University of Alberta

Impacts of partial harvest of riparian buffer strips on cavity-nesting birds in boreal mixedwood forest

by

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ABSTRACT

To alleviate negative effects of forest harvesting on wildlife in boreal forests, forest managers are attempting to emulate patterns of wildfire disturbance in treed riparian buffers using partial-harvesting techniques. I assessed the response of cavity-nesting birds to forest harvesting in riparian buffers, and identified habitat features relevant to bird management across three spatial scales in the Boreal Plains ecozone of SK and MB in 2005 and 2006. The composition of bird assemblages shifted when less than 33% of forest was retained in buffers. Site-use by Brown Creepers (*Certhia americana*), Red-breasted Nuthatches (*Sitta canadensis*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*) and Boreal Chickadees (*Poecile hudsonica*) decreased with increasing amount of harvest. Compared to harvested buffers, burned riparian forest supported more Northern Flickers (*Colaptes auratus*), Tree Swallows (*Tachycineta bicolor*) and House Wrens (*Troglodytes aedon*). Site-use by most species was related to habitat at a scale similar to their territory size.

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CHAPTER 1

THESIS INTRODUCTION

1.1 Thesis Introduction

The boreal forest represents 77% of Canada's total forest area (Canadian Forest Service 2005) and provides breeding habitat for over 300 species of birds (Blancher and Wells 2005). The Boreal Plains ecozone represents the transition zone from the closed boreal forest in the north to the forest/grassland complexes in the south. Industrial development is increasing throughout western Canada and concomitantly, demands on forest resources in this region have also increased (Schneider and Walsh 2005). Timber harvesting, as an example, has been increasing across the Boreal Plains ecozone for the past 30 years, prompting economic and social concern over the economic, social and ecological sustainability of forest resources (Burton et al. 2006).

The Boreal Plains ecozone is shaped by natural disturbances, primarily insect outbreaks, windthrow and wildfire (Brassard and Chen 2006, Burton 2006). Consequently, the landscape is a dynamic mosaic of forest stands varying in age, composition and structure (Cumming et al. 1996, Brassard and Chen 2006). Recent anthropogenic disturbances and conventional forestry activities have contributed to a shift in this "natural" forest structure across managed regions. Forest harvest planning within the Boreal Plains ecozone has typically taken a sustained-yield approach, and followed a two-pass clearcutting system with short rotation age (~70 years) (Bergeron et al. 2002, Schneider 2002). This has led to a reduction in the area of old-growth forest (Schneider and Walsh 2005), and reduced structural heterogeneity of forest stands across the landscape (Schmiegelow and Mönkkonen 2002, Burton et al. 2006, Macdonald and

Fenniak 2007). As a result, the amount of habitat available for some avian species has been reduced (Schmiegelow et al. 1997, Imbeau and Desrochers 2002, Schmiegelow and Mönkkonen 2002).

The effects of harvesting on boreal birds must be considered to conserve bird biodiversity (Schmiegelow and Hannon 1999, Schneider and Walsh 2005, Schieck and Song 2006). Hunter (1993) suggested that effects of traditional clearcutting could be reduced if landscapes were harvested to emulate patterns of natural disturbances. This idea assumes that birds are adapted to natural disturbances and thus should be affected less by harvesting if it approximates forest patterns resulting from natural disturbance events. In the boreal-plains ecozone, wildfire is the predominant natural disturbance (Rowe and Scoter 1973) and can significantly alter forest structure on a large scale (Hunter 1993, Walker et al. 1995, Brassard et al. 2008).

In upland forests, attempts to emulate natural burn patterns include harvesting across large areas to reflect the large extent of burns, and retaining trees in patches and as individuals to mimic fire skips (Walker et al. 1995, Franklin et al. 1997). Retained forest structures can provide habitat for birds in partially-harvested landscapes (Norton and Hannon 1997, Schieck and Hobson 2000, Potvin and Bertrand 2004), however, differences in forest structure exist between stands immediately post-fire and post-harvest (Hobson and Schieck 1999, Schieck and Song 2006). Importantly for birds, post-fire stands generally have a high abundance of fire-killed snags, while post-harvest stands have few snags (Hobson and Schieck 1999). Because burned snags provide nesting habitat and a source of insect prey for several postfire-associated bird species (Murphy and Lehnhausen 1998, Hoyt and Hannon 2002, Stambaugh 2003), partial-harvest may not be a suitable analogue for fire for certain species.

In riparian forests across North America, provincial and state policies have generally required the retention of variable-width intact forest strips, or "buffers", along the edges of waterbodies in harvested landscapes (Lee et al. 2004, Alberta Sustainable Resource Development 2005). Buffers can function to reduce upland run-off and maintain water quality (see Steedman and France 2000) and to conserve fish stocks (Wesche et al. 1987), insect communities (Noel et al. 1986, Whitaker et al. 2000) and nearshore vegetation (Harper and Macdonald 2001). Furthermore, they contribute detritus and downed woody debris to waterbodies, which is necessary to maintain aquatic ecosystems (Decker 2003). However, similar to retained upland forest structures, buffer strips may provide lifeboats for some avian species in recently-harvested landscapes (Whitaker and Montevecchi 1997, Lambert and Hannon 2000, Pearson and Manuwal 2001). A lifeboat refers to a forest structure that maintains species present prior to harvesting over the forest regeneration phase (Matveinen-Huju et al. 2006). Additionally, buffers can provide a source of old growth forest, suitable for old-growth dependent species (Schieck and Hobson 2000).

