A MULTIPLE-SCALE INVESTIGATION
OF CAVITY-NESTING BIRD HABITAT
IN AN INDUSTRIAL FOREST

By

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B.Sc.(Hons), Queen's University, 1997

A thesis submitted in partial fulfilment of
the requirements for the degree of

Master of Science

in the Graduate Academic Unit of Biology

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THE UNIVERSITY OF NEW BRUNSWICK

January, 2004

Abstract

I studied habitat use on multiple scales by cavity-nesting bird species in a late successional industrial forest landscape in northwestern New Brunswick. I investigated the effect of local habitat and landscape composition independent of local habitat on the occupancy of six cavity-nesting bird species. I also explored whether occupancy was a misleading indicator of habitat quality for one species, the Yellow-bellied Sapsucker. Lastly, I described woodpecker nesting and foraging preferences. The occupancy of Boreal Chickadees, Red-breasted Nuthatches, and Hairy Woodpeckers was explained only by features within 100m (local habitat). The occupancy of Downy Woodpeckers and Northern Flickers, the two species associated with open areas or early successional forest, was explained by features within 300m and 1000m (landscape composition). The local occupancy and productivity models for Sapsuckers were similar, although productivity was also related to landscape composition. Foraging substrates preferred by Yellow-bellied Sapsuckers may not be supplied by management focused on nest site needs; Sapsuckers used a wider range of foraging substrates compared to nesting substrates, and preferred different hardwood tree species. These results indicate that the approach to the management of cavity-nesting birds must be multiple-scaled and species-specific. Additional research is needed on extended temporal scales, and in different types of landscapes, to determine how widely these results can be applied.

Preface

This thesis is written in articles format. The data for Chapter 2 were collected by myself and my two field assistants: Sarah Glinz and Marie-Paule Godin. This paper will be submitted to Ecoscience and will be co-authored by myself, Matthew Betts, Antony Diamond, and Graham Forbes. The data for Chapter 3 were collected by myself and my four field assistants: Sarah Glinz, Marie-Paule Godin, Sarah Hui, and Amanda Smith. This paper will be submitted to the Canadian Field Naturalist and will be co-authored by myself, Antony Diamond, and Graham Forbes.

Acknowledgements

This research project has been completed with the help and support of many people. First I would like to acknowledge my co-supervisors Tony Diamond and Graham Forbes for the time and assistance given to me throughout my years here at UNB. I would also like to thank Steve Young and Martin Marshall for paving the way to my introduction to the forests of northwestern New Brunswick. Thanks to NSERC, Nexfor Fraser Papers and the University of New Brunswick for their funding.

This project would not have come so far without the thoughtful input from Laurel Bernard, Jeff Bowman, Kate Devlin, and Lasha Young. Special thanks go to Matt Betts and Maureen Tingley for their invaluable encouragement and guidance. Thanks to Laurel Bernard, Sarah Glinz, Marie-Paule Godin, Sarah Hui, Chris Kusch, Robert Parish, and Amanda Smith for their hard work in the field and laughs on the river.

Thank you to Jessie Vincent and the Cwynar Lab for their friendship. Other friends that have helped my along the way include Laurel and Joey Bernard, Jeff Bowman, Kate Devlin, and Lasha Young. I am at a loss for words to thank my family for all of their love and support throughout the years. Special thanks goes to Robert Parish.

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Chapter 1

General Introduction

1.1 General Introduction

    The sub-boreal Acadian forest of eastern North America is an ecological

transitional zone between the eastern boreal forest and temperate deciduous forest

(Seymour and Hunter 1992, Zelazny and Veen 1997). Unlike that of the true boreal

forest, natural disturbance in the Acadian forest is rarely of such intensity that it replaces

the forest to an even-age condition; the presettlement forests were characterised by high

species diversity and multi-cohort stands maintained by insect outbreaks and windthrow

(Lorimer 1977, Seymour 1992, Seymour and Hunter 1992). Logging since European

settlement has largely disrupted this natural disturbance regime and altered the

composition of species and age classes within the Acadian forest. Pine, spruce, and

hardwood sawlogs were selectively cut in the early 1800s at progressively lower

diameter limits (Seymour 1992). The smaller pulpwood-sized trees were harvested

towards the end of the century with the development of the pulp and paper industry

(Seymour and Hunter 1992). Many harvested stands became dominated by one age

class and the relative abundance of some species (e.g. Red Spruce and pine) declined

while others (e.g. Balsam Fir) increased (Seymour 1992).

    The forest industry remains a very important part of the regional economies

within the Acadian forest. Changes to logging practices are still made today in response

to technological advances, greater understanding of forest ecosystems, and refined

definitions of forest values. Forest management planning in the province of New

Brunswick, Canada has developed considerably over the past two decades. Forest management is designed to intentionally alter the temporal and spatial dynamics of a forest system (Baskerville 1997); actions are implemented in order to achieve forest conditions that are consistent with a set of forest values (Erdle and Sullivan 1998). If there are multiple values, forest management interventions are applied once an acceptable trade-off between the values is found (Erdle 1998). In the early 1980's, maximum even-flow of softwood fibre was the single value guiding most forest management practices on Crown Land (Erdle 1998). More recently, biodiversity and the maintenance of broad vegetation communities important to wildlife have been added to the primary value of timber production (Erdle 1998). Ensuring that mature forests are represented on the landscape is a particular concern given that the maximisation of timber extraction results in the elimination of softwood stands greater than 60 years old (Erdle 1998). Increasingly industry is incorporating similar values into the management of their privately-owned land.

This study was conducted in co-operation with Nexfor Fraser Papers on their Freehold land in northwestern New Brunswick (47°N, 67°W). Nexfor Fraser Papers chose to manage habitat for wildlife associated with mature forest in separate areas fixed on the landscape (Anonymous 1997). The guidelines and standards for management of these Habitat Management Areas (HMAs) are based on the primary value of wildlife habitat maintenance and the secondary value of timber extraction (Anonymous 1997). Management interventions (e.g. clearcuts, plantations, selection cuts) are still applied to the stands, but they are relatively less common (Anonymous 1997). The impetus for my study of primary cavity-nesting birds was the wish of Nexfor Fraser Papers to assess the

suitability of these HMAs to support mature species assocated with mature forest
(Appendix 2).

Primary cavity-nesting birds were chosen for study because they play a keystone
role in forest ecosystems and are associated with stand structures typical of mature
forests. Secondary cavity-nesting birds and small mammals reuse nests excavated by
primary cavity-nesting birds (Kilham 1971, Erskine and McLaren 1972, Short 1979,
Kilham 1983, Daily et al. 1993, Bull and Jackson 1995, Kalcounis and Brigham 1998,
Bonar 2000, McClelland and McClelland 2000). Large trees, snags and logs are
essential to primary cavity-nesting birds as nesting, drumming, and foraging substrates
(Angelstam and Mikusinski 1994, Gunn and Hagan 2000). Because harvesting in
industrial forests often occurs before these structures can develop, I expected primary
cavity-nesting birds to be particularly sensitive to forest management practices.

Avian conservation and management requires an understanding of bird-habitat
relationships. Habitat refers to the environmental components that meet life history
requirements. Often these components are proximate cues for ultimate factors that
influence survival or productivity (Hilden 1965, Rotenberry 1981, Orians and
Wittenberger 1991). For example, vegetation structure may be a good predictor of prey
availability. Although bird-habitat models have traditionally focused on fine spatial
scales, patterns of habitat use can be sensitive to the spatial scale of observation (e.g.
regional, landscape, and multiple local scales) (Wiens et al. 1987, Wiens 1989, Orians
and Wittenberger 1991, Dunning et al. 1992, Jokimaki and Huhta 1996, Morrison et al.
1998). Conclusions drawn from studies may be erroneous if an arbitrarily chosen scale
of investigation does not correspond to the scale of an organism's response, or if the

results from one scale are extrapolated to another (Wiens 1989, Virkkala 1991, McGarigal and McComb 1995, Jokimaki and Huhta 1996). Therefore, I decided to take a multiple-scale approach to studying the habitat of primary cavity-nesting birds.

Studies of forest birds have shown that landscape context influences habitat use by some species (e.g. McComb and McGarigal 1995, Hagan et al. 1997, Lichstein et al. 2002). But this research has focused primarily on songbirds, with few studies specifically looking at how landscape scale factors influence cavity-nesting birds in forested landscapes (but see Lawler and Edwards 2002). My first objective in Chapter 2 was to characterise the relationships between local vegetation and the occurrence of six primary cavity-nesting bird species. Occupancy data were sufficient to model the local and landscape associations of the Boreal Chickadee (*Poecile hudsonica*), Red-breasted Nuthatch (*Sitta canadensis*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus*), and Yellow-bellied Sapsucker (*Sphyrapicus varius*). I expected to be able to develop strong local habitat models for these species because of their association with mature forest structures, whose maintenance is often in conflict with industrial forest management. My second objective was to assess whether landscape composition explained additional variation in the species' occurrence. This aspect of the study was largely exploratory, given the wide range of responses to landscape factors by other bird species (e.g. McGarigal and McComb 1995, Hagan et al. 1997) and the lack of information specific to cavity-nesting birds due to large scale censusing difficulties (Appendix 1). My third objective was to compare habitat models developed using occupancy and productivity. Occurrence or density measures may be misleading indicators of habitat suitability,

although they are often easier to assess than survival or productivity (Van Horne 1983). If species occupancy is a misleading indicator of habitat quality, then the models should be different.

Research and management of primary cavity-nesting birds has traditionally focused on nest site suitability and availability. However, nest sites are not always limiting to breeding populations, and factors such as foraging habitat and food availability can be overlooked (Brawn and Balda 1986, Swallow et al. 1988, Weikel and Hayes 1999). My objectives in Chapter 3 were to describe woodpecker nesting and foraging tree use and preference in my study area, and to directly compare nesting and foraging substrates used by the most commonly detected woodpecker breeding in the area, the Yellow-bellied Sapsucker.

The two chapters complement each other. The study of habitat use at local and landscape scales gives insight into which resources may be limiting to the occupancy or productivity of the six cavity-nesting bird species, while the foraging and nesting study gives insight into why those resources may be limiting to the woodpecker species. In the last chapter I summarise the results from the two chapters and present the scope and limitations of the two studies.

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Chapter 2

The influence of local habitat and landscape composition on cavity-nesting birds in northwestern New Brunswick

2.1 Introduction

By relating the structure and composition of local vegetation to bird presence or productivity, bird-habitat models have traditionally focused on fine spatial scales (Dunning et al. 1992). More recently it has been recognised that habitat variation occurs across a variety of scales and that patterns of habitat use can be sensitive to the spatial scale of observation; different associations may exist between birds and their habitat on biogeographical, regional, landscape, and multiple local scales (Wiens et al. 1987, Wiens 1989, Orians and Wittenberger 1991, Dunning et al. 1992, Jokimaki and Huhta 1996, Morrison et al. 1998). Currently, research is focused on determining whether landscape context influences the occurrence of species in addition to local habitat conditions (Diamond 1999).

'Landscape' can be defined as a mosaic of patches in which a focal patch is embedded (Dunning et al. 1992). The spatial extent of 'landscape' depends on the study organism's perception of scale (Dunning et al. 1992, With 1994). Landscape structure can be defined by composition (proportion of patch types in a predefined area) and configuration (e.g. patch size and shape), and may affect intra- and interspecific interactions, the complementation or supplementation of resources, and movement patterns (Dunning et al. 1992, McGarigal and McComb 1995, Lichstein et al. 2002).

Studies of landscape effects on birds have been conducted largely in agricultural settings (but see Enoksson et al. 1995, McGarigal and McComb 1995, Edenius and

Elmberg 1996, Jokimaki and Huhta 1996, Hagan et al. 1997, Schmiegelow et al. 1997, Drolet et al. 1999, Estades and Temple 1999, Jokimaki et al. 2000, Lichstein et al. 2002). However, landscapes created by agriculture are different from those created by timber harvesting. Fragmentation by agriculture or urbanisation often produces small forest patches that are permanently isolated within a non-forested matrix; landscapes are often characterised by suitable habitat patches embedded in a non-habitat or unsuitable matrix (McGarigal and McComb 1995). In contrast, edges are temporary in industrial forest landscapes and patches are rarely truly isolated (Welsh and Healy 1993, McGarigal and McComb 1995). Moreover, it has been found that few forest birds are restricted to only one habitat or vegetation type, and their perception of forest landscapes may be more in terms of habitat quality (high vs. low) than habitat versus non-habitat. Conclusions derived from agricultural landscape studies therefore may not be applicable to forest landscapes.

Management of industrial forests alters both landscape configuration and composition (Bowman et al. 2001). Landscape configuration is altered when harvest blocks do not reflect the size or shape of stands developed under natural disturbance regimes. Landscape composition is altered by plantations, thinning, herbiciding, and the truncation of age classes. Despite the inclusion of forest values such as biodiversity and wildlife habitat conservation in forest management guidelines, industrial forest stands in New Brunswick are often harvested in short rotations timed to roughly coincide with peak mean annual increment (Freedman et al. 1996, Erdle 1998, Flemming et al. 1999). The productivity of a maturing stand levels off and then drops, and eventually tree mortality exceeds growth. This latter stage is commonly referred to by foresters as

'overmature', and represents an economic loss to the forest industry (Freedman et al. 1996). Consequently, forests have traditionally been managed for early- and mid-seral stages that yield high volumes of desired timber products (Kimmins 1995, Erdle and Sullivan 1998). Even selection harvests of less intensive tree removal often occur at higher frequencies compared to natural disturbance events (Freedman et al. 1996). All of these practices change landscape composition by altering the composition and structure of individual stands. In light of these changes, it is clearly important to adopt a multi-scale approach to wildlife studies in industrial forest landscapes.

I studied habitat use by six cavity-nesting bird species in an industrial forest in northwestern New Brunswick, Canada: Boreal Chickadee (*Poecile hudsonica*), Red-breasted Nuthatch (*Sitta canadensis*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), and Northern Flicker (*Colaptes auratus*). All of the study species are primary excavators; Boreal Chickadee and Red-breasted Nuthatch may also use natural cavities. They excavate their own nests or roosting sites, and play an important role in forest ecosystems by providing cavities for secondary cavity-nesting birds and small mammals (Bull and Jackson 1995, Bonar 2000). Large trees, snags and logs commonly found in old stands supply essential nesting, drumming, and foraging sites for these species (Angelstam and Mikusinski 1994, Gunn and Hagan 2000). Harvesting in industrial forests often occurs before these structures can develop, thereby reducing the structural complexity within stands (Newton 1994). Conditions within stands are further simplified by removing existing structures that would otherwise function as biological legacies in regenerating forests (Hansen et al. 1991, O'Hara et al. 1994, Freedman et al.

1996). Species associated with these structures may be particularly sensitive to industrial forest management practices on a local scale (Newton 1994, Gunn and Hagan 2000, Imbeau et al. 2001). Our understanding and management of these species may be further improved by incorporating multiple scales into the habitat models.

There are three reasons why it is important to invest in new studies of cavity-nesting bird habitat at multiple scales. First, previous studies show that landscape relationships differ widely among species, and the response of one species cannot necessarily be extrapolated to another (McGarigal and McComb 1995, Hagan et al. 1997). For example, McGarigal and McComb (1995) found that late seral species' abundance was generally higher in more heterogeneous landscapes. Hagan et al. (1997) found the opposite relationship, with both early and late seral species more positively associated with homogeneous landscapes. Research into landscape effects on forest birds has focused predominately on songbirds; few studies have specifically assessed landscape effects on cavity-nesting birds in forested landscapes (but see Lawler and Edwards 2002). Due to their large home ranges alone, I might expect that cavity-nesting birds will respond at different scales compared to the commonly studied songbirds; woodpeckers in particular may incorporate more than one habitat patch into their large home ranges (Lawrence 1966, Gutzwiller and Anderson 1987, Angelstam and Mikusinski 1994). Research also suggests that larger birds are more likely to cross gaps within their home ranges, and so may perceive fragmentation on a different scale compared to smaller birds (Grubb and Doherty 1999). Other studies have shown that large birds are more area-sensitive than smaller birds (Estades and Temple 1999).

Second, multiple scales are often investigated separately, which is problematic if relationships at one scale are confounded with those at another (Pearson 1993, Lichstein et al. 2002). If the correlation between the local and landscape variables is not statistically controlled, distinguishing between the two scales can be very difficult and pose problems for species conservation and management (Pearson 1993, Lichstein et al. 2002).

Third, this study will contribute to a growing body of evidence needed to determine habitat use by cavity-nesting birds at multiple scales. The strength of relationships with landscape characteristics changes depending on the proportion of suitable habitat in the surrounding area (Wiens 1989, Andren 1994). It is difficult or impossible to replicate in large-scale studies, so the results of a number of studies must be taken into consideration to provide a more complete picture.

My study had three main objectives. My first objective was to determine how well the local vegetation explained the occurrence of the six cavity-nesting bird species. I expected to find strong local habitat models for these species due to their association with mature forest structures, whose maintenance is often in conflict with industrial forest management. My second objective was to assess whether landscape composition explained additional variation in the species' occurrence. Given the wide range of responses to landscape factors by other bird species, and the paucity of information on the effect of landscape on cavity-nesting birds due to large scale censusing difficulties (Appendix 1), this aspect to the study was largely exploratory. I chose to focus on landscape composition because the number of independent variables was limited by sample size, and research indicates that composition contributes more to the explanation

of bird distribution than landscape configuration (Trzcinski et al. 1999, Lichstein et al. 2002, but see Villard et al. 1999). My third objective was to compare habitat models developed using occupancy and productivity. Although easier to assess than survival or productivity, occurrence or density measures may be misleading indicators of habitat suitability (Van Horne 1983). If species occupancy is a misleading indicator of habitat quality, then the models should be different.

2.2 Methods

2.2.1 Study Area

My study was conducted on the industrial forest of Nexfor Fraser Papers in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). The area is within the Acadian forest region of Canada (Rowe 1972). Well-drained upper slopes are dominated by Sugar Maple (*Acer saccharum* Marsh.), Yellow Birch (*Betula alleghaniensis* Britt.), and Beech (*Fagus grandifolia* Ehrh.) (Rowe 1972). Middle slopes are dominated by mixed hardwoods, Red Spruce (*Picea rubens* Sarg.), White Spruce (*Picea glauca* (Moench) Voss), and Balsam Fir (*Abies balsamea* (L.) Mill.) (Rowe 1972). Spruce, Fir, and Eastern White Cedar (*Thuja occidentalis* L.) dominate Lowland sites (Rowe 1972).

One of the management goals of this privately owned forest is to provide habitat for a variety of wildlife (Anonymous 1997). Nexfor Fraser Papers (Canada) is working to achieve this goal using designated Habitat Management Areas (HMAs) to support species associated with mature habitat conditions. The guidelines and standards for management of these Habitat Management Areas (HMAs) are based on the primary

value of wildlife habitat maintenance and the secondary value of timber extraction (Anonymous 1997). Approximately 12.6% of the Freehold land area is designated as HMA. Management interventions (e.g. clearcuts, plantations, selection cuts) are still applied to the stands, but they are relatively less common (Anonymous 1997). Most of the 74 HMAs on Fraser Freehold land in New Brunswick are grouped into 21 HMA complexes ranging in size from 124 ha to 7 210 ha (personal communication). Census points were located within and outside groups of HMAs in order to sample a wide range of local and landscape conditions.

The study landscape, defined by a 1000m buffer around the census points, is covered by 29% softwood, 23% hardwood, and 19% mixedwood stands, as well as 7% early-aged (regenerating) stands and 19% recent clearcuts ≤10 years old (see Table 2.1 for stand classification).

