated woodpecker	0.27	0.09	0.20	0.05	0.09	0.03	0	0
Black-backed woodpecker	0.23	0.08	0.10	0.03	0.18	0.05	0.33	0.33
Northern three-toed woodpecker	0.02	0.02	0.01	0.01	0.01	0.01	0	0
Red-breasted nuthatch	1.98	0.47	4.14	0.55	3.74	0.46	6.67	4.41
White-breasted nuthatch	0	0	0.01	0.01	0.02	0.01	0	0
Black-capped chickadee	7.43	1.07	9.46	0.80	8.52	0.68	10.67	2.73
Boreal chickadee	0.96	0.27	0.55	0.12	0.52	0.12	0	0
Blue jay	0.35	0.11	0.44	0.08	0.34	0.07	0	0
Gray jay	1.08	0.17	0.57	0.10	0.68	0.10	0.67	0.67
Ruffed grouse	0.33	0.09	0.57	0.11	0.37	0.08	0.33	0.33
Spruce grouse	0.04	0.03	0.01	0.01	0.03	0.02	0	0
White-winged crossbill	1.40	0.47	1.43	0.30	1.94	0.42	5.00	3.61
Red crossbill	0.35	0.35	0.28	0.08	0.23	0.10	0	0
Common redpoll	2.64	0.82	1.60	0.45	1.82	0.60	0	0
Brown creeper	0.10	0.04	0.14	0.05	0.11	0.03	0	0
Pine grosbeak	0.10	0.05	0.16	0.07	0.14	0.05	0.33	0.33
Pine siskin	0.60	0.36	1.38	0.51	1.47	0.49	0	0
American goldfinch	0.58	0.44	0	0	0	0	0	0
Purple finch	0	0	0.01	0.01	0	0	0	0
Golden-crowned kinglet	0.02	0.02	0.05	0.03	0.04	0.04	0	0
Boreal owl	0	0	0	0	0.01	0.01	0	0

Appendix 3. Mean counts (number of pairs) of breeding cavity-nesting bird species in spring by stand types from 1995-2005. (One mature pine stand was converted to a harvested stand in 2003.)

Species	Non-pine mixed wood (n = 4)		Mature pine (n=7, 6)		Old-growth pine (n = 6)		Selection harvested (n = 4, 5)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Downy Woodpecker	2.07	0.24	2.26	0.26	2.81	0.24	2.40	0.22
Hairy woodpecker	1.18	0.19	0.86	0.16	1.23	0.19	1.86	0.22
Pileated woodpecker	0.74	0.13	0.63	0.11	0.81	0.11	0.78	0.18
Black-backed woodpecker	0.15	0.09	0.46	0.12	0.17	0.06	0.46	0.11
Red-breasted nuthatch	2.67	0.45	3.80	0.38	3.23	0.31	3.35	0.45
Yellow-bellied sapsucker	2.85	0.31	2.97	0.37	2.98	0.23	4.05	0.32
Black-capped chickadee	3.11	0.46	3.62	0.49	3.02	0.49	2.57	0.79
Boreal chickadee	0.15	0.09	0.17	0.09	0.13	0.07	0.13	0.07
Brown creeper	0.30	0.14	0.91	0.29	0.41	0.13	0.27	0.16
Common flicker	1.00	0.24	0.97	0.16	0.75	0.14	1.13	0.19