Intact buffer retention, however, is inconsistent with a natural disturbance model based on burn patterns since wildfire can burn to the edge of a waterbody (Andison and McCleary 2002, Everett et al. 2003). To emulate burn patterns, the application of an approach similar to upland partial-harvesting in buffers may be more appropriate. Recently, some companies operating in the Boreal Plains ecozone have been experimenting with such an approach by harvesting buffers and retaining variable amounts of forest as strips, patches, and individual trees within the buffer. Depending on the size, abundance, spatial pattern, and/or composition of residual structures (Franklin et al. 1997, Schieck and Hobson 2000), this harvest approach may retain suitable habitat in buffers for birds or may reduce the amount of, or eliminate, usable riparian forest habitat.

Riparian partial-harvesting is an experimental and controversial management approach across North America. As forest development continues, riparian buffers are expected to retain a disproportionately high amount of old-growth forest across the landscape (Lee and Barker 2005). The loss of this old-growth habitat through buffer harvesting combined with limited knowledge on the effects of buffer harvesting on water quality and biota (Lee et al. 2004) have led to varying levels of acceptance of riparian partial-harvesting among North American jurisdictions.

As with many faunal groups, the effect of partial-harvesting in buffers on avian communities in the Boreal Plains ecozone remains relatively untested (but see Kardynal 2007). Responses by cavity-nesting birds in particular have not been well-assessed and the efficacy of buffer harvesting as an analogue of wildfire, and the influence of retained structures on cavity-nesting bird communities, represents a key knowledge gap in forest management.

Functional relationships exist among cavity-nesters and are described by a nest web (Martin and Eadie 1999). Primary-nesters excavate cavities, weak-excavators excavate cavities or use previously-excavated cavities and secondary-nesters are non-excavators and rely on previously-excavated or natural cavities (Martin et al. 2004). Because of these relationships, certain excavators represent keystone species. Effects of riparian partial-harvesting on these species will exert a strong influence on the entire nest web. Furthermore, primary-nesters are indicators of forest bird richness at a stand scale (Drever et al. 2008). An assessment of cavity-nesting bird responses to riparian partial-harvesting allows forest managers to assess impacts across a broad ecological range.

Riparian forests may be particularly important to cavity-nesters due to a generally high abundance of standing snags, decaying trees and downed woody material: all important substrates for nesting and foraging (Harestad and Keisker 1989, Weikel and Hayes 1999, Gunn and Hagan 2000, Martin et al. 2004, Savignac and Machtans 2006). Furthermore, certain waterfowl species (e.g. Bufflehead (*Bucephala albeola*), Common Goldeneye (*Bucephala clangula*)) are secondary-nesters and rely on certain primary-nesting species in riparian forests for nest-sites (Eadie et al. 1995, Gauthier 1993). Negative responses to riparian harvesting by these primary-nesters may lead to a reduction in suitable waterfowl nesting habitat.

Historically, most studies have related patch use (including buffers) by birds in harvested landscapes to local habitat features only (Lambert and Hannon 2000, Tittler et al. 2001, Morissette et al. 2002, Harrison et al. 2005). However, forest management affects both stand and landscape scales, and changes across the landscape may influence local bird-habitat relationships. Landscape-scale habitat can influence resource availability, inter- and intra-specific interactions, and bird movement (McGarigal and McComb 1995, Crozier and Niemi 2003, St. Clair 2003). These factors may be particularly relevant to cavity-nesters as many species have large territories and home ranges. One approach for relating landscape-level features to birds has been to sample individuals at a landscape scale, and relate their occurrence or abundance to features at that scale (Norton et al. 2000, Woinarski et al. 2000). Alternatively, a more common approach in management studies is to sample individuals within a habitat patch and relate species occurrence or abundance to surrounding habitat features at multiple spatial scales (Fairbairn and Dinsmore 2001, Lee et al. 2002, Melles 2003). This multi-scale method identifies the relative influence of patch vs. landscape-scale habitat on local birds, and can provide forest managers with recommendations across multiple spatial scales.

The purpose of my thesis was to determine the effect of partial harvesting in buffers on cavity-nesting birds, to compare these effects to those in burned riparian forest, and to identify habitat relationships at multiple spatial scales for individual species and bird assemblages. My goal was to evaluate the use of buffer harvesting as a riparian management approach and to provide recommendations on riparian management relevant to cavity-nesting species.

In Chapter 2, I investigated bird assemblages in buffers varying in the amount of forest retained. I also related habitat features at multiple spatial scales to the composition of bird assemblages and species use of sites. My purpose was to determine: 1) the role of the amount of forest retained in buffers, 2) local and landscape-scale habitat features that were important and 3) the relative influence of habitat at different spatial scales, in structuring bird assemblages and determining species site-use of sites.

In Chapter 3, I investigated differences in the composition of cavity-nesting bird assemblages and species use among burned, partially-harvested, and intact riparian forests. I also identified assemblage and species relationships with local habitat features. My purpose was to determine whether recently (≤4 years old) partially-harvested buffers: 1) emulated the effects of recently (2-3 years old) burned riparian forest for bird assemblages, and 2) provided lifeboats for birds in harvested landscapes. Furthermore, I aimed to elucidate specific habitat features across burned, harvested and intact riparian forests that could be used to manage for riparian-using cavity-nesters.