2.2.2 Bird Surveys

Bird surveys were conducted during the 2001 breeding season (mid-May to mid-August). Eight areas within 270 km^2 and ranging in size from 300-900 ha were sampled systematically. Seventy-one points within HMAs were sampled in year 2000 as part of a larger study. Forty-eight out of those 71 points were randomly selected to survey in year 2001, along with an additional 48 in areas surrounding the HMAs (Total N in 2001=96). Points were separated by at least 600m in order to reduce the chance of double counting individuals with large territories. Points closer than 100m from a 'hard edge' were excluded from the analyses, leaving a total of 73 points (38 HMA, 35 non-HMA; Figure 2.1). A 'hard edge' was defined as a boundary between a forested stand and a recent clearcut ≤10 years old.

I used Barred Owl (*Strix varia*) calls and Boreal (*Poecile hudsonica*) and Black-capped Chickadee (*Poecile atricapillus*) mobbing calls to survey the cavity-nesting birds (Appendix 1). I broadcast chickadee mobbing calls (recorded locally) to attract Red-breasted Nuthatches and Boreal Chickadees, and Barred Owl calls (© 1990 Cornell Laboratory of Ornithology and Interactive Audio) to attract woodpeckers.

The points were visited 6 times during the 2001 breeding season. Each visit consisted of a 30-minute count period separated into 5 intervals: 5 minute silent period, 5 minute chickadee mobbing playback, 10 minute silent period, 5 minute Barred Owl playback, and 5 minute silent period. Calls were broadcast on tape players, with the volume set to be heard within 100m by the human ear. To limit observer and temporal biases, three observers were rotated among points for the six visits, as was the time of day at which the points were sampled. Points were visited between sunrise and noon on mornings with winds less than 20 km/h and no rain (Robbins 1981). Long count periods and repeated visits were used in order to incorporate the different playbacks, to increase survey time relative to long travel time between points, and to offset the problem of detecting less conspicuous species. Individuals of each species within 100m of the point were counted during the visits. Sex, age, and whether individuals were part of a pair or family group were recorded when possible.

Determining the productivity of cavity-nesting birds by locating and monitoring cavity nests is prohibitive in terms of time and cost. Therefore, I developed a reproductive index for each species based on my observations (Vickery et al. 1992, Gunn et al. 2000). Species were given a productivity rank from 0-4 at each of the census points (Table 2.2). For the purpose of analyses, I classified points as

'productive' for a species if there was evidence of a pair, nest, or fledglings (rank 3-4) and 'not productive' if the species was absent from the point or if I only observed unpaired individuals (ranks 0-2).

2.2.3 Habitat measurements

Local vegetation characteristics were measured at three 10- by 20-m quadrats within 100m of each census point. One quadrat was placed at the centre of the plot, and two quadrats were placed 75m from the centre at two randomly selected directions: 0 degrees, 120 degrees, or 240 degrees. Each tree $\geq$ 8 cm dbh was tallied, identified to species and decay class (live healthy tree, declining tree, dead tree or snag), and measured for diameter at breast height (dbh). Trees were classified as large ($\geq$ 22 cm dbh) and small (<22 cm dbh) for the purpose of analyses. The presence of a broken top or branches, bark cover class (0-5%, 6-25%, 26-50%, 51-75%, 76-95%, 95-100%), and evidence of woodpecker foraging or nesting were also recorded as part of another study (Chapter 3). Coarse woody debris (cwd) was measured using the line intersect technique (Van Wagner and Wilson 1976). Logs or stumps crossing a 20m transect through the centre of the quadrat were tallied, identified to species, measured for diameter at the point of crossing, and classified on a scale from 1-5 based on decay (recently fallen to very decayed; Maser et al. 1979). Debris < 8cm in diameter at the point at which it crossed the transect was not included. Mean decay class of coarse woody debris was calculated for each point. The data from the three vegetation plots at each point were pooled.

Landscape variables were developed using digital forest inventories and a Geographic Information System (GIS). The GIS data have an accuracy of

approximately 80% (Province of New Brunswick 2001). Stands were classified based on development stage, hardwood, and softwood components (Table 2.1). Development stage was based on the age of the dominant tree species (Table 2.3). 'Medium' aged is equivalent to the 'Young' and 'Immature' stages and 'Mature' is equivalent to the 'Mature' and 'Overmature' stages in the New Brunswick Permanent Sample Plot Database (Porter et al. 2001). I calculated the area in hectares for eight stand classifications within 300m and 1000m of each survey point (Table 2.1).

2.2.4 Data Analysis

I used logistic regression to assess the importance of local habitat and landscape composition to the cavity-nesting bird species. Because the density of each species was so low, habitat occupancy (presence/absence) was used as a surrogate for density. Species were considered present at a point if one or more individuals were detected within 100m of the point during any of the six visits. Occupancy data were sufficient to model Boreal Chickadee, Downy Woodpecker, Hairy Woodpecker, Northern Flicker, Red-breasted Nuthatch, and Yellow-bellied Sapsucker (Table 2.4). Visual observations of Yellow-bellied Sapsuckers were common enough to also model the presence/absence of productivity (rank 0-2 versus 3-4, Table 2.2). Black-backed Woodpeckers (*Picoides arcticus*) and Pileated Woodpeckers (*Dryocopus pileatus*) were excluded from my analyses because of very low detection frequencies (5.5% and 7.4% respectively), and Black-capped Chickadees were excluded because of a very high detection frequency (90.4%).

Large distances between points (600m) do not necessarily ensure that the points are statistically independent of one another. Spatial autocorrelation refers to the

similarity of variables based on a function of geographical distance, whereby data from neighbouring points are more similar than data from farther apart (Rossi et al. 1992, Mathsoft 1996). If ignored, spatial autocorrelation may cause an inflation of the Type I error rate (i.e. the detection of a false effect) (Legendre et al. 2002). For each species, I visually assessed omnidirectional variograms for spatial autocorrelation (Mathsoft 1996). There was no obvious spatial pattern in any of the species' data.

I screened the local vegetation variables statistically and graphically before building local models. I performed Spearman rank correlations on the pairs of local variables and excluded the more specific of the two if $r \geq 0.7$ (Loose and Anderson 1995, Tabachnick and Fidell 1996). For example, the 'number of spruce trees' and 'number of small softwood trees' had a bivariate correlation of 0.910, so I excluded the spruce tree variable. A model for each bird species was fit with the remaining local variables using univariate logistic regression. Those with a $p > 0.5$ were not included in further analyses; Hosmer and Lemeshow (2000) suggested a screening level of 0.25, but I chose a more liberal cut-off so as to not leave out potentially important variables. The adequacy of the univariate models was assessed graphically by grouping each continuous variable and comparing plots of observed proportions and their standard errors with the predicted model (Hosmer and Lemeshow 2000, Bêty et al. 2001). These graphs were also used to suggest transformations of the continuous variables.

I used Akaike's Information Criterion (AIC) to determine variable addition or removal in stepwise logistic regression. The goodness-of-fit of the local models was assessed using the Hosmer-Lemeshow statistic, Pearson chi-square, and deviance (Hosmer and Lemeshow 2000). Highly unusual points were identified by the diagnostic

graphs recommended by Hosmer and Lemeshow (2000). I directly assessed the influence of these points by performing the stepwise procedure again after removing these points. If the final model was different, I rejected the original model as unreliable because of undue influence by one or a few points.

I repeated the univariate screening process for the 300m and 1000m variables. The effects of large scales were tested using sequential and stepwise logistic regression; variables important at the smaller spatial scales were forced to stay in the model while the larger scale variables were added or dropped (Tabachnick and Fidell 1996, Estades and Temple 1999, Freckleton 2002). Using this method I partitioned the variance explained at successively larger spatial scales. The additional effect of 300m variables was assessed after taking into consideration 100m variables, and the additional effect of 1000m variables was assessed after taking into consideration 100m+300m variables. The percent deviance explained and statistical significance ($p < 0.10$) was determined for the 100m model, the partial 300m model, the partial 1000m model, and the full 100m + 300m + 1000m model. I chose an alpha-level of 0.10 because it is more important to reduce the probability of a Type II error (i.e. not detecting a real effect) than a Type I error (i.e. detecting a false effect) when management decisions with important conservation consequences are needed (Tacha et al. 1982, Thompson et al. 1992).

I assessed how well the final models discriminated between species presence/absence (or productivity presence/absence in the case of Yellow-bellied Sapsuckers) using the area under the receiving operating characteristic (ROC) curve. Traditionally, classification tables have been used for this purpose. If the probability

predicted by the model exceeds a certain cutpoint (e.g. p=0.50), then the test result is classified as present or occupied. Sensitivity is a measure of how well the model correctly classifies the occupied cases, and specificity is a measure of how well the model correctly classifies the unoccupied cases (Tyre et al. 2001). The problem with that method is that it uses an arbitrarily chosen cutpoint, and favours classification into the larger group (Hosmer and Lemeshow 2000). The area under the ROC curve avoids these problems. The ROC curve is a plot of proportion of occupied points correctly classified as occupied (sensitivity) vs. the proportion of unoccupied points incorrectly classified as occupied (1-specificity) across the entire range of probability cutpoints (0-1) (Hosmer and Lemeshow 2000). The area under the ROC curve is the proportion of times an occupied site is ranked with a higher probability than an unoccupied site for all pairs of occupied and unoccupied sites (Hosmer and Lemeshow 2000, Tyre et al. 2001).

The variograms were calculated using S+SPATIALSTATS Version 1.0. The habitat models were developed using SPLUS 6.0 Professional. The goodness-of-fit statistics and diagnostic graphs were calculated in SYSTAT Version 9. The ROC curves were calculated using SPLUS code made available by the Mayo Clinic (http://www.mayo.edu/hsr/Sfunc.html).

2.3 Results

Yellow-bellied Sapsuckers were the most common cavity-nesting bird species recorded in my study area aside from Black-capped Chickadees, followed by Red-breasted Nuthatches (Table 2.4).   Evidence of Sapsucker pairs, nests or fledglings was also widespread (Table 2.4). Downy Woodpeckers, Boreal Chickadees, and Hairy

Woodpeckers were observed at about half, and Northern Flickers a little over one third of the census points (Table 2.4).

Depending on the species, 0-58.5% of the deviance of cavity-nesting bird occurrence was explained by local vegetation characteristics within 100m (Table 2.5). Landscape cover variables explained an additional 0-24% at 300m and an additional 0-5.1% at 1000m once the effect of the lesser scales was removed (Table 2.5).

The occurrence of Boreal Chickadees, Red-breasted Nuthatches, Hairy Woodpeckers, and Yellow-bellied Sapsuckers was explained by variables only at the local scale (100m). Boreal Chickadees were positively associated with the number of large and small softwood trees, and negatively associated with the number of small hardwood trees (Table 2.5). Red-breasted Nuthatches showed positive relationships to large softwood trees and the average decay class of coarse woody debris (Table 2.5). Hairy Woodpecker presence was positively related to the number of large hardwood trees and inversely related to the average decay class of coarse woody debris (Table 2.5). Yellow-bellied Sapsucker occupancy was explained by the number of large hardwood trees and large snags (Table 2.5).

Downy Woodpeckers were associated with variables only at the landscape scales (300m and 1000m). Downy Woodpeckers were positively related to the area covered by medium-aged hardwood/mixedwood stands and mature hardwood stands within 300m, and early-aged stands within 1000m (Table 2.5).

The occurrence of Northern Flickers and the productivity of Yellow-bellied Sapsuckers were related to variables at local and landscape scales. Northern Flickers were negatively related to the number of small hardwood trees and positively related to

the average decay class of coarse woody debris at the local scale (Table 2.5). Their occurrence was further explained by negative associations with the area covered by mature mixedwood and medium-aged hardwood/mixedwood stand area 300m, and by a positive association with the area covered by early-aged stands within 1000m of the census point (Table 2.5). Yellow-bellied Sapsucker productivity was positively related to the number of large hardwood trees and large snags within 100m, the area covered by mature mixedwood and medium-aged hardwood/mixedwood stands within 300m, and by mature hardwood stands within 1000m (Table 2.5). In addition, productivity was negatively related to mature mixedwood stand area within 1000m (Table 2.5).

The classification accuracy based on the area under the ROC curves was "outstanding" for the Boreal Chickadee and Northern Flicker models, "excellent" for the Red-breasted Nuthatch, Yellow-bellied Sapsucker, and Yellow-bellied Sapsucker Productivity models, and "acceptable" for the Downy Woodpecker model (terms from Hosmer and Lemeshow 2000, Table 2.6). The area under the ROC curve was 0.64 for the Hairy Woodpecker model, indicating a model that is very weak and shows almost no discrimination between presence and absence (Hosmer and Lemeshow 2000, Table 2.6).

2.4 Discussion

Response to local and landscape features was highly variable within this group of six cavity-nesting birds. Boreal Chickadee, Red-breasted Nuthatch, Hairy Woodpecker and Yellow-bellied Sapsucker occurrence was related only to local vegetation variables (100m radius), while Downy Woodpecker occurrence was associated only with landscape characteristics (300m and 1000m radii). Northern

Flickers were strongly influenced by both landscape and local variables, while the productivity of Yellow-bellied Sapsuckers was only weakly associated to landscape characteristics relative to local characteristics. I placed these relationships in the context of the natural history of each species.

Local scale: 100m

My results suggest a general preference for softwood vs. hardwood stand types by Boreal Chickadees and is in accordance with research showing that they are not confined to mature forests (Ficken et al. 1996). While larger trees are needed for nesting, Boreal Chickadees do not specifically require softwood for nesting; nest site selection is based on heartwood softness rather than tree species (Ficken et al. 1996). I found very strong relationships between Boreal Chickadee occupancy and the number of large and small softwood trees, suggesting that tree size might not be as important as softwood stand type. Similarly, Imbeau et al. (1999) found no difference in Boreal Chickadee abundance between shrub, young forest, and mature forest stages in Quebec, and Hagan et al. (1997) found comparable densities of Boreal Chickadees between medium-aged and mature softwood stands in Maine.

My finding that there is a relationship between Boreal Chickadee occupancy and softwood trees is consistent with a study of avian communities in Newfoundland; Boreal Chickadees were significantly more abundant in 40 and 60 year old mature Balsam Fir stands compared to 80 year old stands (Thompson et al. 1999). Thompson et al. (1999) proposed that Boreal Chickadee density was higher in 'younger' mature stands because these stands had greater numbers of small trees that support spiders, a favoured prey of Boreal Chickadees. Their weak negative association with small hardwood trees also

supports my finding that Boreal Chickadees are showing a general preference for softwood stands in this area. Boreal Chickadee habitat relationships at the local scale were stronger than any of the other cavity-nesting birds, followed by those of another softwood associate, the Red-breasted Nuthatch. McLaren (1975) recorded nest site competition between these two species, and on two occasions saw Red-breasted Nuthatches displace Boreal Chickadees from their nests.

My results indicate that Red-breasted Nuthatches prefer older stands that have highly decayed coarse woody debris and a mature softwood component. This preference is consistent with the known association of Red-breasted Nuthatches with mature coniferous or mixedwood forests (Ghalambor and Martin 1999). For example, Hagan et al. (1997) found that Red-breasted Nuthatch density in Maine industrial forests was highest in mature softwood stands, followed by mature mixedwood. In Quebec, Rail (1996) found that they were common even in predominantly deciduous forests, providing there were a few scattered conifer trees.

Red-breasted Nuthatches use softwood trees for foraging and nesting. They forage primarily on softwood trees throughout the year, relying on large caches of conifer seeds over winter and arthropods during the breeding season (Ghalambor and Martin 1999). They apply softwood resin to their nest cavity entrances as a possible deterrent to nest predators or competitors (personal observation, Rail 1996, Ghalambor and Martin 1999). Although research indicates that these weak excavators select nest trees based on softened wood rather than tree species (Steeger and Hitchcock 1998, Ghalambor and Martin 1999), the three nests found in my study area were all located in

dead or declining softwood trees (Balsam Fir: dbh=19cm, Balsam Fir: dbh=21cm, White Pine: dbh=37cm).

The Hairy Woodpecker model was very weak, and I can only speculate as to the biological significance of large hardwood trees and lower average decay class of coarse woody debris. Nest site availability may explain the positive relationship between Hairy Woodpecker occupancy and large hardwood trees. Although Hairy Woodpeckers do not nest exclusively in hardwood trees throughout their range (Jackson et al. 2002), all five nests found in my study area were in hardwood trees with dbh > 24cm. Their apparent preference for stands with a mature hardwood component is in agreement with other studies which find an association between Hairy Woodpeckers and mature deciduous, mixed, or conifer forests (when in conifer forests, often related to small component of hardwood) (Lemieux 1996a). Hairy Woodpeckers were present at approximately half of the points censused (45%), so the weak local effect is not explained by ubiquity, i.e. they did not occur at every point. This indicates that either an important variable was not included in the habitat model, or that my study area is generally suitable and points were incorrectly classified as 'non-habitat' for Hairy Woodpeckers.

If my study area was generally suitable to Hairy Woodpeckers, they would not exhibit strong habitat selection within it (Åberg et al. 2000). For example, Haila et al. (1996) studied yearly changes in territory locations of 17 boreal bird species in southern Finland over a six-year period. They found that the majority of species did not follow the model of ideal-free distribution for habitat selection; individuals did not simultaneously assess the quality of all habitats and preferentially occupy the highest quality habitat (Haila et al. 1996, Lima and Zollner 1996). Instead, most of the species

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displayed a strong avoidance for certain habitats and only a weak preference for others. Once the avoided habitats were removed from the analyses, territory location from year to year appeared to vary stochastically (Haila et al. 1996). Haila et al. (1996) refer to this as 'searching for satisfying conditions' rather than 'searching for the best possible conditions'. When available habitats are not all used during a sampling period, an apparent lack of specific habitat association may result. Raphael and White (1984) found that Hairy Woodpeckers were habitat generalists with respect to forest type surrounding nests in Sierra Nevada, and Conner (1980) found that they foraged in a diverse selection of forest types in Virginia. In Maine, Hagan et al. (1997) found Hairy Woodpeckers to have low habitat specificity and highest abundance in regenerating stands. It is interesting that other studies have found Hairy Woodpeckers to have an affinity for old growth forest (e.g. Haney 1999), suggesting the importance of regional studies to the understanding of habitat associations throughout a species' range. Only a long-term study would be able to determine whether weak habitat preferences and a generally suitable region were causing this weak habitat relationship.

The Downy Woodpecker was the only study species for which occurrence was not explained in any part by local variables. The generalist nature of Downy Woodpeckers, together with their process of territory and nest selection, may contribute to the lack of significant local effects. Downy Woodpeckers are renowned for their broad habitat tolerance; they are generally present in deciduous forests or coniferous stands with hardwood understories and may even nest in suburban or agricultural areas (Jackson and Ouellet 2002). Downy Woodpeckers forage largely by gleaning or excavating insects just below the tree surface, and appear to be opportunistic feeders

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(Brenner et al. 1992). They are the smallest woodpecker in North America and their

choice of nest and roosting sites is not as restricted by tree diameter (Jackson and

Ouellet 2002). Downy Woodpecker pairs establish broad territories early in the

breeding season that may cover over 10 ha (Kilham 1983a). Once a nest site is chosen,

the defended territory shrinks to centre on the nest. Therefore it is possible that the

occurrence of Downy Woodpeckers is more reflective of their early territories, i.e.

broader characteristics at a larger scale.

Northern Flicker occupancy in my study was positively related to average coarse

woody debris decay class and negatively related to small hardwood trees. The positive

relationship with the average decay class of coarse woody debris may indicate nest site

suitability. Flickers are weak excavators and snags are important nesting substrates

(Harestad and Keisker 1989). Higher average decay class of coarse woody debris may

be an indication of the decay of snags available in the area. I did not detect a

relationship to snags, but the density of snags within 100m of the census point is likely a

poor measurement of nest site availability for a species with such a potentially large

home range (up to 65 ha, Lemieux 1996b).

Unlike the other cavity-nesting birds, Northern Flickers generally prefer to settle

in open habitats with few trees (Bull et al. 1986, Conner et al. 1975, Conner and

Adkisson 1977, Moore 1995). Almost one half of the summer diet of Northern Flickers

consists of ants, for which they forage on open ground (Bull et al. 1986, Moore 1995).

The negative relationship to the number of small hardwood trees is consistent with the

Flicker's association with open areas. Univariate models of local vegetation further

imply the relationship between Flickers and open areas in my study, although these

variables were not included in the final model due to intervariable correlation. The models showed a strong negative relationship between Flickers and the number of large hardwood trees and a moderate negative relationship with the number of small softwood trees. It is curious that there was no negative association with the number of large softwood trees, particularly since previous research has found stand structure to be more important to Flickers than tree species (Conner et al. 1975).

Yellow-bellied Sapsucker occurrence and productivity models at the local scale were similar. The Sapsucker occupancy model showed a strong positive relationship to the number of large hardwood trees and a moderately positive relationship to the number of large snags. The Sapsucker productivity model showed a strong positive relationship to large snags, a weak positive relationship to the number of small hardwood trees, and a weak negative relationship to the average decay class of coarse woody debris. The Sapsucker association with large and small hardwood trees accords with research showing a foraging preference for birch sap and to a lesser extent maple sap at the peak of the breeding season (Kilham 1964, Tate 1973). Hardwood trees are also preferred nesting substrates, perhaps explaining the importance of large hardwood trees in the occupancy model (Walters et al. 2002).

The relationship to large snags is also likely related to nesting. In my study area, 27 out of 52 Sapsucker nests found in years 1999-2001 were in dead trees. This contrasts with the large body of research showing that Sapsuckers typically nest in live aspen trees with heartwood decay fungus (Kilham 1971, Kilham 1983b, Runde and Capen 1987, Harestad and Keisker 1989, Walters et al. 2002). My results are more similar to those of another study in New Brunswick by Gibbon (1970). Few aspen grew

on his study sites and the majority of Sapsucker nests were in birch and maple snags (37 out of 38; Gibbon 1970). The negative relationship to coarse woody debris decay class may indicate a preference for younger-aged stands, but the relationship is too weak to make any further inferences.

Landscape scales: 300m, 1000m

Boreal Chickadee, Red-breasted Nuthatch, and Hairy Woodpecker occurrence was not affected by larger scale factors once the effect of local vegetation was removed. Schmiegelow et al. (1997) found that Red-breasted Nuthatch abundance declined two years after forest fragments were isolated by 200m clearcut buffers, and Hagan et al. (1997) found that Boreal Chickadees were more likely to be present in homogeneous landscapes. However Hagan et al. (1997) did not take into account local habitat models, and the relationship may have disappeared if the confounding effect of local vegetation had been removed.

Downy Woodpeckers are generally found in deciduous forests throughout their range (Jackson and Ouellet 2002). This is consistent with my findings: Downy Woodpecker occupancy was positively related to medium-aged hardwood/mixedwood stands and mature hardwood stands within 300m, and early-aged stands within 1000m. As suggested above, the landscape model may characterise early territory selection. But the model was weak overall, and may be attributed again to their broad habitat tolerance. Saab (1999) also found a relationship between the occurrence of Downy Woodpeckers and landscape features. She looked at habitat use by breeding birds in riparian forests simultaneously at three spatial scales. Downy Woodpeckers were detected more often

in open cottonwood riparian forest patches surrounded by an agricultural landscape (Saab 1999).

Northern Flickers in my study were related to stand cover types within 300m and 1000m. Lawler and Edwards (2002) also found that Northern Flickers were sensitive to landscape characteristics, although they did not remove the confounding effect of local vegetation. They built models to predict the nesting habitat of cavity-nesting birds in Utah using landscape composition and configuration variables measured over a range of scales (0.8-98 ha). The model with the highest nest classification rate for Flickers corresponded to the 56.3 ha scale, and the strongest predictors were associated with open areas (Lawler and Edwards 2002). My model similarly shows the association of Flickers and open areas; Flickers were negatively related to medium-aged hardwood and mixedwood stands and mature mixedwood stands within 300m, and positively related to early-aged stands within 1000m.

Home range size may also be contributing to the importance of larger scale variables to the Downy Woodpecker and Northern Flicker. These two species may have home ranges that extend farther than the 'local' 100m buffer. There have been no detailed studies of territory or home range for either of these species, and the recorded sizes in the literature vary widely (Downy Woodpecker: 2-15 ha, Northern Flicker: 5-65 ha; Kilham 1974, Lemieux 1996b, Lemieux 1996c). I did not measure home range sizes in my study, so further research is required to verify this possibility.

Interestingly, while the Yellow-bellied Sapsucker local presence and productivity models were alike, the productivity of Yellow-bellied Sapsuckers was also explained by variables at a landscape scale. According to Van Horne (1983), increased

competition may cause individuals to settle in inferior habitat when population densities are high. Yellow-bellied Sapsuckers were very common across my study area (present at 85% of the points), so the landscape variables distinguish higher quality habitat selected by productive individuals. Although the use of occupancy may obscure the finer details of habitat quality compared to productivity, I would not go so far as to conclude that occupancy is a misleading indicator. The local variables accounted for the greatest proportion of explained deviance in Sapsucker productivity, and were similar to those in the occurrence model.

Yellow-bellied Sapsucker productivity was positively related to medium-aged mixedwood/hardwood and mature mixedwood stand areas within 300m. Likewise, Gibbon (1970) found that Sapsuckers in his New Brunswick study were abundant in open mixedwood stands, rare along hardwood slopes, and absent from dense conifer stands. The 300m landscape model for Yellow-bellied Sapsucker productivity may be related to foraging, particularly with respect to the mixedwood stands. The diet of Yellow-bellied Sapsuckers varies throughout the breeding season. In early spring they feed primarily on conifer phloem sap and bast (i.e. soft inner bark and sap associated with it) while deciduous trees are still dormant. After leaf-out they switch to deciduous trees such as birches, and to a lesser extent maples, with their higher sugar content (Kilham 1964, Tate 1973). Perhaps more fit Sapsuckers are able to key in on these mixed stand characteristics and outcompete others when setting out their territories.

Yellow-bellied Sapsucker productivity was positively related to mature hardwood stands and negatively to mature mixedwood stands within 1000m. The positive relationship to mature hardwood stand area may be related to foraging and

nesting substrate availability (see local section). The negative relationship to mature mixedwood stand area is curious, especially given that the relationship was positive in the univariate analysis and there was a positive relationship to mature mixedwood stand area within 300m. Perhaps this points towards some sort of threshold in mixedwood preference, but this is only speculation given the small amount of deviance explained (2.4%).

Trends in local vs. landscape scales

Generalisations are difficult to make in light of the large variation in species response but, as I expected, smaller scale factors play a greater role in explaining the species data on average; 1000m variables generally explained the least amount of deviance (0-5.1%) once the effects of lesser scales were removed. A study of songbird abundance by Lichstein et al. (2002) also found that landscape effects were less important than local habitat in a mid- to late successional study area. Similarly, McGarigal and McComb (1995) found that while landscape did play a part in explaining breeding bird abundance in fragmented forest landscapes, local vegetation variables were not measured and there was a large amount of unexplained variation. They could not conclude that landscape structure was a dominant factor related to species' abundance, and found that landscape relationships varied widely among species (McGarigal and McComb 1995).

Based on a review of bird and mammal studies from landscapes with different proportions of suitable habitat, Andren (1994) concluded that landscape effects might not become apparent until the amount of suitable habitat remaining in a landscape dropped below a threshold of 10-30%. Over half of my study area is covered in late

successional forest (51%), followed by medium-aged (19%), early-aged (7%), and clearcut (19%), so it would make sense that early-successional species would be affected more strongly by landscape effects than late successional species. Indeed, Downy Woodpeckers and Northern Flickers, the two study species generally associated with younger seral stages, exhibited the strongest landscape effects relative to their local habitat models.

The diversity of responses that I observed indicates that landscape investigations should be species-specific and models are best understood in terms of each species' natural history. Analyses that group species together may miss important relationships if one species' response counteracts that of another.

Table 2.1. Forest stand classification

Stand Type	Description
Recent clearcut	age=recent clearcut
Early-aged	age=early
Medium-aged hardwood [a]	>75% hardwood, age=medium
Medium-aged softwood [b]	>75% softwood, age=medium
Medium-aged mixedwood	50-75% hardwood or softwood, age=medium
Mature hardwood [a]	>75% hardwood, age=mature
Mature softwood [b]	>75% softwood, age=mature
Mature mixedwood	50-75% hardwood or softwood, age=mature

[a]Sugar Maple (*Acer saccharum* Marsh.), Red Maple (*Acer rubrum* L.), White Birch (*Betula papyrifera* Marsh.), Yellow Birch (*Betula alleghaniensis* Britt.), Beech (*Fagus grandifolia* Ehrh.), Trembling Aspen (*Populus tremuloides* Mich.)
[b]Red Spruce (*Picea rubens* Sarg.), White Spruce (*Picea glauca* (Moench) Voss), Black Spruce (*Picea mariana* (Mill.) BSP), Balsam Fir (*Abies balsamea* (L.)), Eastern White Cedar (*Thuja occidentalis* L.), White Pine (*Pinus strobus* L.)

Table 2.2. Productivity ranks for species based on observations at each census point

Rank	Description
0	not present
1	male or unknown individual present once
2	territory[a]
3	pair, nest, or nestlings
4	fledglings

[a]female detected once or species detected more than once

Table 2.3. Stand development stage based on the age of the dominant tree species.

Species	Recent clearcut (years)	Early-aged (years)	Medium-aged (years)	Mature (years)
Balsam Fir	0-10	11-25	26-50	50+
Red Spruce	0-10	11-30	31-70	70+
Black Spruce	0-10	11-30	31-70	70+
White Spruce	0-10	11-20	21-60	60+
White Pine	0-10	11-30	31-90	90+
Red Pine	0-10	11-20	21-70	70+
Eastern White Cedar	0-10	11-30	31-70	70+
Tolerant Hardwood	0-10	11-30	31-80	80+
Intolerant Hardwood	0-10	11-20	21-40	40+

Table 2.4. Occupancy data for cavity-nesting bird species (n=73 census points)

Species	Occurrence
Boreal Chickadee	36
Red-breasted Nuthatch	52
Downy Woodpecker	38
Hairy Woodpecker	33
Northern Flicker	27
Yellow-bellied Sapsucker	62
Yellow-bellied Sapsucker Productivity[a]	44

[a]evidence of productivity (rank 3-4, Table 2.2)

Table 2.5. Results of logistic regression models relating cavity-nesting bird species occurrence to variables measured at successively larger spatial scales. Direction of relationships is indicated by a (+) or (-). For all models, n=73.

Species	Spatial Scale	Variable[a]	Variable		Spatial Scale[b]		Model[c]	
			Deviance (%)	p	Deviance (%)	p	Deviance (%)	p
Boreal Chickadee	local	(+) large sw trees	34.3	3.83E-09	58.5	8.66E-13	58.5	8.66E-13
		(+) small sw trees	19.4	9.24E-06				
		(-) small hw trees	4.8	0.028				
Red-breasted Nuthatch	local	(+) large sw trees	28.7	5.30E-07	31.8	8.90E-07	31.8	8.90E-07
		(+) average decay of cwd	3.1	0.100				
Downy Woodpecker	300 m	(+) medium-aged hw and mw stand area	5.2	0.022	8.2	0.016	10.9	0.012
		(+) mature hw stand area	3.0	0.081				
	1000 m	(+) early-aged stand area	2.7	0.098	2.7	0.098		
Hairy Woodpecker	local	(+) large hw trees	2.7	0.096	4.9	0.083	4.9	0.083
		(-) average decay of cwd	2.2	0.137				
Northern Flicker	local	(-) small hw trees	15.0	1.48E-04	22.1	2.42E-05	48.9	5.60E-09
		(+) average decay of cwd	7.1	0.009				
	300 m	(-) mature mw stand area	11.5	8.80E-04	24.0	9.75E-06		
		(-) medium-aged hw and mw stand area	12.5	5.30E-04				
	1000 m	(+) early-aged stand area	2.8	0.100	2.8	0.100		

Table 2.5 continued.

Species	Spatial Scale	Variable[a]	Variable		Spatial Scale[b]		Model[c]	
			Deviance (%)	p	Deviance (%)	p	Deviance (%)	p
Yellow-bellied Sapsucker	local	(+) large hw trees	13.7	0.004	21.7	0.001	21.7	0.001
		(+) large snags	8.0	0.026				
Yellow-bellied Sapsucker Productivity[d]	local	(+) large snags	18.5	2.03E-05	23.1	4.79E-05	34.2	2.09E-05
		(+) small hw trees	1.3	0.254				
		(-) average decay of cwd	3.2	0.075				
	300 m	(+) mature mw stand area	3.1	0.080	6.0	0.051		
		(+) medium-aged hw and mw stand area	2.9	0.090				
	1000 m	(+) mature hw stand area	2.6	0.109	5.1	0.083		
		(-) mature mw stand area	2.4	0.121				

[a]hw: hardwood, sw: softwood, mw: mixedwood; deviance explained and significance of adding a new variable to the model that already includes the variables listed above it (likelihood-ratio test)

[b]deviance explained and significance of adding a new spatial scale to the model that already includes the smaller spatial scales listed above it (likelihood-ratio test)

[c]deviance explained and significance of full model

[d]presence/absence of productivity (rank 0-2 vs. 3-4, Table 2.2)

Table 2.6. Model deviance and the receiving operating characteristic (ROC) curve area for the full species' models

Species	Model Deviance (%)	Area Under ROC
Boreal Chickadee	58.5	0.95
Red-Breasted Nuthatch	31.8	0.87
Downy Woodpecker	10.9	0.72
Hairy Woodpecker	4.9	0.64
Northern Flicker	48.9	0.92
Yellow-bellied Sapsucker	21.7	0.82
Yellow-bellied Sapsucker Productivity	34.2	0.88
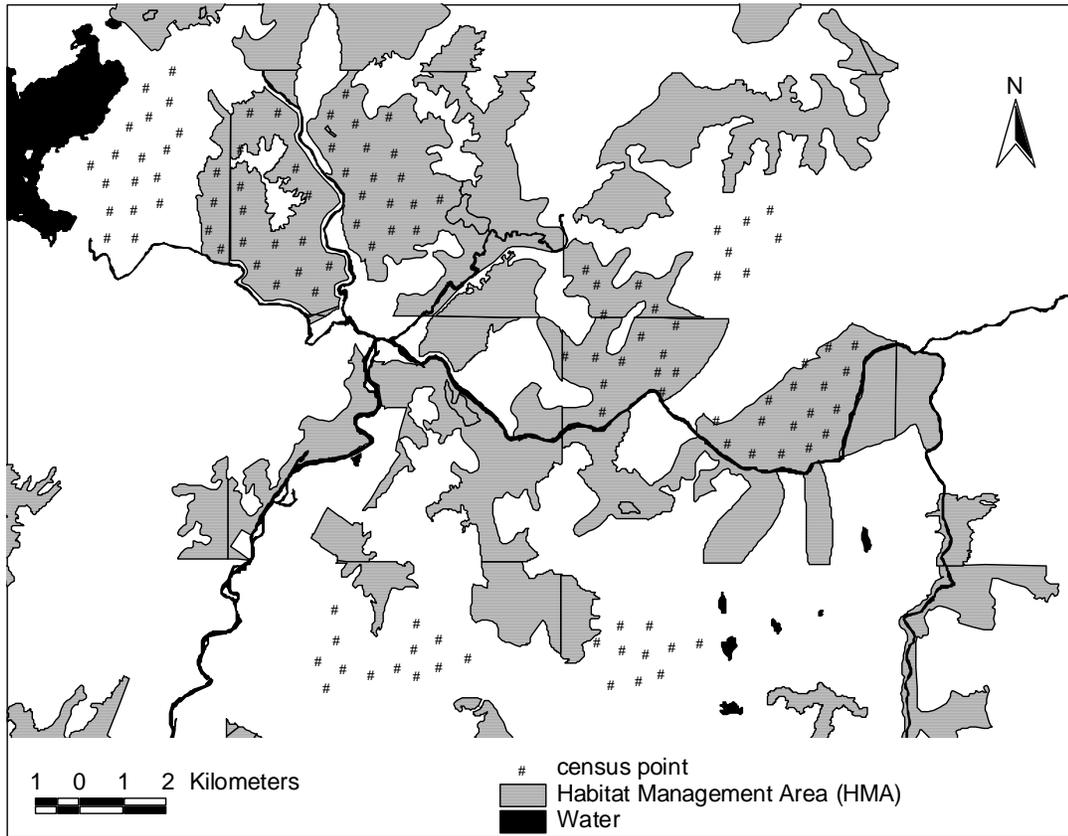
Figure 2.1. Location of 2001 census points in northwestern New Brunswick (47°N, 67°W) on Freehold land owned by Nexfor Fraser Papers.
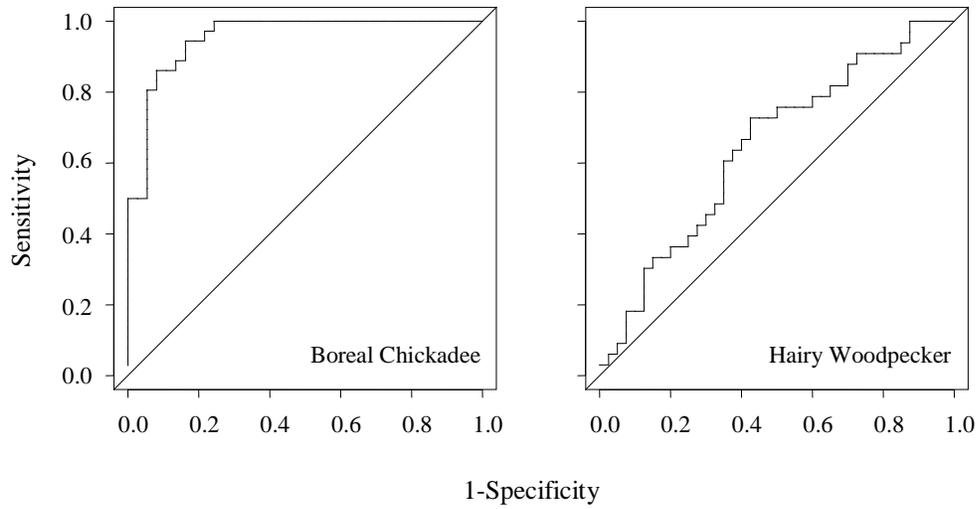
Figure 2.2. Receiver operating characteristic (ROC) curves for Boreal Chickadee and Hairy Woodpecker. Area under the ROC curve for Boreal Chickadee (0.95) indicates that the model has outstanding classification of presence and absence, while the area under the ROC curve for Hairy Woodpecker (0.64) indicates that the model has very poor classification.

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Chapter 3

Characterising woodpecker nesting and foraging substrates

3.1 Introduction

Woodpeckers excavate their own nests and play an important role in forest ecosystems by supplying cavities for secondary cavity-nesting birds and small mammals (Kilham 1971, Erskine and McLaren 1972, Short 1979, Kilham 1983, Daily et al. 1993, Bull and Jackson 1995, Kalcounis and Brigham 1998, Bonar 2000, McClelland and McClelland 2000). Large trees, snags and logs are essential to these species as nesting, drumming, and foraging substrates (Angelstam and Mikusinski 1994, Gunn and Hagan 2000). Because harvesting in industrial forests often occurs before these structures can develop, the provision of woodpecker habitat has been the focus of many forest management recommendations.

Nest site selection often is the dominant factor that determines where individuals settle (Orians and Wittenberger 1991). Therefore, cavity-nesting bird research and management has traditionally focused on nesting habitat. The results of some studies indicate limitation by nest site availability (e.g. Zarnowitz and Manuwal 1985, Eberhardt 1994, Dobkin et al. 1995, Loose and Anderson 1995), while other studies have found that suitable cavity trees do not appear to be limiting to woodpeckers (e.g. Welsh and Capen 1992). Where nest sites are present in excess, other factors such as foraging habitat and food availability may limit breeding population density (Brawn and Balda 1986, Newton 1994). Management approaches often assume that by providing adequate nesting habitat, foraging habitat will also be supplied. This assumption may be

false if characteristics differ between nesting and foraging sites (Swallow et al. 1988, Weikel and Hayes 1999).