Finally, Chapter 4 provides a summary of my work, outlines key management recommendations, and indicates future research directions.

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CHAPTER 2

RESPONSES OF CAVITY-NESTING BIRDS TO PARTIAL-HARVESTING IN RIPARIAN BUFFERS AND HABITAT MEASURED AT THREE SPATIAL SCALES IN THE BOREAL PLAINS ECOZONE

2.1 Introduction

Across the Boreal Plains ecozone, increasing harvesting pressure by forest companies and other resource industries has resulted in loss and fragmentation of older forest (Schneider and Walsh 2005). Conventional harvest practices in boreal forests of Canada have primarily involved a clearcutting system with two harvest passes and a short rotation age (~70 years) (Bergeron et al. 2002, Schneider 2002). This has reduced the amount of old-growth forest across the landscape and the structural heterogeneity of forest stands (Schmiegelow and Mönkkonen 2002, Burton et al. 2006, Macdonald and Fenniak 2007). For some forest birds, these landscape alterations can limit the amount of available habitat and lead to decreases in their abundance (Imbeau et al. 2001, Imbeau and Desrochers 2002, Schmiegelow and Mönkkönen 2002).

In upland forests, some forest companies have adopted a natural disturbance model in an attempt to reduce negative effects on ecosystems from forest loss (Hunter 1993, Niemela 1999, Burton et al. 2006). This is a coarse-filter approach that assumes organisms are adapted to natural disturbances and thus should be affected less by harvesting that approximates natural disturbance events than by traditional harvesting practices (Hunter 1993). Because fire is the dominant stand-replacing natural disturbance across the Boreal Plains ecozone (Rowe and Scotter 1973, Weir et al. 2000), it may be appropriate as a harvest model (Hunter 1993). Patches of forest and individual trees are retained within variable-sized cutblocks to represent natural fire-skips across a range of fire sizes (Eberhart and Woodard 1987).

In riparian forests, general practice has been to leave uncut, fixed-width buffers adjacent to watercourses (Lee et al. 2004) to conserve water quality (Lee and Smyth 2002) and fish stocks (Wesche et al. 1987). Buffer strips provide habitat for birds and help maintain a diversity of bird species in harvested landscapes (Triquet et al. 1990, Darveau et al. 1995, Whitaker and Montevecchi 1999, Hannon et al. 2002). However, riparian and upland forests are often similarly affected by fire (Andison and McCleary 2002, Everett et al. 2003) and thus retention of intact strips may be inconsistent with a natural disturbance model. Harvesting in buffers is not universally accepted: only 62% of North American boreal jurisdictions (most occurring in Canada) allow this practice (Lee et al. 2004). However, some forest companies are partially-harvesting buffers in a way similar to upland forest, and experimenting with buffer width and the amount of forest retained within them.

While partial-harvesting in buffers represents a fine-scale disturbance that may directly influence the suitability of buffers for birds, suitability may also be affected by larger-scale landscape features. Forest management influences both stand and landscape structure and a fine-scale (i.e. buffer-centric) approach to riparian management may not conserve all riparian birds. If an individual bird's territory extends beyond the buffer, surrounding habitat features may influence its presence in the buffer. Similarly, surrounding landscape elements, such as watercourses and forest patches, may serve as either dispersal barriers or corridors into a buffer, depending on the species (Gustafson and Gardner 1996, Desrochers and Hannon 1997, Belisle et al. 2001, Gobeil and Villard

2002, St. Clair 2003). Focusing on fine-scale habitat alone ignores the influence of spatial habitat variation and can provide an incomplete description of species-habitat relationships (Pearson 1993, Saab 1999, Melles et al. 2003, Warren et al. 2005). Avian responses to spatial scale need to be determined and forest planners may need to consider habitat features at the scale with the strongest influence on bird assemblages or individual species.

In this study, I investigated the effect of partial-harvesting, and the influence of local and landscape-level habitat, on riparian cavity-nesting birds in western Manitoba. I focused on cavity-nesting birds because certain excavators are keystone species and provide nesting habitat for non-excavating species (Martin and Eadie 1999). Effects on these excavators will exert a strong influence on the entire cavity-using community. Furthermore, riparian forests in conventional buffers represent a major source of older forest across harvested landscapes (Lee and Barker 2005). Many cavity-nesters rely on older forest structures such as large decaying trees, standing snags, and downed woody material (DWM) (Lee et al. 1997) for nesting and foraging (Harestad and Keisker 1989; Weikel and Hayes 1999; Gunn and Hagan 2000; Hoyt and Hannon 2002; Aitken and Martin 2004; Martin et al. 2004; Savignac and Machtans 2006). Forest resources important to cavity users may be more abundant in riparian forests. Beaver activity creates standing snags and downed woody material (Rosell and Parker 1996, Martell et al. 2006) and high winds can uproot old trees, adding downed woody material (Stevens et al. 1995). Finally, high humidity levels may promote fungal growth and tree decay (Jackson and Jackson 2004), providing standing trees for excavation.

My objectives were to determine: 1) how species assemblages were influenced by the degree of harvesting within riparian buffers, 2) what local (i.e. within-buffer) and landscape-level habitat features influence the composition of bird assemblages and site-use by five species: Northern Flicker (*Colaptes auratus*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), Boreal Chickadee (*Poecile hudsonica*), Tree Swallow (*Tachycineta bicolor*) and Brown Creeper (*Certhia Americana*) and 3) the scale at which habitat features have the strongest influence on assemblage composition or species site-use.

2.2 Methods

2.2.1 *Study Area*

The study occurred within and around Louisiana Pacific Canada Ltd.'s Forest Management Unit #13 in the Duck Mountain Provincial Forest (DMPF) (51° 39' 58"N and 100° 54' 52" W) of western Manitoba (Fig. 2.1). The DMPF is situated in the Mid-Boreal Uplands ecoregion of the Boreal Plains ecozone, encompasses approximately 3760km^2 (Kenkel et al. 2003) and is dominated by trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). Less dominant tree species include: white spruce (*Picea glauca*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*). Forest stands are predominantly aspen or mixed-conifer, interspersed with many lakes, streams, and black spruce- and tamarack-dominated wetlands. Understory plant species vary in deciduous stands and commonly include river alder (*Alnus rugosa*) and willow (*Salix* sp.). Feather moss (*Pleurozium schreberi*) dominates the understory in conifer forests (Tardif 2004).

The main regional land-use activities in the region are forestry and agriculture (Environment Canada 2007) and fire is the dominant natural disturbance (Rowe and Scotter 1973). Forest harvesting has occurred on a small scale across the Forest Management Unit for the past 100 years, but has intensified significantly in the past 10 years (Donnelly 2001). In harvested landscapes, a 50m-wide buffer is maintained along permanent watercourses. Two years prior to the study some riparian forests were experimentally partially-harvested in one of two general patterns: 1) harvested to the edge of the watercourse and retaining only 5-12% of the forest (similar to retention in the upland) or 2) retaining a 10m-wide unharvested buffer strip along the edge of the watercourse, with an adjacent 30m-wide, partially-harvested strip where 25% of the forest was retained as patches and individual trees. In these latter buffers, forest was typically retained either in a castellated pattern or as a long narrow strip.

2.2.2 *Site Selection*

In total, 66 riparian sites were surveyed, each a 400m-long, 40m-wide strip, situated along the forest/riparian zone edge. Sites were grouped into three broad classes according to total forest retention without consideration of the size, shape or distribution of retained forest structures. Eleven low retention (0-33% forest by area), 14 medium retention (34-66% forest by area), and 22 high retention (66-100% forest by area) buffers were sampled (see Fig. 2.2 for examples; see results for more precise site ranges). In addition, 19 intact riparian forests were sampled (Fig. 2.2), resulting in a total of 4 treatments: 3 buffer types and intact forest. All sites were situated within recently harvested landscapes (harvested 1-2 years previous) except for unharvested sites, which were surrounded by at least a 1km radius of unharvested forest. Cutblocks in the landscape ranged from 5-95ha. Retention within each cutblock left 5-10% of representative tree species and sizes as individual trees or in various-sized patches (Louisiana-Pacific Canada Ltd. 2004-2005). Sites were distributed non-randomly across the study area due to the non-random location of harvest activity however attempts were made to establish an equal number of treatment types in each general harvest region (~300km^2; Fig. 2.1). Based on forest inventory data, all forests sampled were between 77 and 132 years old (mean age=99 years ±1.5 SE) and were aspen-dominated mixedwood (>50% aspen). Sites were situated adjacent to waterbodies (open wetlands and small shallow lakes) ranging from 2ha to 67ha. The width of the riparian zone (the distance between the riparian forest edge and the watercourse edge) varied among sites and ranged from ~5-100m. Riparian zones were typically characterized by an abundance of low-lying shrubs or young aspen trees (<4cm dbh) with some grasses and sedges closer to the water's edge. Only one site per waterbody was established and sites were at least 500m apart to reduce the chance of double-counting birds with large territories. Sites were chosen to minimize the variability in vegetation composition across them.

2.2.3 *Bird Sampling*

Surveys were conducted from 15 April to 27 June, 2006. One of three trained observers surveyed birds along a 400m-long line transect (Bibby et al. 1992) which ran through the centre of each site. All birds, excluding flyovers, that were detected within 20m on either side of the transect were recorded. Observers traveled at a slow and even pace along the transect, stopping and listening for 3 minutes at 100m intervals. This increased detection of birds that may have stopped vocalizing due to observer movements. Because of high shrub density and reduced detection ability in some sites, in all sites observers also stopped briefly (one minute) at 50m intervals to increase the number of birds detected. To decrease the risk of observer bias, 10 pre-season practice surveys were conducted simultaneously by each observer. Inconsistent results among observers were identified and behaviours leading to those differences were corrected. Practice surveys continued until results among observers were minimized to the extent possible. Observers remained inconsistent in their identification of Brown Creepers based on call alone. Therefore, while most species were identified by call, song and/or drumming, Brown Creepers were only recorded if they were singing.