The objectives of my study were to describe woodpecker nesting and foraging tree use and preference in northwestern New Brunswick, and to directly compare nesting and foraging substrates used by the most commonly detected woodpecker breeding in the area, the Yellow-bellied Sapsucker (*Sphyrapicus varius*). The results from this study may be applied towards the revision of forest management plans and the protection of cavity-nesting birds in northwestern New Brunswick industrial forests.

3.2 Methods

3.2.1 Study Area

My study was conducted on the industrial forest of Nexfor Fraser Papers in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). The area is within the Acadian forest region of Canada (Rowe 1972). Well-drained upper slopes are dominated by Sugar Maple (*Acer saccharum* Marsh.), Yellow Birch (*Betula alleghaniensis* Britt.), and Beech (*Fagus grandifolia* Ehrh.) (Rowe 1972). Middle slopes are dominated by mixed hardwood of Red Spruce (*Picea rubens* Sarg.), White Spruce (*Picea glauca* (Moench) Voss), and Balsam fir (*Abies balsamea* (L.) Mill.) (Rowe 1972). Spruce, Fir, and Eastern White Cedar (*Thuja occidentalis* L.) dominate Lowland sites (Rowe 1972).

One of the management goals of this privately-owned forest is to provide habitat for a variety of wildlife (Anonymous 1997). Nexfor Fraser Papers (Canada) is working to achieve this goal using designated Habitat Management Areas (HMAs) to support

species associated with mature habitat conditions. Management interventions (e.g. clearcuts, plantations, selection cuts) are still applied to the stands, but they are relatively less common (Anonymous 1997). Sampling points were located in four groups of HMAs and four groups of non-HMAs as part of a larger study. The eight areas were within 270 km^2 and ranged in size from 300-900 ha.

3.2.2 Nesting and foraging and observations

Surveys were conducted during the 2000 and 2001 breeding seasons (mid-May to the end of August). 71 points within HMAs were sampled in year 2000 and year 2001, and 48 additional points were sampled in areas surrounding the HMAs in year 2001. All points were separated by at least 600m. Nests were found through chance observations, by the sound of excavation, nestlings calling, or by following parents to the nest. Woodpeckers commonly start more than one potential nest hole early in the breeding season (Conner 1978, Short 1979). Some researchers propose that potential cavity trees are abandoned if they are not suitably decayed (Conner et al. 1976), but Short (1979) suggests that the excavation of partial holes may be adaptive, allowing pairs to renest quickly after the loss of their first nest due to predation or competition. A nest was confirmed as active based on evidence of incubation, fecal sac removal, nestlings calling within a nest, or by observing parents bringing food into the nest. Due to logistic restrictions the nests were revisited only approximately every two weeks to confirm whether they were active. Some of the excavations without confirmation may have been active nests, and some may have been excavated as suitable alternates. Therefore, while 87% of the nests were confirmed as active (n=66), all nests were included in the analysis.

Foraging surveys were conducted in the morning by walking 100m in each cardinal direction from the sampling points; every point was sampled at least once during the breeding season. Species, sex, age, activity, location and height on tree were recorded. I also located birds while walking between points. Initial observations only were used in the analyses due to concerns over the lack of independence of sequential observations (Hejl et al. 1990, Raphael 1990, Recher and Gebski 1990).

3.2.3 Description of nesting and foraging trees

I recorded tree species, diameter at breast height (dbh), bark cover class, presence of broken top or branches, decay class (healthy tree, declining tree, and snag), cavity orientation and nest height for each nesting or foraging tree. Most of the available trees (>90%) were covered by 96-100% bark, which caused the expected frequency of used trees in the other five classes (0-5%, 6-25%, 26-50%, 51-75%, 76-95%) to be extremely low. Therefore, the use and availability of all six classes are displayed graphically, and the six classes of bark cover were simplified into two classes (0-95% and 96-100% cover) for analyses. Nesting and foraging data from years 2000 and 2001 were combined in order to increase sample sizes. There were insufficient data to test for differences in nest tree character use between years. The sample of foraging bouts by Yellow-bellied Sapsuckers was large enough to test for differences in all characteristics except for tree species. There was no difference in the proportion of tree characteristics (hardwood trees, trees with broken branches, trees with broken tops, trees with missing bark, decay stages) used by foraging Yellow-bellied Sapsuckers in year 2000 and year 2001 (all tests: p>0.05, contingency table analyses).

3.2.4 Description of available trees

Local vegetation characteristics were measured at three 10- by 20-m quadrats within 100m of each sampling point. One quadrat was centred at the point, and two quadrats were placed 75m from the point in two randomly selected directions: 0 degrees, 120 degrees, or 240 degrees. Each tree ≥ 8 cm dbh was tallied, identified to species, and measured for dbh, presence of a broken top or branches, bark cover class, and decay class.

3.2.5 Statistical Analyses

Nesting

Yellow-bellied Sapsuckers dominated the nest sample, so I analysed the data separately for Sapsuckers, and for all other species pooled together.

The randomness of nest cavity orientations was tested using the Rayleigh test (Gutzwiller and Anderson 1987, Zar 1999); mean angles are reported with angular deviation, a measure analogous to linear standard deviation (Zar 1999).

Non-random use of tree diameters was tested using Mann-Whitney U-tests. Contingency tables were used to compare the proportions of tree character use and availability in the study area; Fisher exact tests were used to analyse 2x2 contingency tables and the chi-square statistic was used to analyse variables with more than two levels (Zar 1999). Average expected frequencies in the contingency tables exceeded the minimum recommendations set out by Zar (1999). When a test between more than two categories was significant, multiple comparisons were made using confidence intervals for the difference between the used and available proportions. A negative interval indicates use in greater proportion to availability, a positive interval indicates use in lesser proportion to availability, and an interval that includes zero indicates no

significant relationship. The Dunn-Šidák method was used to adjust the α-levels of the individual tests to ensure an experimentwise error rate of α=0.05 (Sokal and Rohlf 1995).

The evaluation of resource preference using this method is critically dependent on the definition of available substrates because the presence of some items can influence the apparent preference of others (Johnson 1980, Harestad and Keisker 1989). Therefore, tree species were removed from the nesting analyses if they constituted less than 1% of the total number of trees and were not used by nesting woodpeckers at any time; Balsam Poplar (*Populus balsamifera*), and Pin Cherry (*Prunus pensylvanica*) were excluded from the analyses of nesting woodpeckers, and Eastern White Pine (*Pinus strobus*) was also excluded from the analyses of nesting Yellow-bellied Sapsuckers. Although Yellow Birch and Eastern White Cedar were not used for nesting by any species, they were present in the study area in relatively large amounts (6.8% and 8.8% respectively). Therefore, the nesting analyses were repeated with, and without, these two tree species. The results were all the same except that the significant relationship between Sapsuckers and maple trees became non-significant with the exclusion of Yellow Birch and Eastern White Cedar. Only the results including these species are shown, but it is important to note that I am not confident in the relationship shown between Yellow-bellied Sapsuckers and maple trees. Trees were also excluded from the analyses if they were smaller than the minimum dbh of nest trees found in this study (pooled woodpecker nests dbh $\geq$ 18.8cm, Yellow-bellied Sapsucker nests dbh $\geq$ 21cm) (Runde and Capen 1987, McClelland and McClelland 2000).

Foraging

Less than ten bouts of foraging were recorded for each of four species of woodpeckers: Black-backed Woodpecker (*Picoides arcticus*), Northern Flicker (*Colaptes auratus*), Pileated Woodpecker (*Dryocopus pileatus*), and Three-toed Woodpecker (*Picoides tridactylus*) (Table 3.1). Therefore, they were eliminated from the dataset, and the remaining three species, Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), and Yellow-bellied Sapsucker, were analysed separately. I omitted foraging observations with missing data, so the sample sizes are lower than the total number of initial bouts for some tests. Observations (n=7) of woodpeckers foraging on substrates with dbh ≤ 8cm were omitted because only trees with dbh ≥ 8 cm were measured as available in the vegetation plots. Four Yellow-bellied Sapsuckers and three Hairy Woodpeckers were observed foraging on trees with diameters ranging from 4.5-7.0 cm. These observations represent only 3.2% of the total number of initial bouts, and their exclusion should not affect the final conclusions.

Non-random use of tree diameter was tested using Mann-Whitney U-tests. Contingency tables and confidence intervals for the difference between proportions were used to compare tree character use and relative availability in the study area, and Fisher exact tests were used to analyse the 2x2 contingency tables (Zar 1999). As with the nesting analyses, tree species not used and constituting less than 1% of the available trees were excluded; Mountain Ash (*Sorbus sp.*), Willow (*Salix sp.*), Eastern White Pine, Balsam Poplar, and Pin Cherry were excluded from all of the foraging analyses. Snags not identified to species (n=48) were pooled into one category for tree species use and availability comparisons.

Yellow-bellied Sapsucker: nesting versus foraging substrates

Categorical variables of Yellow-bellied Sapsucker nesting trees were compared to foraging trees using contingency tables and confidence intervals for the difference between proportions. The difference in diameter between nesting and foraging trees was tested using a Mann-Whitney U-test.

3.3 Results

Nest sample

I found 18 woodpecker nests in year 2000 and 54 in year 2001. Also included in the analyses are 4 nests found in the study area in 1999. I found over half of the nests (57%, n=43) by following foraging adults and through chance observations. An additional 16 nests (21%) were discovered by the sound of excavating pairs and 17 nests (22%) by the sound of calling nestlings. Sixty-six nests (87%) were confirmed as active. Seven out of the ten nests without confirmation were discovered during the excavation period.

Yellow-bellied Sapsuckers were by far the most common woodpecker species observed nesting in the study area (n=52). Black-backed Woodpecker (n=2), Downy Woodpecker (n=6), Hairy Woodpecker (n=5), Northern Flicker (n=9) and Pileated Woodpecker (n=2) nests were also found. The nest tree diameters and cavity heights were within the normal range found in the Maritime Provinces (Table 3.2). The cavity entrances did not differ significantly from random orientation for either Yellow-bellied Sapsucker nests (p>0.05, Rayleigh's Test) or the pooled sample of other woodpecker nests (p>0.05, Rayleigh's Test) (Figure 3.1a, b).

Nest tree diameter

The minimum dbh for Yellow-bellied Sapsucker nest trees was 21 cm, representing the upper 29% of the trees available ≥ 8cm dbh. The mean dbh (± SD) of trees used by Sapsuckers for nesting was 37.1 ± 11.5 cm. The minimum dbh for the other woodpecker nest trees was 18.8 cm, representing the upper 35% of the trees available ≥ 8cm dbh. The mean dbh (± SD) of trees used by the other woodpeckers for nesting was 39.5 ± 17.1 cm. Two of the six Downy Woodpecker nest trees had dbh's smaller than 21 cm, accounting for the lower minimum dbh for the pooled woodpecker sample. Both the Yellow-bellied Sapsucker nests and the pooled sample of other woodpecker nests were in trees with disproportionately large diameters compared to those available ($p<0.0001$, Mann-Whitney U-tests, Figure 3.2).

Nest tree species

Yellow-bellied Sapsuckers showed a preference for nesting in hardwood trees (Table 3.3). Trembling Aspen and maple trees were used in greater proportion than their availability, and Balsam Fir and spruce trees were used in lesser proportion than their availability (Table 3.4). Maple species were pooled in the tree species analyses because of the large number of nests in unidentified maple snags; these unidentified snags were likely Red or Sugar Maple. Yellow Birch and Eastern White Cedar trees were not used for nesting and the analyses were repeated without these species. When these two species were removed, the relationship between Sapsucker nest use and availability of maple trees was non-significant. The sample size was too low to test for tree species preference by the other woodpeckers, but they did show a significant preference for hardwood trees (Table 3.3, Table 3.4).

Nest tree condition

Yellow-bellied Sapsuckers were more likely to nest in trees with broken tops, broken branches, and missing bark (Table 3.3, Figure 3.3). Their nest trees were more likely to be dead and less likely to be alive than the trees available, while declining trees were used in proportion to their availability (Table 3.3). However, these results mask differences in selection of nest tree condition between tree species. Trembling Aspen and maple trees were used most frequently for nesting by Yellow-bellied Sapsuckers, and the relationships to tree condition differed markedly between the two species. Sapsuckers showed no preference for broken tops, broken branches, missing bark, or decay stage in trembling aspen nests (Table 3.3). However, they did show strong preferences for nesting in maple trees with broken tops, broken branches and missing bark (Table 3.3). Nests in maple trees were also found more often in dead trees and less often in live trees than expected based on their availability (Table 3.3).

The sample size was too low for the pooled woodpecker nest sample to similarly separate the analyses by nest tree species, but overall the other woodpeckers showed preferences for trees with broken tops, broken branches, and missing bark (Table 3.3). They were also more likely to nest in dead rather than live trees, and used declining trees in proportion to their availability (Table 3.3).

Foraging sample

A total of 211 initial bouts of foraging woodpeckers was recorded in years 2000 and 2001. Over half of the bouts were of Yellow-bellied Sapsuckers (n=135, 59%), followed by Downy Woodpeckers (n=44, 21%) and Hairy Woodpeckers (n=26, 12%).

The remaining bouts were of Black-backed Woodpeckers, Northern Flickers, Three-toed Woodpeckers, and two unidentified woodpecker species (Table 3.1).

Foraging tree diameter

Yellow-bellied Sapsuckers, Downy Woodpeckers, and Hairy Woodpeckers foraged on trees disproportionately larger than those available (all tests: $p < 0.0001$, Mann-Whitney U-tests, Figure 3.4).

Foraging tree species

All three species of woodpeckers showed a foraging preference for hardwood trees (Table 3.5). While foraging use of tree species was significantly non-random, the woodpeckers focused their nesting activities on fewer tree species compared to foraging activities. For example, while over 80% of Sapsucker nests were found in just two tree species, 80% of the foraging bouts were observed on seven tree species (Table 3.4, Table 3.6).

Yellow-bellied Sapsuckers used Yellow and White Birch in greater proportion to their availability, Balsam Fir and spruce in lesser proportion to their availability, and did not use Striped Maple (*Acer pensylvanicum* L.) (Table 3.6). Downy Woodpeckers also used Balsam Fir and spruce in lesser proportion to their availability (Table 3.6). The sample size was too low to test for species preference by Hairy Woodpeckers.

Foraging tree condition

All three woodpecker species were more likely to forage on trees with broken branches and missing bark (Table 3.5, Figure 3.5). Unlike the other two species, Downy Woodpeckers used trees with broken tops in proportion to their availability. Although the three species showed significant preferences for trees based on decay, the

relationships differed. Yellow-bellied Sapsuckers preferred declining trees and avoided live trees (Table 3.5). Hairy Woodpeckers also avoided live trees, but showed preferences for both declining and dead trees (Table 3.5). The relationship with tree decay was weakest for Downy Woodpeckers (p=0.035), and use was not significantly different from availability for the individual decay classes based on confidence intervals (Table 3.5).

Yellow-bellied Sapsucker: nesting vs. foraging

Yellow-bellied Sapsuckers used significantly different tree species for foraging and nesting (p<0.0001, chi-square statistic, Figure 3.6). Sapsucker nests were found more often in Trembling Aspen, and less often in birch and Eastern White Cedar compared to the trees at which they were found foraging (all tests: p<0.05, confidence limits on differences in proportions). Nesting trees were significantly larger than foraging trees (p<0.0001, Mann-Whitney U-test, Figure 3.7) and were more likely to be hardwoods, trees with broken tops, and trees with broken branches (Table 3.7). There was no significant difference in use with respect to bark cover, but the difference between tree use and decay stage was highly significant; more nests were found in snags and fewer in declining trees compared to foraging trees, while live trees were used in similar proportions (Table 3.7).

3.3 Discussion

Nesting

The woodpeckers in my study showed very strong preferences with respect to tree size, species, and condition for nesting. Large trees hold larger nest cavities,

provide thicker walls for protection against predators, and may be less likely to break at cavity height compared to small trees (Short 1979, Conner et al. 1975, Harestad and Keisker 1989). The importance of stable nesting structures may also explain the avoidance of certain tree species. Balsam Fir and spruce have shallow root systems and are highly vulnerable to windthrow, perhaps making them risky choices for nesting substrates (Seymour and Hunter 1992, Farrar 1995). Indeed, Balsam Fir and spruce dominated the sample of available softwood trees, and softwood trees were avoided by nesting woodpeckers.

The type of decay typically associated with each different tree species may also influence woodpecker preference. Tree decay facilitates excavation, and the lack of suitably decayed trees may delay or prevent nesting (Conner 1978). Woodpeckers are well adapted to excavation; they have hard chisel-like bills, shock-absorbing muscles, thickened brain cases, toes adapted for vertical clinging, and tails modified to prop their bodies away from tree surfaces (Winkler et al. 1995). Despite these highly developed features, woodpeckers cannot excavate easily in just any tree of sufficient diameter. Studies indicate that strong excavators such as the Hairy Woodpecker, Pileated Woodpecker, and Yellow-bellied Sapsucker require trees with decayed heartwood, and weak excavators such as the Downy Woodpecker and Northern Flicker require trees with both softened heartwood and sapwood (Erskine and McLaren 1972, Conner et al. 1975, Conner 1978, Kilham 1983, Runde and Capen 1987, Harestad and Keisker 1989, Daily 1993, Bonar 2000).

Yellow-bellied Sapsuckers most strongly preferred to nest in Trembling Aspen trees, which are softer than most hardwoods and highly susceptible to heart rot

(McClelland and McClelland 2000, Daily 1993). The sapwood of Trembling Aspen is typically spared by decay, thus providing protection against nest competitors and predators (Kilham 1971). Aspen is widely used for nesting by woodpeckers and particularly Yellow-bellied Sapsuckers throughout their ranges (Lawrence 1966, Runde and Capen 1987, Harestad and Keisker 1989, Li and Martin 1991, Loose and Anderson 1995, Martin and Eadie 1999).

Correctly classifying aspens suffering from heartwood decay using external characteristics can be difficult. The fungi do not necessarily present themselves with obvious fruiting bodies, and even the number of fungal conks have been found to be weak indicators of tree hardness in this species (Conner et al. 1976, Schepps et al. 1999). Yellow-bellied Sapsuckers in my study used Trembling Aspen trees of various decay stages (live, declining, dead) in proportion to their availability. My results are consistent with an Arizona study which found that woodpeckers were able to select softer aspen trees for nesting based on tree characteristics unrelated to external appearance (i.e. live, declining, dead) (Schepps et al. 1999). Similarly, Harestad and Keisker (1989) found that dead and live aspen trees were used for nesting in proportion to their availability by the Yellow-bellied Sapsucker, Pileated Woodpecker, and Hairy Woodpecker.

Yellow-bellied Sapsuckers also exhibited no preferences in aspen trees for the other measures of tree condition (broken tops, broken branches, or missing bark). This may be related to the primary mode of fungal entry. While trees in some studies were likely infected by fungi through a dead branch stub (e.g. Conner et al. 1976, Runde and Capen 1987, Schepps et al. 1999), Daily (1993) found that most of the aspen trees used

for nesting by Red-naped Sapsuckers (*Sphyrapicus nuchalis*) were infected by heartwood decay at or near the base. If heartwood fungi entered initially via the roots, I would not expect a strong relationship to factors such as broken stubs and wounds.

My results were surprising in that the disproportionate use of aspen by nesting Yellow-bellied Sapsuckers was followed by the disproportionate use of maple (likely Red or Sugar Maple) trees. This relationship was weak however, and disappeared when Yellow Birch and Eastern White Cedar were removed from the analyses. In any case, the relationship may indicate that aspen is not widely available throughout my study area and that Sapsuckers are using the second most suitable tree species. Runde and Capen (1987) also found that Red Maple trees were used by woodpeckers in Vermont second most frequently (20%) behind trembling aspen (52%). Furthermore, a study of nesting Yellow-bellied Sapsuckers in central New Brunswick attributed the overwhelming use of Red Maple and birch snags (37 of 38 nests) to a near absence of aspen in the area (Gibbon 1970).

Maple trees have harder wood and thicker tough bark compared to aspen trees (Farrar 1995), and it is understandable that woodpeckers would require maples to be at a more advanced stage of external decay for nesting. Yellow-bellied Sapsuckers nesting in maple trees showed strong preferences for all measures of poor tree condition. Over 73% of the maple trees used for nesting were dead compared to 26% of aspen trees. Most of the nests in living maples were actually in dead portions of living trees; three nests were in dead broken branch or trunk stubs, one nest was located immediately below a broken branch, and only one nest was in an apparently healthy tree, although it did have broken branches.

The other woodpeckers showed strong preferences for nesting in dead trees, trees with broken tops, broken branches, and/or missing bark. Insufficient data make it impossible to determine whether preferences differ between tree species as in the case of the Yellow-bellied Sapsucker. Even if it were possible, the weaker excavators dominated the pooled woodpecker sample (Downy Woodpecker n=6, Northern Flicker n=9), and the differences in condition preferences within tree species may not be as marked.

Various theories have been proposed to explain random and non-random orientation of woodpecker nests. Exposure to the south or east may confer needed light and warmth to nests and may even indicate low quality nest sites, whereby woodpeckers attempt to compensate for the low capacity for insulation of smaller trees (Lawrence 1966, Conway and Martin 1993). Conversely, nest bearings may vary according to microhabitat features or as a consequence of tree angle (Conner 1975). Dobkin et al. (1995) proposed that woodpeckers in their study oriented their nest cavities in response to thermal and microhabitat features; entrances were facing east and southwest, and were significantly oriented toward woodland edges. The nest entrances of Yellow-bellied Sapsuckers and other woodpeckers in my study were not significantly oriented in any particular direction. My results are in agreement with some studies (e.g. Gutzwiller and Anderson 1987), but contrast with others (e.g. Lawrence 1966, Inouye 1976, Dobkin et al. 1995) that detected general orientations to the south or east. I did not measure microclimate, microhabitat or tree angle, but there appears to be little or no thermal compensation at work in the nests found in my study based on cavity orientation.

Foraging

Three woodpecker species were most commonly observed foraging: Downy Woodpecker, Hairy Woodpecker, and Yellow-bellied Sapsucker. Downy and Hairy Woodpeckers forage opportunistically throughout their ranges (Jackson and Ouellet 2002, Jackson et al. 2002). While they both forage on tree surfaces and subsurfaces, Hairy Woodpeckers have better excavating abilities, and Downy Woodpeckers spend more time foraging superficially (Lawrence 1966, Conner 1981). Yellow-bellied Sapsuckers are unique in that they exploit tree sap as an important food resource in addition to insects, fruit, and bast (Tate 1973). Sapsuckers extract xylem sap from trees early in the spring, but rely on phloem sap for the bulk of the breeding season (Eberhardt 1994). They peck long columns of holes out of which sap flows, focusing most of their effort on major sap wells in a few individual trees. Because of their unique foraging behaviour, Yellow-bellied Sapsuckers are discussed separately from Downy and Hairy Woodpeckers. Foraging studies of warblers indicate that a minimum sample size of 30 individuals (Morrison 1984) and even up to 60-70 individuals (Recher and Gebski 1990) is required for the analysis of single point observation data. Therefore, the analyses for Downy Woodpeckers (n=44) and Hairy Woodpecker (n=26) should be interpreted with caution.

The disproportionate use of larger trees by Downy and Hairy Woodpeckers may be related to foraging efficiency (Weikel and Hayes 1999). Arthropod abundance and diversity are influenced by tree age and size as bark becomes thicker and rougher (Jackson 1979). Raphael and White (1984) suggested that cavity-nesting birds spent less time foraging on small trees because small trees supported a lower abundance of

prey. In their study, the birds appeared to balance energy gains (prey availability) and

losses (travel time); medium-sized trees were used in the greatest proportion to their

availability and for the longest periods of time, while rare large trees were used in

proportion to their availability (Raphael and White 1984). The preferences for larger

trees exhibited by Downy and Hairy Woodpeckers in my study supports this premise.

Foraging by Downy and Hairy Woodpeckers was associated with hardwood

trees. I found that Downy Woodpeckers used spruce and Balsam Fir trees in lesser

proportion to their availability, and although no study has shown similar results, Downy

Woodpeckers are generally associated with deciduous forests (Jackson and Ouellet

2002). Because regional preferences for tree species by foraging Downy Woodpeckers

often appears to be driven by insect infestations (Jackson and Ouellet 2002), the

measurement of arthropod abundance in this area may shed insight into tree species

preference and avoidance. The use of tree species by foraging Hairy Woodpeckers

varies widely throughout their range (Jackson et al. 2002). Even the preference of

softwood versus hardwood trees changes from one region to another (Jackson et al.

2002). My observations correspond most closely with those in Quebec and Ontario

boreal forests, where Hairy Woodpeckers used Trembling Aspen and birches more

frequently than softwood trees in summer (Jackson et al. 2002).

Downy and Hairy Woodpeckers did not use trees of different condition in

proportion to their availability. Downy Woodpeckers were only weakly associated with

decay stage, and the multiple comparisons were not significant with adjusted α-levels.

However, the preferences for trees with broken tops and missing bark suggests the

relationship may be with declining and/or dead trees. Relationships may have been

clearer if my data were not pooled across stand types, but the small sample size precluded separating the data. Conner and Crawford (1974) found that Downy Woodpeckers foraged primarily on live trees in mature stands, and snags or downed woody debris in clearcuts.

Hairy Woodpeckers observed in my study favoured declining and dead trees, and avoided live healthy trees as foraging substrates. Their preference for dead and declining trees is also reflected in their disproportionate use of trees with broken tops, broken branches, and missing bark. Preferences for tree decay by foraging Hairy Woodpeckers are not consistent throughout their range (Jackson et al. 2002).

As suggested above for Downy and Hairy Woodpeckers, foraging efficiency may explain the use of larger trees by Yellow-bellied Sapsuckers. Sapsuckers stimulate phloem sap flow in their sap wells by excavating new holes above old ones (Eberhardt 1994). Eberhardt (1994) found that sap flow was correlated with the number of new holes added to the sap well. The new holes produce sap for an average of 3.1 days before going dry (Eberhardt 1994). Because only the uppermost holes produce sap, I propose that tree diameter could limit the potential number of holes and total amount of active sap flow from a sap well.

The strong relationships between Yellow-bellied Sapsuckers and Yellow and White Birch that I detected are consistent with observations of summer feeding by Sapsuckers in New Hampshire (Kilham 1964), Maine (Rushmore 1969), Ontario (Lawrence 1966), New Brunswick (Gibbon 1970), and Michigan (Tate 1973). Yellow-bellied Sapsuckers may prefer species based on sap flow rates and sugar concentration (Walters et al. 2002). The sugar content of Yellow and White Birch phloem sap

measured during their breeding season ranged from 9-28%, with averages around 16-18% (Kilham 1964, Tate 1973, Southwick and Southwick 1980). Amino acids in the phloem may be of secondary importance to feeding Yellow-bellied Sapsuckers. Declining trees often release amino acids into their phloem sap, and Sapsuckers may feed preferentially on declining trees to take advantage of this source of dietary nitrogen (Eberhardt 1994). Future research is needed to address this possibility, but I too observed the disproportionate use of declining trees by Sapsuckers in my study.

It can be difficult to determine whether Sapsuckers select trees initially based on decay stage or ultimately cause the decline. Yellow-bellied Sapsuckers may cause the decline of trees by drilling preliminary holes called primary or satellite bands and by repeated wounding (Kilham 1964, Tate 1973, Eberhardt 1994). It is possible that Sapsuckers exploit declining trees when available, and otherwise create their own. Kilham (1964) observed that virtually all of the original main feeding trees used in three Sapsucker territories were declining as a result of old wounds or infections unrelated to woodpecker activity (Kilham 1964). But in the same season, Sapsuckers laid down primary bands on healthy birches surrounding their main feeding trees, and subsequently used them as main feeding trees the following year (Kilham 1964). Sapsuckers in my study showed significant relationships to trees with broken tops, branches, and/or missing bark, which may indicate preferences for declining conditions unrelated to the construction of sap wells.

Yellow-bellied Sapsucker: nesting vs. foraging

Sapsuckers were the most abundant woodpecker in my study area, and the only species abundant enough to make direct comparisons between nesting and foraging

substrates. Superficially, it appeared that Sapsuckers selected similar substrates for nesting and foraging (preference for large hardwoods, avoidance of healthy trees), however, this was not the case. Although they did prefer to nest and forage on large trees, nest tree size is more restrictive than foraging tree size – they physically cannot nest in a small tree. Furthermore, the similar selection of hardwood trees masks very important differences between actual tree species used for nesting (aspen and maple) versus foraging (Yellow and White Birch). Lastly, nesting and foraging trees differed significantly with respect to tree decay and condition. Nest trees were more likely to be dead and foraging trees were more likely to be in a state of decline. Nest trees were also more likely to have broken tops and broken branches.

Swallow et al. (1988) also found that woodpeckers appear to be more tolerant of variations in tree size and condition for foraging than nesting. My results stress the importance of considering both nesting and foraging substrates for the management of this species.

Table 3.1. Observations of initial foraging bouts (year 2000, 2001).

Woodpecker species	initial bouts
Black-backed Woodpecker	7
Downy Woodpecker	44
Hairy Woodpecker	26
Northern Flicker	1
Pileated Woodpecker	4
Three-toed Woodpecker	2
Yellow-bellied Sapsucker	125
Unknown woodpecker	2
Total	211

Table 3.2. Comparison of mean dbh (cm) and cavity height (m) of nest trees for the six woodpecker species.

	Present study				Towers et al. 1992 [a]			
	Mean	SD	Range	N	Mean	SD	Range	N
Nest tree dbh (cm)								
Black-backed Woodpecker	22.7	1.9	21.3-24.0	2	23.4	4.3	17.0-30.5	17
Downy Woodpecker	37.8	27.6	18.8-84.6	6	27.6	9.8	15.0-43.0	7
Hairy Woodpecker	35.6	10.7	24.9-49.2	5	32.8	16.3	12.0-91.4	26
Northern Flicker	43.3	12.4	29.2-70.2	9	33.0	14.5	15.2-77.0	29
Pileated Woodpecker	54.4	2.7	52.5-56.3	2	44.5	13.0	25.4-61.0	10
Yellow-bellied Sapsucker	37.1	11.5	21.0-64.7	52	31.3	11.9	16.5-76.2	41
Cavity height (m)								
Black-backed Woodpecker	5.0	2.1	3.5-6.5	2	3.8	1.9	0.6-10.8	42
Downy Woodpecker	9.0	5.0	4.0-16.0	6	5.3	3.3	1.2-15.4	43
Hairy Woodpecker	10.0	4.2	5.5-16.5	5	6.5	3.0	1.5-15.4	101
Northern Flicker	9.4	3.5	6.5-17.3	9	4.3	2.8	0.5-15.4	170
Pileated Woodpecker	14.3	1.8	13.0-15.5	2	7.4	2.9	3.1-18.5	22
Yellow-bellied Sapsucker	10.4	3.6	3.3-22.0	52	7.3	3.3	1.8-16.9	81

[a] data collected from New Brunswick, Nova Scotia, and Prince Edward Island nest records in Maritimes Nest Records Scheme 1895-1989, and nests from 1990-91 wildlife habitat studies in Nova Scotia (n=17) and Prince Edward Island (n=14)

Table 3.3. Woodpecker use of tree characteristics for nesting

| Variable | All tree species | | Trembling Aspen | Maple spp. |
	Yellow-bellied Sapsucker[c] n=52	Other Woodpeckers[d] n=24	Yellow-bellied Sapsucker n=23	Yellow-bellied Sapsucker n=19
Hardwood trees	$p < 0.0001$	$p < 0.0001$		
Broken tops	$p < 0.0001$	$p < 0.0001$	$p=0.209$	$p < 0.0001$
Broken branches	$p < 0.0001$	$p < 0.0001$	$p=0.366$	$p < 0.0001$
Missing bark	$p < 0.0001$	$p < 0.0001$	$p=0.400$	$p < 0.0001$
Decay	$p < 0.0001$	$p < 0.0001$	$p=0.370$	$p < 0.0001$
	live[a]	live[a]	live	live[a]
	declining	declining	declining	declining
	dead[b]	dead[b]	dead	dead[b]

[a]foraging intensity significantly less than expected at $p<0.05$ based on positive confidence limits on difference between used and available proportions
[b]foraging intensity significantly greater than expected at $p<0.05$ based on negative confidence limits on difference between used and available proportions
[c]p-values from Fisher Exact Tests and chi-square analyses of contingency tables comparing tree species use versus availability
[d]Black-backed Woodpecker (n=2), Downy Woodpecker (n=6), Hairy Woodpecker (n=5), Northern Flicker (n=9), and Pileated Woodpecker (n=2)

Table 3.4. Woodpecker use of tree species for nesting

Tree species[c]	Yellow-bellied Sapsucker		Other Woodpeckers[h]	
	available[f] (%) n=1466	used (%) n=52	available[g] (%) n=1786	used (%) n=24
Balsam Fir	29.5	1.9 [a]	30.0	4.2
Yellow Birch	7.2	0.0 [a]	6.2	0
White Birch	4.2	5.8	4.5	8.3
American Beech	3.3	9.6	3.1	8.3
Maple spp.	16.0	36.5 [b]	15.3	37.5
Eastern White Pine[d]			0.2	4.2
Trembling Aspen	6.8	44.2 [b]	6.0	29.2
Spruce spp.	22.4	1.9 [a]	21.0	8.3
Eastern White Cedar	10.6	0.0 [a]	9.0	0
Pearson Chi-square[e]		137.63		not tested
probability		1.00E-15		not tested

[a]foraging intensity significantly less than expected at p<0.05 based on positive confidence limits on difference between used and available proportions

[b]foraging intensity significantly greater than expected at p<0.05 based on negative confidence limits on difference between used and available proportions

[c]woodpecker nests: Red Maple (n=3), Sugar Maple (n=5), unidentified maple snags (n=20); available: Red Maple (n=102), Sugar Maple (n=169), unidentified maple snags (n=12), Striped Maple (n=1), Mountain Maple (n=3)

[d]not included in Yellow-bellied Sapsucker analysis because species not used and percent availability <1%

[e]chi-square analysis of contingency table comparing tree species use versus availability

[f]trees ≥21.0cm dbh (minimum nest tree size)

[g]trees ≥18.8cm dbh (minimum nest tree size)

[h]Black-backed Woodpecker (n=2), Downy Woodpecker (n=6), Hairy Woodpecker (n=5), Northern Flicker (n=9), and Pileated Woodpecker (n=2)

Table 3.5. Woodpecker use of tree characteristics for foraging

Characteristic	Yellow-bellied Sapsucker[c] n = 125	Downy Woodpecker n = 44	Hairy Woodpecker n = 26
Hardwood trees	$p < 0.0001$	$p < 0.0001$	$p = 0.002$
Broken tops	$p = 0.032$	$p = 0.138$	$p = 0.001$
Broken branches	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
Missing bark	$p < 0.0001$	$p < 0.0001$	$p = 0.003$
Decay	$p < 0.0001$ live[a] declining[b] dead	$p = 0.035$ live declining dead	$p < 0.0001$ live[a] declining[b] dead[b]

[a]foraging intensity significantly less than expected at p<0.05 based on positive confidence limits on difference between used and available proportions

[b]foraging intensity significantly greater than expected at p<0.05 based on negative confidence limits on difference between used and available proportions

[c]p-values from Fisher Exact Tests and chi-square analyses of contingency tables comparing tree species use versus availability

Table 3.6. Woodpecker use of tree species for foraging

Tree Species	Available[d]	Use			
		All Woodpeckers	Yellow-bellied Sapsuckers	Downy Woodpeckers	Hairy Woodpeckers
	(%)	(%)	(%)	(%)	(%)
	n=5048	n=209	n=125	n=44	n=25
Balsam Fir	35.9	11.5 [a]	10.4 [a]	9.1 [a]	16.0
Striped Maple	1.4	1.0	0.0 [a]	4.5	0.0
Red Maple	5.6	11.5	12.8	6.8	20.0
Sugar Maple	7.9	6.2	4.8	11.4	8.0
Mountain Maple	2.4	1.0	0.0 [a]	4.5	0.0
Yellow Birch	5.3	17.7 [b]	20.0 [b]	15.9	12.0
White Birch	8.7	17.2 [b]	23.2 [b]	11.4	4.0
American Beech	3.0	5.3	4.8	9.1	4.0
Trembling Aspen	5.0	8.1	8.0	9.1	12.0
Spruce spp.	19.9	9.1 [a]	5.6 [a]	2.3 [a]	12.0
White Cedar	4.1	7.2	8.0	9.1	0.0
Unidentified Snag	1.0	4.3	2.4	6.8	12.0
Pearson Chi-square[c]		162.84	137.80	54.18	not tested
probability		1.00E-15	1.00E-15	1.10E-07	not tested

[a]foraging intensity significantly less than expected at $p<0.05$ based on positive confidence limits on difference between used and available proportions
[b]foraging intensity significantly greater than expected at $p<0.05$ based on negative confidence limits on difference between used and available proportions
[c]chi-square analysis of contingency table comparing tree species use versus availability
[d]trees ≥8cm dbh

Table 3.7. Nesting vs. foraging use of tree characteristics by Yellow-bellied Sapsuckers

Variable	Nest tree vs. Foraging tree[c]
Hardwood trees	$p = 0.001$
Broken tops	$p < 0.0001$
Broken branches	$p = 0.001$
Missing bark	$p = 0.134$
Decay	$p < 0.0001$
	live
	declining[a]
	dead[b]

[a]nest trees significantly less than foraging trees at $p<0.05$ based on positive confidence limits on difference between proportions
[b]nest trees significantly more than foraging trees at $p<0.05$ based on positive confidence limits on difference between proportions
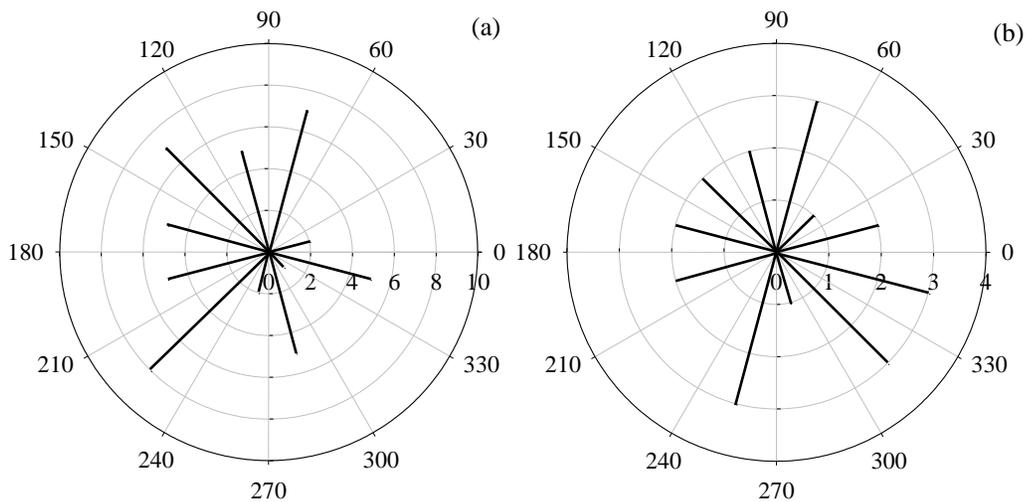[c]p-values from Fisher Exact Tests and chi-square analyses of contingency tables