Mean survey duration was 49 minutes. To decrease the risk of diurnal bias, the daily survey period (0600-1200 hrs) was divided into three intervals: 0600-0800, 0800-1000, and 1000-1200, and whenever possible each site was sampled once in each interval during the sampling period. Surveys commenced later than many bird studies (e.g. Darveau et al. 1995, Hobson and Schieck 1999) because most cavity-nesting species do not engage in a pre-dawn chorus and their activity appeared highest post-sunrise to early afternoon (*personal observation*). Treatments surveyed were alternated across days and the order in which sites were surveyed was the same in each survey round to avoid seasonal bias. Surveys were not conducted in very windy (Beaufort >6), rainy or snowy conditions. A high Beaufort cut-off level relative to conventional studies (e.g. Schmiegelow et al. 1997) was used since riparian forests tend to be windier than upland forests (Stevens et al. 1995) and because the sampling radius was small. It was assumed that birds were detected with equal probability across treatments because the sampling radius was small.

The maximum abundance of each species over all three surveys rounds was used in analyses. This measure was better suited than mean abundance as it was applied to sampling areas that may have encompassed only a portion of a bird's territory (Toms et al. 2006), and individuals with large territories may only have been present for one or two sampling sessions. Species abundances however, were low (generally 0-3 individuals per site) and results are more indicative of differences in species use rather than abundance among sites.

2.2.4 *Local Habitat Sampling*

To characterize forest composition within each site, six habitat variables, identified as important foraging or nesting structures in past studies, were measured: 1) the density of large (≥25cm dbh) trembling aspen trees with at least one *Phellinus tremulae* fungal conk, 2) the density of large (≥25cm dbh) snags (decay class D1-D6; Appendix 2.1), 3) the density of conifer trees ≥4cm dbh, 4) the density of live birch trees ≥4cm dbh, 5) the mean dbh of deciduous trees ≥12cm dbh, and 6) the abundance of decaying downed woody material (Stauffer and Best 1980, Harestad and Keisker 1989, Villard 1994, Johnson 1998, Weikel and Hayes 1999, Gunn and Hagan 2000, Savignac et al. 2000, Hoyt and Hannon 2002, Alberta Sustainable Resource Development 2003, Aitken and Martin 2004, Martin et al. 2004, Warren et al. 2005, Savignac and Machtans 2006, Koivula and Schmiegelow 2007).

Variables 1-5 were determined by sampling vegetation in plots. In harvested sites, plots were situated in remaining forest patches only. Attempts were made to sample a total forest area of $2000m^2$, however because the amount of remaining forest varied among sites, (sometimes less than $2000m^2$) this was not always possible and area sampled varied among sites. Depending on the dimensions of the forested patch, plots were 10mx10m, 10mx20m, 10mx30m, 10mx40m, or 20mx20m. Plots were square or rectangular rather than circular to better match the shapes and sizes of remaining forested patches in order to maximize the area of forest surveyed. Plots were distributed evenly across the forested areas of each site whenever possible. In all intact sites, $2000m^2$ of forest was sampled by dividing the transect widthwise into five equally-sized sections and sampling one 20mx20m plot in each section. In sample plots of harvested and intact sites, the dbh, decay class (1 of 9 classes; Appendix 2.1), and presence of the fungal conk *Phellinus tremulae* for each tree ≥4cm dbh was recorded and abundance values for variables 1-4 were determined. These values were summed over all plots in a site and for each variable the total abundance was divided by the total area of forest sampled across all plots to yield density values. Densities were then multiplied by the total area of forest remaining per site to estimate the abundance of each variable across the entire site. Because sample area varied slightly among sites, values were further divided by the local sample area (obtained from GIS data: see below), to yield the final density value (#/ha) in each site for each variable. Variable 5 was determined by averaging dbh values for deciduous trees ≥12cm dbh across all plots in site.

Downed woody material was sampled across both forested and non-forested areas in each site by dividing the transect widthwise into five equal sections. In each section, along a 20m-long transect running upland from the riparian forest edge, the number of decaying downed woody material (decay class >1; Appendix 2.1) ≥12cm diameter where intersected by the transect (the minimum size deemed appropriate as foraging substrate) were counted. Within a section, this transect was situated at one of three spatial intervals: 0m (riparian tree line)–20m upland, 10m-30m upland, or 20m-40m upland. To avoid sampling bias, the location of a transect was systematically rotated within and among sites. The number of decaying downed woody material was summed over all five transects in each site for a final site abundance value (#/m).

The amount of forest retained within each site was calculated by overlaying the boundaries of each transect onto an aerial image of the site and then digitizing the boundaries of each forest patch (minimum mapping unit 10m) using ArcView 9.0 (ESRI Inc. 2004). Total forest area in the site was divided by local sample area to yield the percent of site forested.

2.2.5 *Landscape Habitat Sampling*

Landscape habitat variables were measured using Louisiana-Pacific Canada Ltd and Manitoba Conservation Forestry Branch (LP&MC) Forest Lands Inventory (2004) (hereafter: Manitoba dataset) and forest cover data provided by the Ministry of Environment (SK)(1978) (hereafter: Saskatchewan dataset). The latter were used only for three sites that fell outside the FMU but were within Saskatchewan (Fig. 2.1). Both data sets were in vector format, were projected in UTM zone 14N in the geographic coordinate system of North American Datum 1983, and measured linear units in meters. Mapping resolution for the Manitoba dataset was 1:15,000 and for the Saskatchewan dataset was 1:12,500. Both datasets provided information on vegetation composition, wetland characteristics, lakes and rivers. For the Saskatchewan dataset, all forested muskeg was assumed to be conifer dominated and composed only of mature (>70 years old) forest, as this level of detail was not provided. These assumptions were based on the fact that: 1) the majority of muskeg identified in the Manitoba dataset was conifer-dominated and 2) disturbance (natural and anthropogenic) had not recently occurred around the Saskatchewan site, resulting in older forest stands.