Figure 3.1. Circular histograms of cavity orientations from (a) 52 Yellow-bellied Sapsucker nest cavities (mean $\theta = 162° \pm 71°$), and (b) 24 other woodpecker nest cavities (mean $\theta = 39° \pm 77°$) (other woodpecker nests: Black-backed Woodpecker n=2, Downy Woodpecker n=6, Hairy Woodpecker n=5, Northern Flicker n=9, and Pileated Woodpecker n=2).
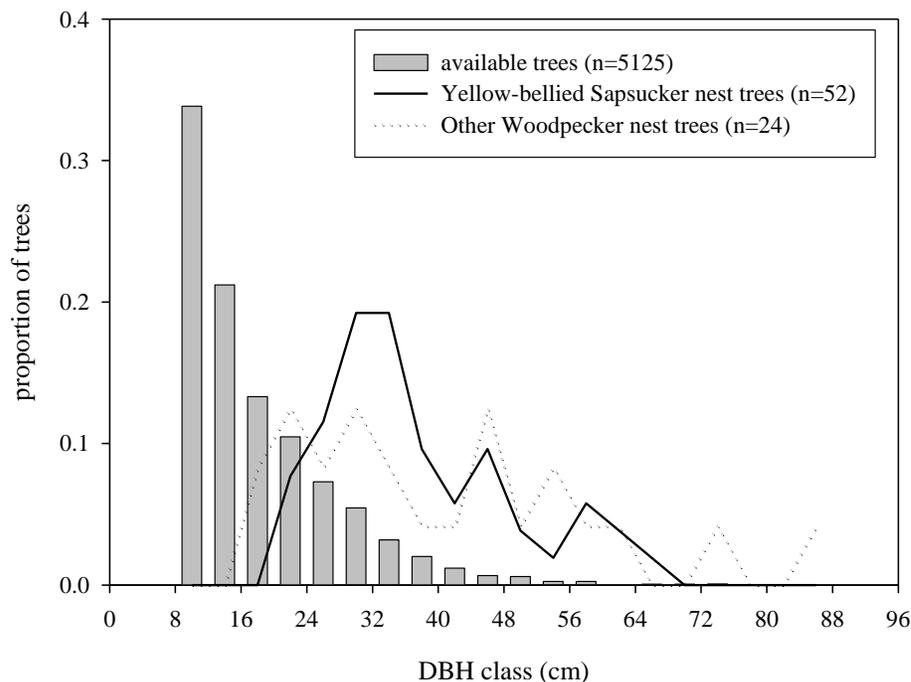

Figure 3.2. Yellow-bellied Sapsucker and other woodpecker use of nesting trees by diameter class (dbh) vs. availability (other woodpecker nests: Black-backed Woodpecker n=2, Downy Woodpecker n=6, Hairy Woodpecker n=5, Northern Flicker n=9, and Pileated Woodpecker n=2).
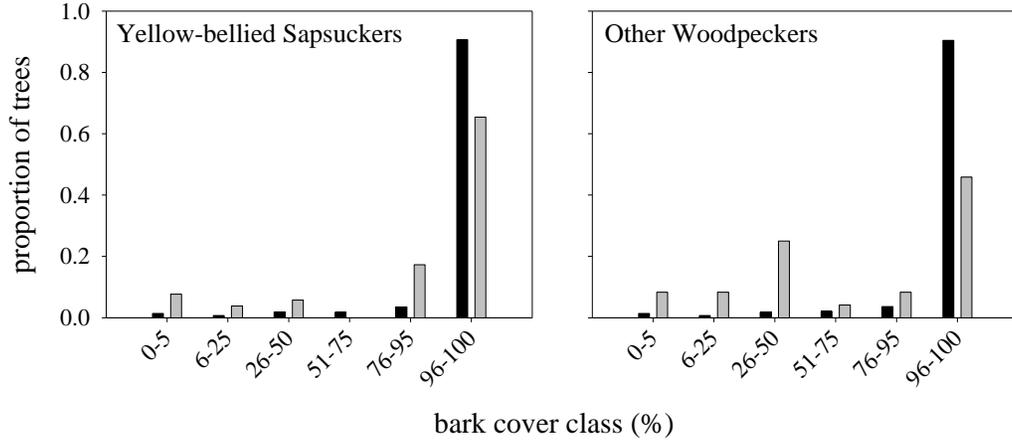
Figure 3.3. Woodpecker nesting use of trees (grey) vs. availability (black) by bark cover class (trees available to Yellow-bellied Sapsuckers n=1473; Yellow-bellied Sapsucker nests n=52; trees available to other woodpeckers n=1794; other woodpecker nests n=24; other woodpecker nests: Black-backed Woodpecker n=2, Downy Woodpecker n=6, Hairy Woodpecker n=5, Northern Flicker n=9, and Pileated Woodpecker n=2).

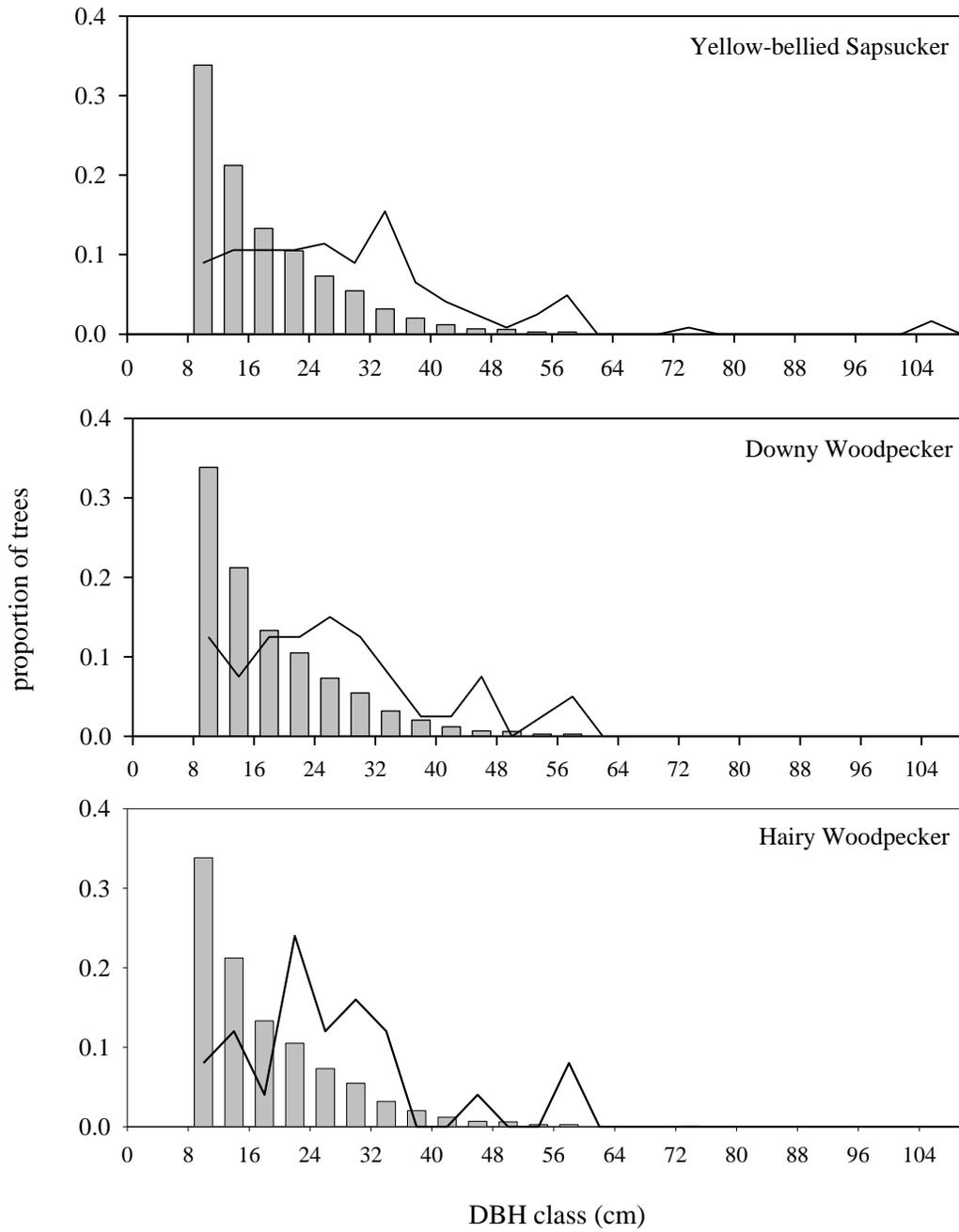Figure 3.4. Woodpecker foraging use of trees (lines) vs. availability (bars) by diameter class (dbh) (available trees n=5125, Yellow-bellied Sapsuckers n=123, Downy Woodpeckers n=40, Hairy Woodpeckers n=25).
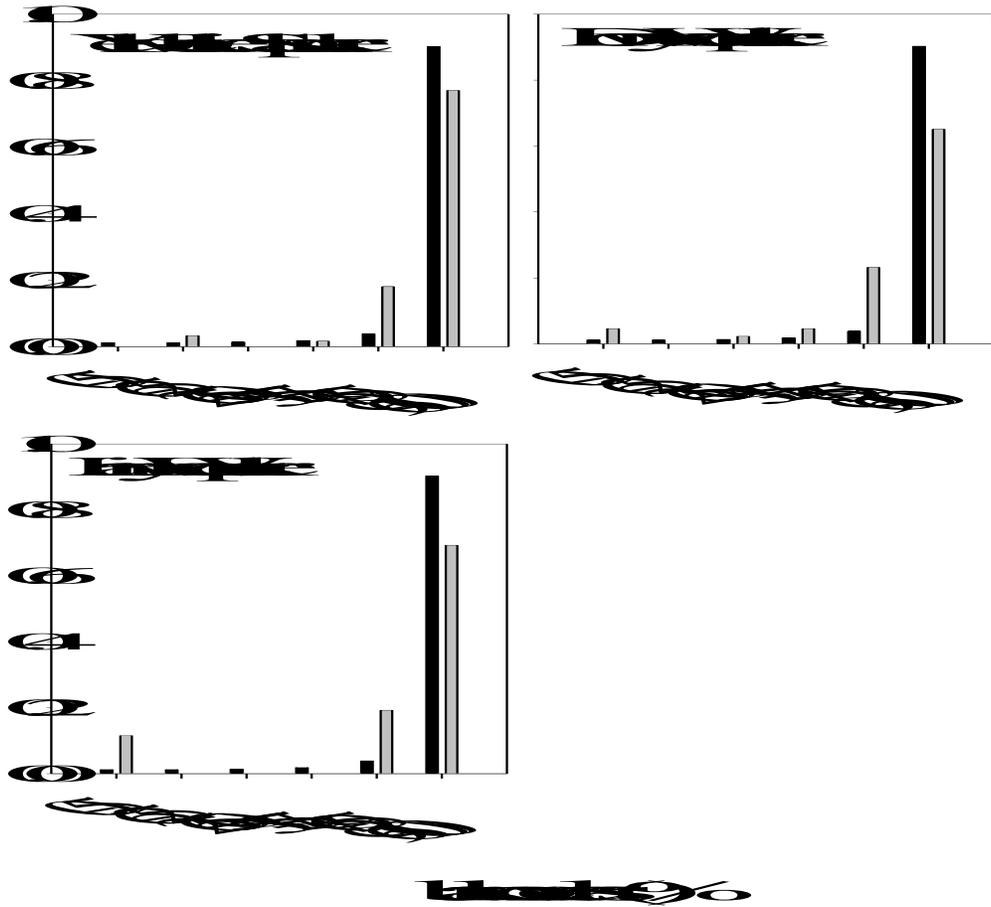
Figure 3.5. Woodpecker foraging use of trees (grey) vs. availability (black) by bark cover class (available trees n=5048, Yellow-bellied Sapsuckers n=122, Downy Woodpeckers n=43, Hairy Woodpeckers n=26).

Figure 3.6. Nesting vs. foraging use of tree species by Yellow-bellied Sapsuckers. Points above the line indicate nesting tree species use in greater proportion to foraging, and points below the line indicate foraging tree species use in greater proportion to nesting.

Figure 3.7. Yellow-bellied Sapsucker use of nesting and foraging trees by diameter
class (dbh).

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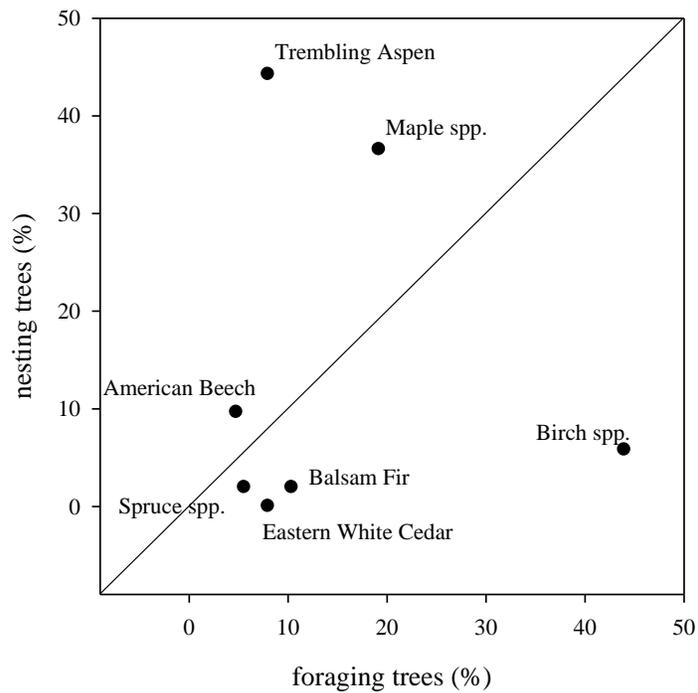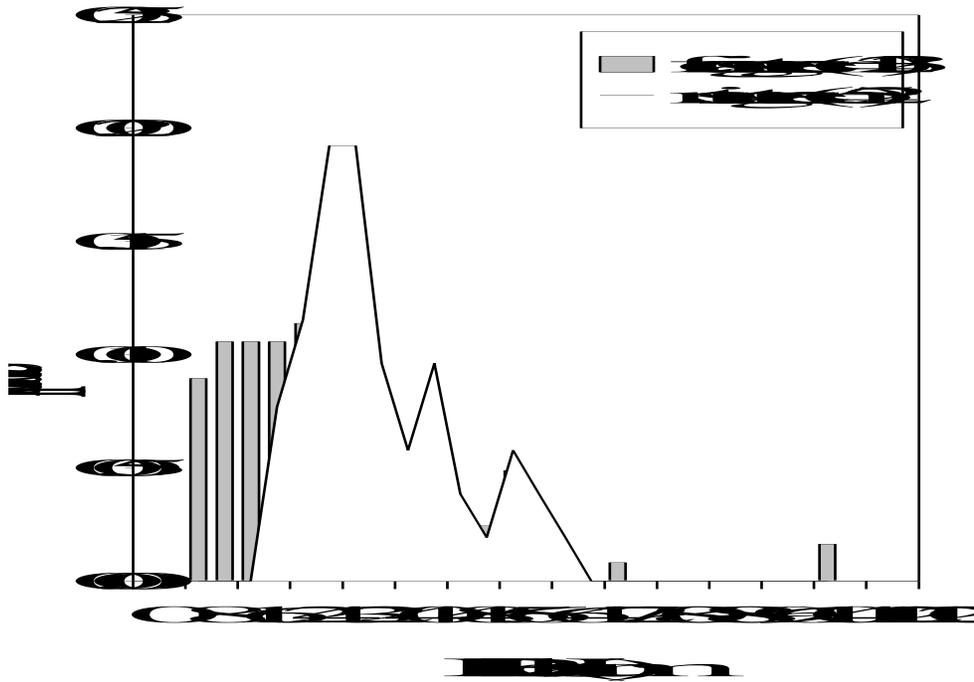
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Chapter 4

Synthesis

4.1 Synthesis

Multiple scales of study are important to the understanding of habitat associations; birds may respond differently to habitat variation depending on the scale of observation. With widespread anthropogenic change to forest landscapes, the importance of larger scales has been given increasing attention. My research indicates that larger landscape scales (within 300m and 1000m of a census point) generally explained little of the variance in primary cavity-nesting bird species occupancy not already explained by the smaller local scale (100m). The exceptions were Downy Woodpeckers (*Picoides pubescens*) and Northern Flickers (*Colaptes auratus*).

The significance of landscape composition to Downy Woodpeckers and Northern Flickers might be explained by their association with younger forest or open areas; species may be influenced by large-scale factors once the amount of suitable habitat in the landscape drops below a threshold (Andren 1994). Late successional forests were predominant in the study landscape, and the early successional species were understandably more strongly affected by landscape factors. The effect of landscape on the occupancy of Boreal Chickadees (*Poecile hudsonica*), Red-breasted Nuthatches (*Sitta canadensis*), Hairy Woodpeckers (*Picoides villosus*) and Yellow-bellied Sapsuckers (*Sphyrapicus varius*) may be more evident in early successional landscapes.

The habitat relationships at local and landscape scales were highly variable between the study species. Although this study was restricted to a guild of primary

cavity-nesting birds, the guild contains hardwood and softwood associates, weak and strong excavators, and species relying on very different foraging techniques (e.g. gleaning, excavating, sapsucking). Clearly the approach to cavity-nesting bird management must be multiple-scaled and species-specific.

My investigation into whether occupancy may be a misleading indicator of habitat quality was limited to Yellow-bellied Sapsuckers. The local occupancy and productivity models were very similar, but the deviance in Sapsucker productivity was also explained in small part by landscape composition within 300m and 1000m. While occupancy may obscure the finer details of habitat quality, the similarity between the two models suggest that occupancy is not a misleading indicator of habitat quality in this case.

The models of species occupancy, abundance, or productivity indicated the habitat characteristics that may be limiting, but reasons as to how, or why, were inferred based on the natural history of the species (Chapter 2). In contrast, the fine-scale selection study detailed the direct use of resources by individuals, but did not indicate whether these resources were limiting (Chapter 3). The study of woodpecker nesting and foraging substrate preferences gives insight into some of the species-habitat models.

The Yellow-bellied Sapsucker was the most abundant woodpecker species in the area and I was able to compare its nesting and foraging preferences. I found that nest substrate characteristics were more restrictive than foraging, and that preferred foraging substrates may not be supplied under the provision of suitable nest sites. The number of large hardwood trees and the number of small hardwood trees were important variables in the occupancy and productivity models respectively. Because the sample size was

too low to model tree species individually, the relationships to hardwood trees could indicate either nesting or foraging substrate limitation. But the number of large snags figured prominently in both models and suggests nest site limitation, because Sapsuckers in my study showed a nesting but not foraging preference for dead trees.

Although Downy and Hairy Woodpeckers exhibited strong preferences for certain foraging substrates, the literature suggests that they forage opportunistically (Jackson and Ouellet 2002, Jackson et al. 2002). Downy and Hairy Woodpeckers preferred to forage on larger trees, hardwood species, and trees in poor condition. If the Sapsucker models are any indication, snags and large hardwood trees are not distributed uniformly across the landscape and I might expect the occupancy of Downy and Hairy Woodpeckers to be related to these characteristics. However, their local occupancy models were very weak (Hairy Woodpecker) or non-existent (Downy Woodpecker), indicating that the preferred substrates are not limiting. It is important to note that the sample sizes are low, and more research is needed to verify these results.

4.2 Future research

The scope and limitations of this thesis indicate the direction for further research. First, both studies would have benefited from larger sample sizes. The impetus for this study was to assess the suitability of Habitat Management Areas (HMAs, see Appendix 2) for cavity-nesting birds in an industrial forest managed by Nexfor Fraser Papers. The sample size was limited for logistical reasons, and also by the availability of HMA complexes on the landscape. Occurrence was used as a surrogate for fitness in most of the species-habitat models because of the small number of observed reproductive

behaviours. But primary population parameters (e.g. productivity or survival) may be more directly linked to environmental change (Temple and Wiens 1989). It would be interesting to see whether more landscape effects appear in the productivity compared to occurrence models for the other species, as in the case of Yellow-bellied Sapsuckers.

A larger sample size would allow the inclusion of more specific variables in the local models important to the characterisation of bird habitat (e.g. tree species; Rotenberry 1985). Given the high diversity of forest structures and species typical of Acadian forests, this study was limited to structural (e.g. dbh) and broad floristic (e.g. hardwood) variables to describe the bird habitats. A larger sample size would also allow the investigations of landscape configuration as well as composition variables.

The small number of foraging observations forced me to pool the data for males and females, despite known intersexual niche partitioning by Downy and Hairy Woodpeckers (Jackson 1970, Jackson and Ouellet 2002, Jackson et al. 2002). It also forced me to pool foraging observations from across the entire study area, even though defining available substrates with respect to stand types or territories may be more relevant to the study species (Raphael and White 1984, Raphael and Maurer 1990, Carlson 1998, Jones 2001).

Second, future research should investigate the issue of temporal scale. The conclusions of these studies are based on data collected in one or two breeding seasons, but species-habitat relationships can fluctuate through time (Wiens 1989). For example, resident species may occupy different parts of their territory ranges or alter their foraging behaviour in winter, causing within-year variation (Conner 1981, Van Horne 1983). Changes to food availability, predator populations, and abiotic environmental

factors can cause between-year variation (Van Horne 1983, Raphael and White 1984). Furthermore, the effect of habitat change may not be apparent until later if site fidelity may cause time lags in the distribution of birds (Van Horne 1983, Temple and Wiens 1989). A long term study spanning all seasons could address these temporal issues on seasonal and yearly scales.

Third, I recommend a species-centred approach to the definition of habitat patches in the landscape. The 300m and 1000m landscape variables were defined using a GIS forestry database, and these classifications may not be functionally relevant to the species that I studied (Wiens 1989, McGarigal and McComb 1995, Azevedo et al. 2000).

Lastly, I strongly suggest that the multiple scale study be replicated in different landscapes. Habitat selection may be influenced by regional abundance of individuals and habitat types, and studies in different areas would indicate whether my results can be readily applied beyond this study region (Wiens 1989, Andren 1994, Trzcinski et al.1999, Lichstein et al. 2002).

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Appendix 1

Using chickadee mobbing and Barred Owl playbacks
to census cavity-nesting birds

A1.1 Introduction

Studying patterns of habitat use across large spatial scales can be very

challenging for species with low detection frequencies (Johnson et al. 1981). Few

studies have investigated the effects of landscape on cavity-nesting birds, largely due to

their low detection probabilities (e.g. Derleth et al. 1989, McGarigal and McComb

1995). A species' detection frequency refers to the proportion of times that a species is

recorded where it occurs and it depends on the individual detection frequency and the

density of individuals (Buskirk and McDonald 1995).

Aural stimuli can effectively supplement point counts and increase the detection

of birds that do not vocalise consistently or frequently (Johnson et al. 1981, Lynch

1995). For example, Gunn et al. (2000) used chickadee mobbing playbacks to

significantly increase the number of visual observations of birds compared to passive

point counts. Similarly, Barred Owl (*Strix varia*) calls have been successfully used to

elicit a defensive response in woodpeckers and increase their detection (Shackelford and

Conner 1997, personal observation). Mobbing or alarm calls communicate the presence

of a predator and often result in mixed-species mobbing (Altmann 1956, Hurd 1996).

I used Barred Owl (*Strix varia*) calls and Boreal (*Poecile hudsonica*) and Black-

capped Chickadee (*Poecile atricapillus*) mobbing calls to survey cavity-nesting birds

throughout a forested landscape as part of a larger study. The objective of this paper

was to determine how the audio and visual detection of cavity-nesting bird species using these playbacks compared to traditional silent point counts.

A1.2 Methods

My study was conducted on the industrial forest of Nexfor Fraser Papers in the Appalachian forest of northwestern New Brunswick (47°N, 67°W).   Bird surveys were conducted during the 2001 breeding season (mid-May to mid-August). Eight areas within 270 km^2 and ranging in size from 300-900 ha were sampled systematically. 96 census points were separated by at least 600m in order to reduce the chance of double counting individuals with large territories.

I used Barred Owl calls (© 1990 Cornell Laboratory of Ornithology and Interactive Audio), and Boreal and Black-capped Chickadee mobbing calls (recorded locally) to survey the cavity-nesting birds. Calls were broadcast on tape players, with the volume set to be heard within 100m by the human ear.

The points were visited 6 times during the 2001 breeding season. Each visit consisted of a 30-minute count period separated into 5 intervals: 5 minute silent period, 5 minute chickadee mobbing playback, 10 minute silent period, 5 minute Barred Owl playback, and 5 minute silent period. Three observers were rotated among points for the six visits, as was the time of day at which the points were sampled. Points were visited between sunrise and noon on mornings with winds less than 20 km/h and no rain (Robbins 1981). Individuals of each species within 100m of the point were counted during the visits, and sex, age and behaviour were recorded when possible.

Species detection was so low that occurrence was used as the dependent variables for many of the analyses in the larger study (Chapter 2). Therefore, I used the number of visits in which a species occurred for the purpose of comparison. The low frequency of detection also necessitated the pooling of data from all six rounds. Therefore there were 576 possible opportunities to detect the presence of a species (6 rounds x 96 points). Although these data are pseudoreplicated, I still believe that my conclusions are valid. I analysed the data separately for seven cavity-nesting bird species: Black-capped Chickadee (*Poecile atricapillus*), Boreal Chickadee (*Poecile hudsonica*), Red-breasted Nuthatch (*Sitta canadensis*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus*), and Yellow-bellied Sapsucker (*Sphyrapicus varius*).

I used contingency tables to compare the number of visits the species were detected in three 5 minute sampling periods: the initial silent period, the chickadee mobbing broadcast period, and the Barred Owl broadcast period. If the chi-square test indicated a significant difference, I performed multiple comparisons using confidence intervals for the difference between the proportions of species' 'detection' and 'no detection'. The Dunn-Šidák method was used to adjust the α-levels of the individual tests to ensure an experimentwise error rate of α=0.05 (Sokal and Rohlf 1995).

I analysed the data for each species four different ways in order to take into consideration both the type of detection and time of day. Because occurrence or density of a species may not accurately reflect habitat quality (Van Horne 1983), visual observations of breeding behaviour can be used to develop reproductive indices (Vickery et al. 1992, Gunn et al. 2000). A method that increases visual observations

would aid the development of such indices. Therefore, I analysed the data with audio and visual observations pooled, and separately for just visual observations.

Bird song activity often decreases throughout the day, and standard point counts are performed within four hours of sunrise (approximately 10 am) (Ralph et al. 1995). However, because the mobbing technique does not rely solely on bird vocalisations, points were visited until noon to maximise the data collected for the larger study. To verify that lower numbers of observations in the silent period were not artefacts of the time of day, the data were analysed with all data, and separately for data collected prior to 10 am.

A1.3 Results

Sunrise until approximately noon: audio and/or visual

The proportions of periods at which the species were detected were significantly different for every species except for the Red-breasted Nuthatch (Table A1.1, Figure A1.1). Black-capped Chickadees were detected in more chickadee mobbing periods, and fewer silent and Barred Owl periods than expected (Table A1.1). Boreal Chickadees were detected in relatively fewer Barred Owl periods (Table A1.1). Downy Woodpeckers, Hairy Woodpeckers, Northern Flickers, and Yellow-bellied Sapsuckers occurred in more Barred Owl periods, and fewer chickadee periods (Table A1.1). Yellow-bellied Sapsuckers were also absent more often from the silent periods (Table A1.1).

Sunrise until approximately noon: visual

The proportion of periods in which the species were seen was significantly different for every species (Table A1.2, Figure A1.2). Black-capped Chickadees, Boreal Chickadees, and Red-breasted Nuthatches were seen in more chickadee mobbing periods and fewer silent periods than expected by chance (Table A1.2). Boreal and Black-capped Chickadees were also seen in relatively fewer Barred Owl periods (Table A1.2). Downy Woodpeckers, Hairy Woodpeckers, Northern Flickers, and Yellow-bellied Sapsuckers were all seen in more Barred Owl periods than expected (Table A1.2). Downy Woodpeckers were also detected in relatively fewer silent periods, while Hairy Woodpeckers were detected in relatively fewer chickadee mobbing periods. Yellow-bellied Sapsuckers and Northern Flickers were absent more often from both the silent and the chickadee mobbing periods.

Sunrise until 10 am

The relationships using data collected up to 10 am were identical to those found using all of the data for every species except the Boreal Chickadee. The proportion of periods at which Boreal Chickadees were detected by audio and/or visual means were not significantly different. While Boreal Chickadees were not seen in equal proportions (p<0.0001, Chi-square test), the difference was driven by the chickadee and Barred Owl periods; Boreal Chickadees were detected in proportion to the expected value in the silent period.

A1.4 Discussion

The use of chickadee mobbing calls and Barred Owl call playbacks successfully increased the detection of cavity-nesting bird species. The Barred Owl calls attracted

the woodpeckers while the chickadee mobbing calls attracted the other species. These different responses may be attributed to predator risk and body size. Predators have been known to attack and kill their mobbers (Sordahl 1990). Perhaps the risk incurred during mobbing of Barred Owls is too large for the smaller cavity-nesting bird species. Boreal and Black-capped Chickadees will mob in response to a mount and tape of the smaller Saw-whet Owl (*Aegolius acadicus*) (personal observation), suggesting that predator size may be a factor in their decision to mob.

The visual detection of species was relatively higher in the playback periods compared to the pooled audio and visual data. These playbacks may be particularly useful for studies relying on visual confirmation of breeding behaviour. For example, Gunn et al. (2000) found that reproductive indices based on cues from mobbing Ovenbirds (*Seiurus aurocapillus*) and Black-throated Blue Warblers (*Dendroica caerulescens*) followed the same trends in productivity found by intensive nest monitoring.

Limiting the data collection to the standard point count hours had no effect on the conclusions for most of the species in my study. Only the results for Boreal Chickadees changed, and in the opposite direction than expected. I anticipated that the differences in the proportion of occurrences in the sampling periods would be more marked using the full data set because of reduced unsolicited activity later in the morning. It is recommended that point counts be conducted within approximately four hours of sunrise (Ralph et al. 1995), but there is no similar standard for this mobbing method. Sampling until noon appears satisfactory, but it is possible that these species could be surveyed further into the afternoon.

These preliminary results suggest a promising new method to survey cavity-nesting birds across large spatial scales. However the data were collected as part of a larger study not designed to rigorously test this method. Future research is needed to understand how these species' mobbing response vary temporally and with respect to life history. Birds may alter their mobbing responses not only throughout the day, but within and even between seasons. Some bird species mob only during the breeding season (e.g. Shedd 1982). Others may vary the intensity of their mobbing in accordance with the age of their young (e.g. Regelmann and Curio 1983, Shedd 1983). I recommend that future research also determine whether adults are more likely to mob within their own territory boundaries. These are important factors to know when constructing bird-habitat models using occurrence, abundance, or productivity.

Table A1.1. The audio and/or visual detection of cavity-nesting bird species in three, 5 minute sampling periods (n= 96 points*6 visits). Data collected from sunrise until approximately noon. (BCCH: Black-capped Chickadee; BOCH: Boreal Chickadee; RBNU: Red-breasted Nuthatch; DOWO: Downy Woodpecker; HAWO: Hairy Woodpecker; NOFL: Northern Flicker; YBSA: Yellow-bellied Sapsucker)

period	BCCH n = 347	BOCH n = 122	RBNU n = 115	DOWO n = 69	HAWO n = 63	NOFL n = 66	YBSA n = 332
silence	-						-
chickadee	+			-	-	-	-
owl	-	-		+	+	+	+
probability[a]	<0.0001	0.040	0.144	0.001	0.004	<0.0001	<0.0001

[+] species detected significantly more than expected at $p < 0.05$ based on confidence limits
[-] species detected significantly less than expected at $p < 0.05$ based on confidence limits
[a] p-values from Chi-square analysis of contingency table

Table A1.2. The visual detection of cavity-nesting bird species in three, 5 minute sampling periods (n= 96 points*6 visits). Data collected from sunrise until approximately noon. (BCCH: Black-capped Chickadee; BOCH: Boreal Chickadee; RBNU: Red-breasted Nuthatch; DOWO: Downy Woodpecker; HAWO: Hairy Woodpecker; NOFL: Northern Flicker; YBSA: Yellow-bellied Sapsucker)

period	BCCH n = 172	BOCH n = 43	RBNU n = 38	DOWO n = 35	HAWO n = 48	NOFL n = 43	YBSA n = 229
silence	-	-	-	-		-	-
chickadee	+	+	+		-	-	-
owl	-	-		+	+	+	+
probability[a]	<0.0001	<0.0001	<0.0001	<0.0001	0.001	<0.0001	<0.0001

[+] species detected significantly more than expected at $p < 0.05$ based on confidence limits
[-] species detected significantly less than expected at $p < 0.05$ based on confidence limits
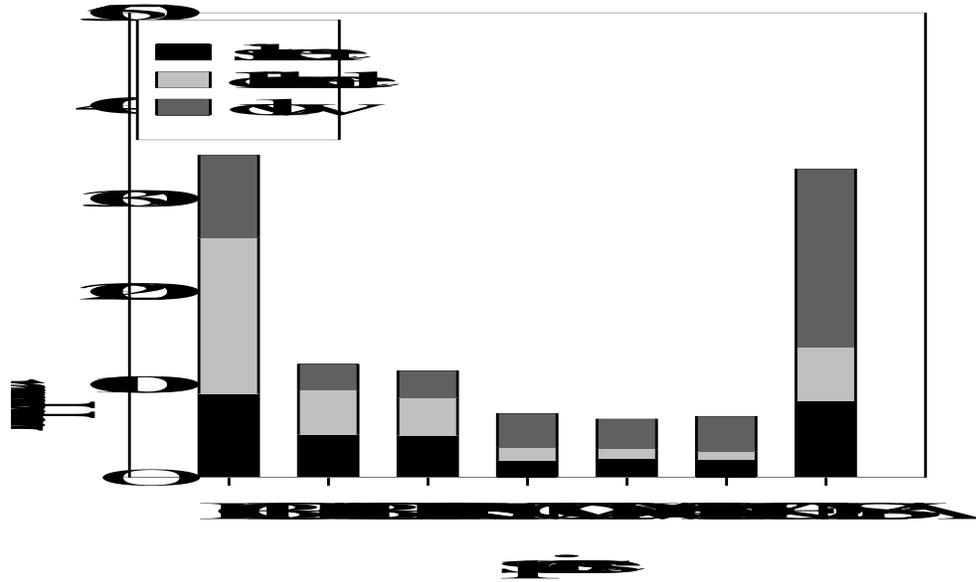[a] p-values from Chi-square analysis of contingency table

Figure A1.1. The audio and/or visual detection of cavity-nesting bird species in three, 5 minute sampling periods (n= 96 points*6 visits). Data collected from sunrise until approximately noon. (BCCH: Black-capped Chickadee; BOCH: Boreal Chickadee; RBNU: Red-breasted Nuthatch; DOWO: Downy Woodpecker; HAWO: Hairy Woodpecker; NOFL: Northern Flicker; YBSA: Yellow-bellied Sapsucker).

Figure A1.2. The visual detection of cavity-nesting bird species in three, 5 minute sampling periods (n= 96 points*6 visits). Data collected from sunrise until approximately noon. (BCCH: Black-capped Chickadee; BOCH: Boreal Chickadee; RBNU: Red-breasted Nuthatch; DOWO: Downy Woodpecker; HAWO: Hairy Woodpecker; NOFL: Northern Flicker; YBSA: Yellow-bellied Sapsucker).
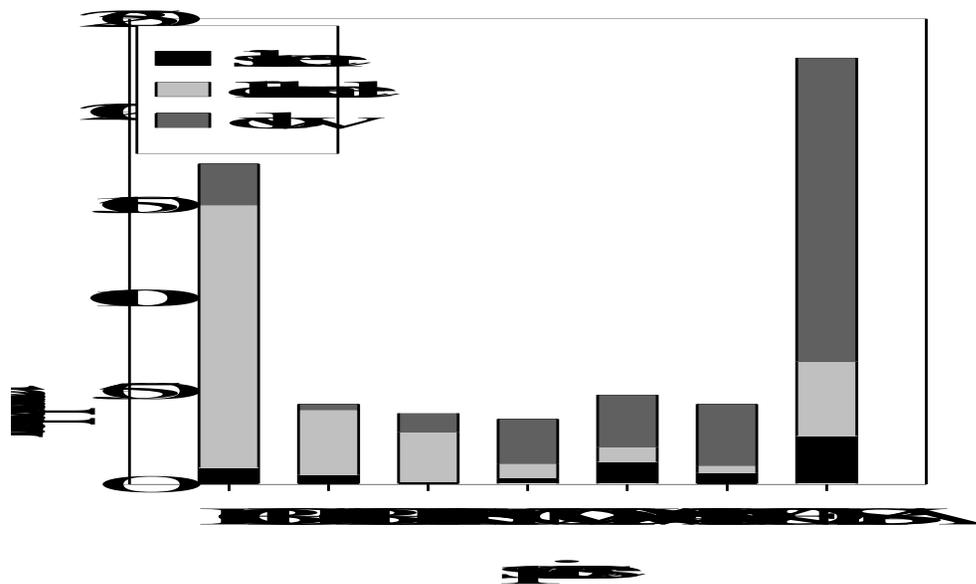
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Appendix 2

Monitoring Recommendations for Nexfor Fraser Papers

The design of a monitoring program depends largely on the purpose of the monitoring. For example, a program to monitor nesting success must be very intensive and requires many repeat visits to the same site during a breeding season. In contrast, a program such as the North American Breeding Bird Survey is extensive; it is set in place to monitor broad geographical population trends, requires only one visit per season, and relies on the effort of hundreds or thousands of volunteers.

Logistics must also play a part in the development of a monitoring program. There is often a necessary trade-off between detail and scale due to monetary constraints, and managers or researchers must determine *a priori* which is more important to their particular needs. Ideally, surveys conducted once in the season would allow managers to draw specific conclusions about species-habitat associations. However, monitoring can be difficult for species that do not advertise as consistently as songbirds sing. Erroneously categorising species as 'absent' at points because of low detection will weaken the overall habitat model and lessen the chance of seeing a clear relationship. My research partially addressed this problem by employing mobbing playbacks to attract individuals (Appendix 1).

The impetus for my study of primary cavity-nesting birds was the wish expressed by Nexfor Fraser Papers to assess the suitability of wildlife habitat in designated Habitat Management Areas (HMAs) on their privately-owned land in northwestern New Brunswick. Nexfor Fraser Papers chose to provide habitat for

wildlife associated with mature forest in separate areas fixed on the landscape (Anonymous 1997). The primary value of these Habitat Management Areas is the maintenance of wildlife habitat and the secondary value is timber extraction. Nexfor Fraser Papers wished to apply the results of this study towards the development of a long term monitoring program for cavity-nesting birds, and towards the amendment of their guidelines and standards for habitat management on their New Brunswick Freehold land. They wanted the monitoring to assess both the suitability of stand types and age classes for these species, and the function of HMAs as a whole. The constraints on time and effort placed on future monitoring programs were that sampling had to be carried out within one month by one or two individuals, and if possible by one visit per point.