Two spatial extents, related to cavity-nesting bird behaviour, were selected for the landscape analyses. The first extent was related to the territory size of many cavity-nesters. Some birds detected on a transect may have had territories that extended beyond the transect and been affected by larger-scale features. To delineate a landscape buffer that encompassed features within species territories (hereafter called the medium scale), it was assumed that: 1) individual birds were moving randomly within their territory and 2) if a bird was observed at least once over all three sampling rounds, the transect encompassed at least one third of its territory. Five hectares was selected to represent territory size as this was the maximum area that encompassed the full territories of most of the common (observed in >20% of sites) cavity-nesting species, excluding Northern Flicker and Boreal Chickadee (Elchuck and Wiebe 2003, Poole 2007). These species were excluded as their territories were significantly larger than many of the other common cavity-nesting species, and habitat within their territory could be captured in the large-scale buffer (described below). The size of Pileated Woodpecker territories far exceeded all other species, and was not considered in the selection of landscape scales. To delineate the medium-scale buffer, I assumed that if territories were circular and one third of a 5ha territory (1.67 ha) fell within the 40m-wide transect, the radius of the remaining 3.33ha outside the transect was 159m. Therefore, 159m was measured out from all edges of the transect using ArcView 9.0 (ESRI Inc. 2004) and a medium scale buffer, averaging 23ha, was delineated around each site (Fig. 2.3a).

The second extent used to characterize the landscape (hereafter called the large scale) was related to the influence of landscape barriers on bird movement and to the territory size of Northern Flicker and Boreal Chickadee. From a bird's perceptual range, barriers may prevent immigration to and/or selection of riparian buffers for use. Features in the surrounding landscape that could be movement barriers were water bodies and cutblocks (Desrochers and Hannon 1997, St. Clair 2003). Buffers are situated on the edge of both cutblocks and waterbodies and thus the extent of these specific barriers may influence dispersal into buffers. On average, cutblocks were larger than water bodies so to maximize representation of the area that may influence movement, cutblock area was used to determine the extent of the large scale. Median cutblock size, averaged over the two years prior to the study, was 49ha (Louisiana-Pacific Canada Ltd. Annual Report 2004-2005; 2005-2006). Assuming cutblocks were square (700mx700m) and sites were situated on the cutblock edge, an individual would be required to cross 700m on average to reach the riparian forest. Therefore, a large-scale buffer, measuring 700m out from all edges of the local sample area and averaging 211ha, was delineated around each site using ArcView 9.0 (ESRI Inc. 2004) (Fig. 2.3b.)

Within the area covered by each medium- and large-scale buffer, including the local sample area, eight variables were measured using ArcView 9.0 (ESRI Inc. 2004): the proportion of area covered by 1) cutblock (harvested over the previous 10 years), 2) intact forest (>10 years old), 3) open water, 4) closed (i.e. treed; >6% tree cover) wetland, 5) deciduous-dominated forest (>10 years old, >50% deciduous *spp.*), 6) conifer-dominated forest (>10 years old, >50% conifer *spp.*), 7) total mature forest (>70 years old), and 8) total young forest (10-70 years old). Variables 2, 7 and 8 included both deciduous- and coniferous-dominated forest. If sites overlapped, only one site was used to avoid pseudoreplication. Selection of sites was designed to maximize variation in landscape composition in the remaining sample. In two sites, medium- and large-scale buffers extended beyond the study area, and these sites were excluded from landscape-scale analyses.

2.2.6 *Data Analyses*

For all significance tests, an error-wise alpha rate of 0.1 was used. This reduced the chance of committing Type II errors, which can have greater consequences for conservation outcomes than Type I errors in applied research (Smith 1995). Specifically, by incorrectly accepting a hypothesis of no difference, future harvesting may apply treatments that may detrimentally affect birds. Correlation among predictor variables at each scale was tested using a Spearman Rank Correlation (Appendix 2.2). For all analyses, only uncorrelated predictor variables (rho<0.7) were used. When two or more variables were correlated, the variable retained was that which was either correlated with multiple variables (to minimize the number of remaining variables) or was expected to be more broadly available to forest managers using GIS data (i.e. more applicable for management use).

All multivariate analyses were conducted using the program PC-ORD 4.2 (McCune and Mefford 1999). For all methods except the Indicator Species Analysis, species abundance values were relativized by site using a general relativization (McCune and Grace 2002). I removed sites with no bird detections, sites greater than 2 standard deviations from the mean distance measure (Sorenson or Chi-squared depending on the analysis) among sites, and species that were present in fewer than 5% of sites, as suggested by McCune and Grace (2002).

2.2.6.1 *Effect of Forest Retention on Bird Assemblages*

To determine whether the species using buffers with low, medium or high forest retention were similar, Non-Metric Multidimensional Scaling (NMDS) (Kenkel and Orloci 1986, Clarke 1993) was used to visually assess the response of bird assemblages to treatments. Multiple Response and Permutation Procedures (MRPP) (Mielke 1984, Zimmerman et al. 1985) were used to quantify differences among the three treatments and Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) was used to identify species that were using sites more frequently in a particular treatment. Intact sites were not used in these analyses because they were situated adjacent to unharvested forest and thus were not buffers.

NMDS is a non-parametric multivariate analysis that ranks sites based on differences in species composition. The data were analyzed using the Sorenson (Bray-Curtis) distance measure and the "slow and thorough" autopilot mode with default settings. Forty iterations with real data, and 50 with randomized data, were run for each of 1 to 6 dimension solutions. The fit of the final solution was indicated by its stress value. The strength of the solution was assessed by the Pearson correlation coefficient of determination (r^2) which describes the amount of variation in the original data matrix that was explained by the reduced data matrix. To evaluate the relationships between site scores and species, the r^2-values between species and each ordination axis were calculated. When r^2-values were >0.3 (deemed sufficiently high), species-site relationships were defined using Pearson correlation coefficients (r). These r-values were calculated for each axis and indicated the linear relationship between site scores and each species. To determine whether bird assemblages were responding to vegetation composition in addition to the degree of harvesting, all local habitat features were indirectly related to the structure of assemblages using overlays. This method differs from direct ordination techniques (e.g. Canonical Correspondence Analysis) in that it relates habitat to a more accurate representation of true assemblages (i.e. one that has not been constrained by habitat). Assemblage-habitat relationships were evaluated by calculating r^2-values between each habitat variable and each axis of the NMDS solution.

MRPP is a non-parametric equivalent of Discriminant Function Analysis. Differences in the composition of bird assemblages among treatments were analyzed using a Sorenson distance measure, and a natural group weighting factor $n_i/\Sigma\, n_i$ (where n_i is the number of sample plots in each group). When treatments differed significantly, pair-wise comparisons were conducted between them to determine where specific differences occurred (McCune and Mefford 1999). Statistical significance was assessed using p-values and a full Bonferroni-corrected alpha value, while effect size was evaluated using the chance-corrected within-group agreement test statistic (A).

The ISA was run using species abundance data (Dufrêne and Legendre 1997). The significance of each species' indicator value (INDVAL) was assessed using a Monte Carlo simulation of 10,000 runs. A species was considered a significant indicator only when $p<0.1$ and INDVAL>25 (Dufrêne and Legendre 1997).

2.2.6.2 *Effect of Habitat on Bird Assemblages*

The previous analyses tested for retention treatment effects on bird assemblages in buffers. To determine the direct relationships of bird assemblages to habitat variables, Canonical Correspondence Analyses (CCA) (ter Braak 1986) were used. Sites in both buffers and intact forest were combined in this analysis to better represent the range of habitat variation across the landscape. To determine what local-, medium- and large-scale habitat features influenced the composition of bird assemblages, and the scale at which habitat had the strongest influence on the composition of bird assemblages, I conducted a separate CCA analysis using habitat from each scale (i.e. 3 CCAs) and compared results across scales. Only sites with non-overlapping medium- or large-scale buffers were analyzed ($n=45$).

CCA is a direct gradient analysis that forces ordination axes to be linear combinations of known environmental variables, therefore directly relating assemblage and environmental variation (ter Braak 1986). CCA was selected over other direct gradient ordination techniques because it is based on unimodal models of species abundance along environmental gradients. In this study, many species abundances were distributed unimodally as indicated by a Detrended Correspondence Analysis (DCA) (length of first axis gradient = 4.3 standard deviations; as a general rule, unimodality is >4 standard deviations., Jongman et al. 1995).

For all CCAs, local habitat values were standardized using a general relativization (McCune and Grace 2002) while landscape-scale variables were not, as they were proportional data. All three CCAs were conducted using a Chi-squared distance measure and the significance of each model was determined by testing the hypothesis of no difference between species and habitat matrices using Monte Carlo permutation tests with 999 iterations. Assemblage-habitat relationships were evaluated using intraset correlation coefficient values between habitat variables and ordination axes. The importance of habitat variables in defining the composition of assemblages was indicated in each CCA by the percent of variance in the original species data explained by the CCA. Local sample area was included as a covariate in all models. For a summary of habitat variables included at each scale, see Tables 2.1 and 2.2.

2.2.6.3 *Individual Species Analyses*

To determine the relationship between habitat variables and individual species site-use, I examined five species: Yellow-bellied Sapsucker, Northern Flicker, Boreal Chickadee, Tree Swallow and Brown Creeper. These species were selected because they were relatively common (present in >9% of sites), have a range of territory sizes, migratory behaviours, and habitat requirements, are of particular management interest. Yellow-bellied Sapsuckers and Northern Flickers are likely keystone species (Bunnell et al. 2002, *Cooke personal communication*), providing nest-sites for many secondary-nesters. Brown Creepers are uncommon, old-growth obligates, whose abundance in the western boreal forest is relatively unknown and of increasing concern (Alberta Sustainable Resource Development 2003). Across Canada, Boreal Chickadee populations have been declining for the past 40 years (Downes and Collins 2007) while Tree Swallows are among aerial insectivorous species which have recently begun to decline (McCraken 2008).