Preliminary analyses (Table A2.1) indicated that the woodpecker species were not significantly associated with Habitat Management Areas, so the monitoring program is discussed with respect to Black-capped Chickadees (*Poecile atricapillus*), Boreal Chickadees Boreal (*Poecile hudsonica*), and Red-breasted Nuthatches (*Sitta canadensis*). Based on the results from Appendix 1, I recommend that these three species be monitored using chickadee mobbing call playbacks: 5 minute silent period, 5 minute chickadee mobbing playback, 5 minute silent period. Data collected in year 2000 and 2001 (see Chapter 2 for detailed methods) are explored graphically. In order to make these results comparable to future data, only the data collected during those first 15 minutes are used for the following graphs and analyses. The feasibility of achieving the multiple objectives given the logistical constraints is discussed.

Bird-habitat models based on stand type and age

In order to determine whether one visit is adequate for the development of specific habitat models for these species, I asked the following questions:

1) Is there a peak in the detection of the different species during the breeding season? This could indicate the most appropriate time to conduct the survey.

2) Does the accumulated number of points at which each species is found present level off? If so, after how many visits? The point at which a graph levels off indicates the number of visits needed to get an accurate account of species presence. If the number of new points that a species is detected continues to increase every round, it suggests more sampling is needed and that species at some points may still be incorrectly classified as absent.

3) How well does one (or more) visit reflect the results pooled from 6-8 visits?

1) There was no peak time of species detection common to all three species (Figure A2.1).

2) Furthermore, there was no obvious levelling off in accumulated species detection (Figure A2.2).

3) Lastly, even the single *peak* round for every species was a poor representative of the results pooled from six and eight rounds for year 2001 and 2000 respectively. In year 2000, the peak round indicated only 58% of the points that Black-capped Chickadees were found present within eight rounds, 43% of Boreal Chickadee points, and 42% of Red-breasted Nuthatch points. In year 2001, the peak round indicated 58% of the points that Black-capped Chickadees were found present within six rounds, 46% of Boreal Chickadee points, and 50% of Red-breasted Nuthatch points. I conclude that one visit

per breeding season will not likely allow researchers or managers to model specific local habitat associations of these species based on a similar sample size. This may be attributed in part due to the low detection probability of the species (despite the playback), and to territory sizes which extend farther than the censused 100m (if the bird is on its territory but not within audio range of the playback, it may not respond).

Function of Habitat Management Areas as a whole

Based on the above results and the limits imposed by time and effort, I suggest that Nexfor Fraser Papers take a landscape approach and focus on the functioning of entire HMAs. The sampling unit would therefore be the HMA (or HMA complex) rather than an individual stand. The changes to relative abundance of species may then be related to the management of particular HMAs and HMA complexes. Permanent sample points can be set up in order to gauge the changes to species levels over time.

Any project that sets out to evaluate the suitability of HMAs for wildlife must also evaluate the suitability of non-HMAs. If not, the changes in wildlife abundance levels cannot be attributed solely to the conditions within the HMAs; conditions in the surrounding Freehold forests may contribute to the increase or decrease of wildlife within the HMAs. The number of points at which Black-capped Chickadees, Boreal Chickadees, and Red-breasted Nuthatches were present was higher in the HMAs based on graphs of year 2001 data (Figure A2.3, Figure A2.4). Logistic regression models confirmed these relationships. Black-capped Chickadees, Boreal Chickadees, and Red-breasted Nuthatches were positively associated with Habitat Management Areas (p=0.049, p=1.8e-007, p=6.5e-005 respectively). These analyses are pseudoreplicated

because my sample size is really in fact 8 (4 HMA groups and 4 non-HMA groups), rather than 94 (48 HMA points and 46 non-HMA points).

To crudely explore what might be driving the relationships, I electronically buffered the year 2001 points by 300m using a GIS program, clipped the stand data, and compared the forest type areas between the HMAs and non-HMAs. Over 75% of the HMA area was covered by mature stands, compared to less than 18% of the non-HMA area (Table A2.1). While only 8.0% of the HMA area was covered by medium-aged or mature hardwood (mixedwood and softwood split fairly evenly), almost 44% of the area outside the HMAs was covered by medium-aged and mature hardwood (Table A2.1). This indicates that the reasons behind the association with HMAs may be confounded by stand type and age. It is impossible to tease out the importance of softwood/hardwood availability and stand maturity based on this type of investigation. Therefore, I urge caution when interpreting these and future results based on this design.

Final recommendations

The low detection probabilities of these species makes their monitoring difficult. Although the use of playbacks did increase their detection, one visit per season of a small number of points (e.g. less than 100) will not likely allow managers or researchers to draw any definite habitat associations at the *local* level. Instead, a cruder HMA vs. non-HMA comparison may be more feasible if Nexfor Fraser Papers is willing to sacrifice statistical rigour (i.e. pseudoreplication) and the confounding effects of forest type and age. If so, I make the following recommendations:

1. Sample size

The issue is whether it is better to invest more time into increasing sample size or repeating visits. I re-analysed the HMA vs. non-HMA data based on two rounds instead of six. I tested whether more species were detected in HMAs compared to non-HMAs in two ways: 1) using the data from the highest two rounds, and 2) using data from the lowest two rounds. Except for the two highest rounds for Black-capped Chickadee, all tests showed that species were more likely to occur in HMAs compared to non-HMAs (Table A2.2). Therefore, I suggest using two visits, and increasing the sample size to 75-100 points each in HMAs and non-HMAs.

2. Setting up points

My study species included woodpeckers, which can have large territories. Therefore, I spaced my points at least 600m apart to reduce the chance of double counting individuals. Based on estimates of territory sizes in the literature for the three target species, I recommend that points are spaced at least 400m apart. Ideally the sampling should be set up to encompass the representative forest types within the HMA and non-HMA areas. Roadside surveys run the risk of sampling just that – roadside habitat. However, if logistic difficulties prevent the sampling of more remote areas that are far from the road (my points were often >300m away from the road, and up to 2km), then I would suggest walking in 100m from the road to sample. If Nexfor Fraser Papers is also interested in the future analysis of data at stand scales, then points should be placed at least 100m from stand edges.

3. Playback preparation

If more than one observer is participating in the monitoring, all must have the same tape player equipment. Before monitoring begins, the tape players must be

calibrated in a wide variety of forest types. The sampling distance is 100m, so tape player volumes should be set accordingly. One observer may stand 100m away, and using a whistle, indicate to the other observer when they can first detect the playback sounds. The average volume at which the playback is heard at 100m across forest types should be marked on the tape players and used in the monitoring.

Tape players should be placed on the ground. While hanging the players above the ground may improve sound transmission, there may not be not suitable places to hang the player up at every point.

4. Birding preparation

Before censusing, observers should be very confident with their visual and audio identification of the study species. They should train in the field using the playback, and be comfortable using binoculars and keying in on the birds.

Training should also include distance estimates of calling birds. String boxes are useful tools to measure out exact distances of calling birds during training so that observers will be able to accurately estimate distance categories (0-50m, 50-100m, >100m) in the monitoring. One observer estimates the distance of a singing bird, and one finds the bird and measures the exact distance. String boxes should also be used to refine visual estimates of distance. This can be practised even without birds (e.g. estimate distance to a tree or rock, and then measure it).

4. Monitoring

Once reaching the point, record individuals seen or heard in three 5 minute periods: silence, playback of Boreal and Black-capped Chickadee mobbing, 5 minute silent period after the mobbing. Observers should record the distance at which the

individuals were detected (within 50m, 50-100m, >100m). Weather condition should also be recorded, along with time of day, observers name, date, and location.

5. Time of day

Monitoring should start at sunrise and end by noon (Appendix A1).

6. Second visit

Points visited early in the morning should be sampled later in the second visit and vice versa in order to reduce bias from the time of day. Observers should also try to rotate to points that they did not visit the first time.

5. Weather

Bad weather can impede the activity and detection of birds. Therefore I suggest adopting the weather guidelines set out by the Breeding Bird Survey (Robbins 1981).

Table A2.1. Testing whether the occupancy of woodpecker species is different at HMA points (n=48) versus non-HMA points (n=46), using logistic regression. Occupancy data were collected in year 2001 using chickadee and Barred Owl playbacks.

Woodpecker species	HMA vs. non-HMA
Downy Woodpecker	p=0.403
Hairy Woodpecker	p=0.933
Northern Flicker	p=0.137
Yellow-bellied Sapsucker	p=0.257

Table A2.2. Percent of area by different forest types within 300m of HMA points (n=48) and non-HMA points (n=46), year 2001.

label	forest type	area in ha	percent
HMA	mature hardwood	84.6	6.3
	medium-aged hardwood	21.5	1.6
	mature mixedwood	396.5	29.7
	medium-aged mixedwood	64.2	4.8
	mature softwood	532.0	39.9
	medium-aged softwood	48.9	3.7
	early-aged	15.6	1.2
	recent clearcuts	149.4	11.2
	other[a]	21.6	1.6
	total	1334.3	100.0
non-HMA	mature hardwood	133.2	10.4
	medium-aged hardwood	428.8	33.5
	mature mixedwood	49.7	3.9
	medium-aged mixedwood	32.4	2.5
	mature softwood	39.7	3.1
	medium-aged softwood	18.5	1.4
	early-aged	149.9	11.7
	recent clearcuts	409.2	32.0
	other[a]	18.7	1.5
	total	1280.2	100.0

[a]unclassified (e.g. roads, gravel pits, wetlands, rivers)

Table A2.3. Testing whether the presence of species in two rounds (2 highest rounds, 2 lowest rounds) is different in HMAs versus non-HMAs, year 2001. Significant p-values indicate that species are more likely to occur in HMAs compared to non-HMAs using logistic regression.

	Black-capped Chickadee	Boreal Chickadee	Red-Breasted Nuthatch
high rounds	p=0.131	p=1.6e-004	p=0.002
low rounds	p=7.6e-005	p=1.4e-006	p=1.1e-004
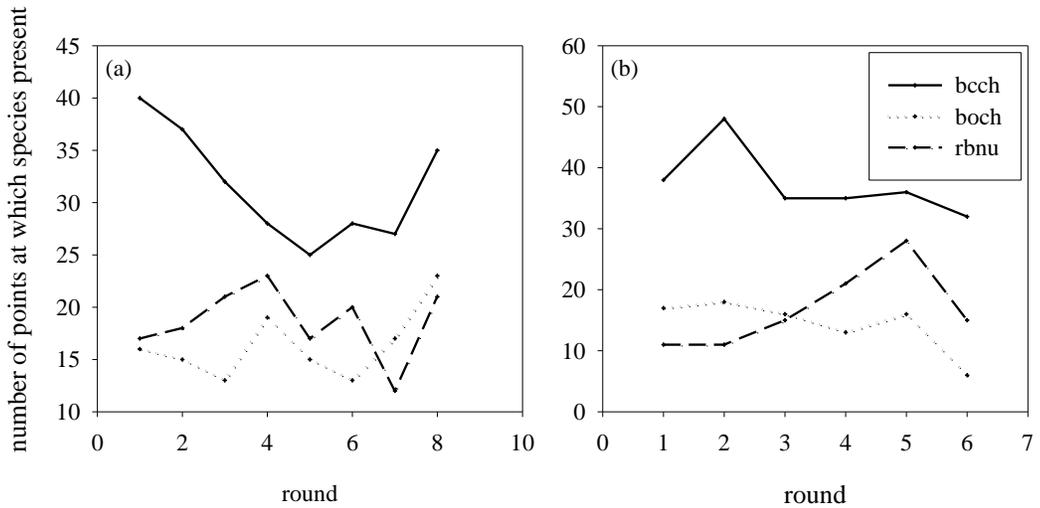
Figure A2.1. Total number of points at which each species was present within 100m per round for a) year 2000, and b) 2001 (bcch: Black-capped Chickadee; boch: Boreal Chickadee; rbnu: Red-breasted Nuthatch).
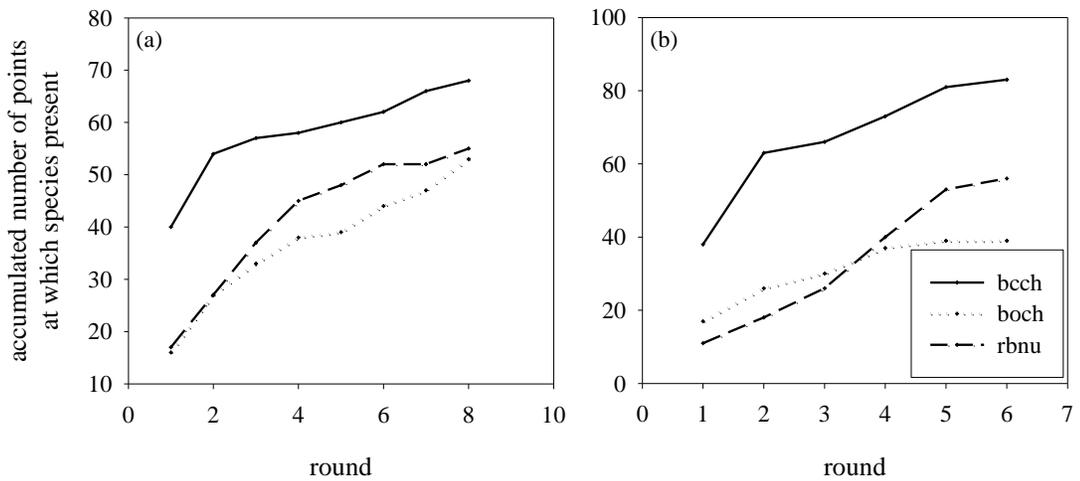

Figure A2.2. Accumulated number of points at which each species is present within 100m, per round for a) year 2000, and b) 2001 (bcch: Black-capped Chickadee; boch: Boreal Chickadee; rbnu: Red-breasted Nuthatch).
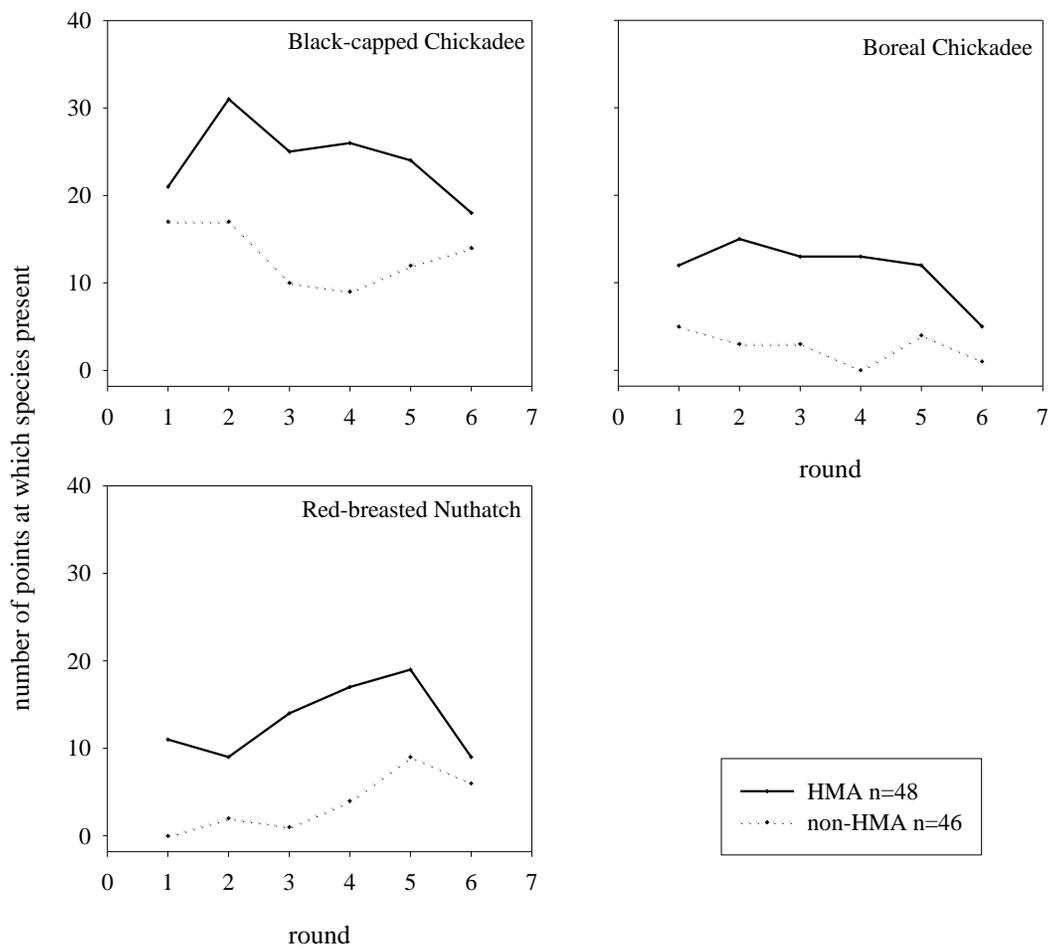
Figure A2.3. Total number of points at which target species were present within 100m per round in Habitat Management Areas (HMAs) and non-HMAs, year 2001.
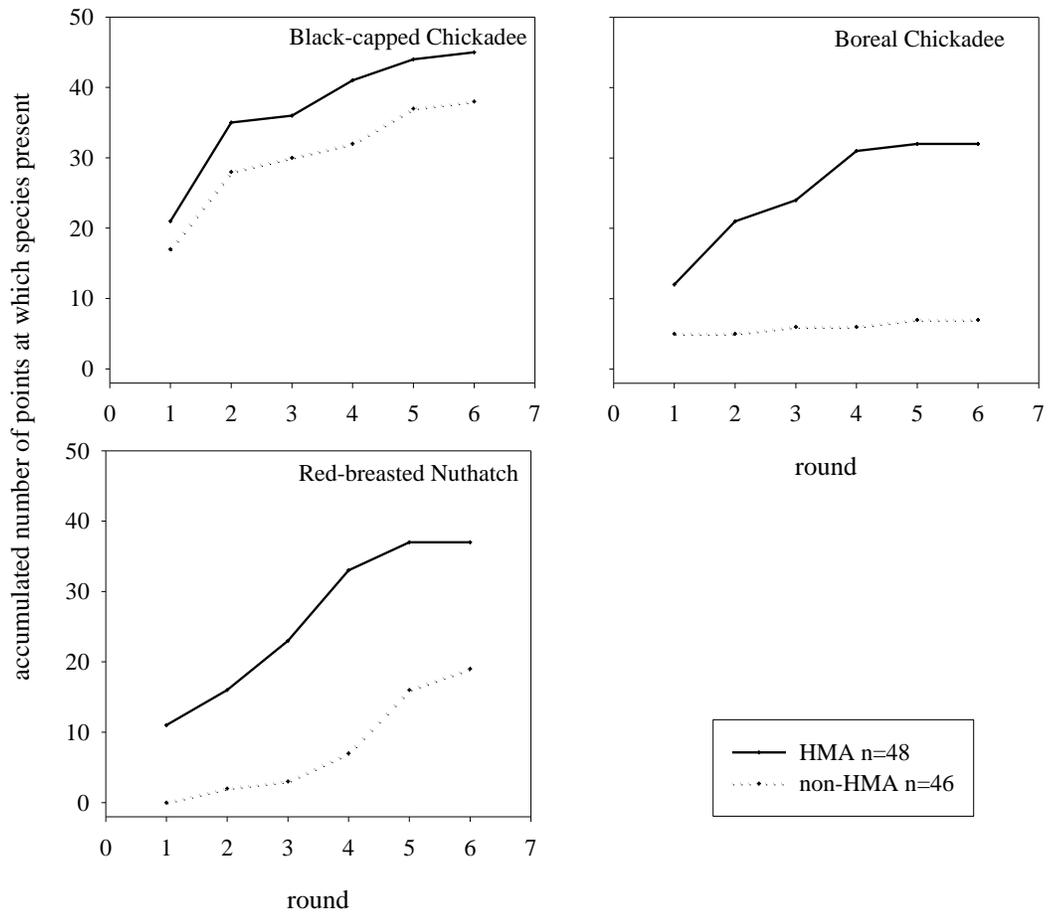
Figure A2.4. Accumulated number of points at which target species were present within 100m per round in Habitat Management Areas (HMAs) and non-HMAs, year 2001

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