Abundance of each species was related to habitat variables using generalized linear models (S-plus; Insightful Corp. 2005). I analyzed bird abundance in both buffers and intact forest to increase the range of habitat variation represented across the landscape. Abundance data for most species were not overdispersed and were Poisson-distributed (Kolomogrov Smirnoff Test, $p>0.1$; Appendix 2.3), thus were analyzed using multiple Poisson regressions. Data for Brown Creeper were overdispersed so I used a negative binomial model. For Boreal Chickadee models, one outlier site was removed. Model covariates included only uncorrelated habitat variables and the local sample area was included in all models to control for its effect on species abundance. Model fit was assessed by the amount of deviance (a measure of difference between observed and fitted values) it explained. If a model explained at least 10% deviance it was deemed appropriate for interpretation.

Depending on management goals, forest managers may be interested in key habitat features at multiple spatial scales that influence bird abundances, or in the particular scale to which individual species respond most strongly. For the former, I determined what habitat variables at local, medium and large scales most strongly influenced the abundance of each species. To do this, models were run at each spatial scale for each species. Covariates selected for local-scale models varied among species and were chosen from among all local variables measured based on known species-habitat associations (Table 2.3). Covariates in medium- and large-scale models included all variables measured at each respective scale. Model fitting followed a multi-step process. First, for each species at each scale, a series of models was run. At the local scale, this included (1) a model with amount of forest retained only to test the independent effect of forest retention, (2) models containing all possible combinations of selected composition variables, and (3) a global model containing the amount of forest retained and all selected composition variables. At medium and large scales, the series included a model for each possible combination of habitat variables and a global model. Within each series, a set of models with substantial supporting evidence (Δ AICc <2; Burnham and Anderson 2002) was identified using Akaike's Information Criterion (AIC) (Anderson et al. 2000) (Appendix 2.4). Specifically, AICc, which accounts for small sample sizes (i.e. $n/K < \sim 40$) was used.

Using all competing models, AIC parameters were recalculated and the potential of each variable to predict each species' abundance (i.e. predictability value) was determined by summing the Akaike weights (w_i) over all models for that species in which a variable appeared. This value ranged from 0 to 1 and was meaningful only in relation to the other model variables. Variables with a predictability value of 1 were either present in all models or were the only variable present. Although all final model variables were important in predicting species abundance to some degree, variables meeting the following criteria were deemed the best predictors: 1) they had a high predictability value ($\geq$0.85) for one or more species or 2) they had a moderate predictability value ($\geq$0.40) for three or more species. Standardized coefficient values for each variable in model subsets were determined using weighted averaging (Burnham and Anderson 2002).

Next, to determine which scale (or multiple scales) was best in describing habitat relationships for each species, multi-scale models were created. These models were run using all sites with non-overlapping medium- or large-scale buffers (n=45). First, the most parsimonious model (Δ AICc = 0) for each species at each scale was selected. Then, for each species, a series of models including the final model at each scale, models for all combinations of scales (i.e. local + medium, medium + large, etc.) and a global model were analyzed. Again, a set of competing models with substantial supporting evidence (Δ AICc <2) was identified (Appendix 2.4). The predictability value of model variables for each species was determined using the same approach as individual-scale analyses (see above). To determine the importance of each scale for each species, the predictability values of model variables were compared among scales for each species. This modeling approach was used to identify the relative importance of scale rather than particular species-habitat relationships per se. A broader suite of habitat relationships was defined for each species in scale-specific models and as such, results from those models should be applied when managing for habitat at a given scale.

2.3 Results

In total, 14 species were observed in 66 sites (Table 2.4; for summary statistics see Appendix 2.5). Yellow-bellied Sapsucker was the most common species followed by Brown Creeper and Black-capped Chickadee. All other species were present in fewer than 30% of sites (Table 2.4). Tree Swallows were observed in low and medium retention sites only, while Boreal Chickadees and Red-breasted Nuthatches were detected in all except low retention sites, and Downy Woodpeckers were detected in all except medium retention sites (Fig. 2.4). Pileated Woodpeckers, Black-backed Woodpeckers, Three-toed Woodpeckers, and White-breasted Nuthatches were observed in less than 5% of sites. Black-backed Woodpeckers were observed only in high retention buffers and intact forest, Three-toed Woodpeckers were detected only in low retention buffers, and White-breasted Nuthatches were observed only in intact forest (Fig. 2.4). Pileated Woodpeckers were observed in all treatments except intact forest (Fig. 2.4). All other species were observed in all treatments.

2.3.1 *Composition of Bird Assemblages*

2.3.1.1 *Effect of Forest Retention on Bird Assemblages*

I identified a three-dimensional solution, accounting for 78% of the variation in the original species-distance matrix using NMDS (Table 2.5). The final stress value was relatively high (Table 2.5), indicating the potential for the projected assemblage structure to be misleading (McCune and Grace 2002). Overall, treatments were poorly separated in ordination space, particularly medium and high retention buffers, suggesting bird assemblages were not distinct (Fig 2.5). The MRPP analysis, however, indicated that medium and high retention buffers had similar bird assemblages, but assemblages in medium and high retention sites differed from those in low retention buffers (Table 2.6). These differences were relatively weak, indicated by low A-values in the MRPP analysis (Table 2.6).

Only Axis 1, which accounted for 20% of the variation in the species data, was correlated (r^2>0.3) with amount of retention, however this correlation was relatively low (Table 2.7). Along a gradient from high to low retention, assemblages shifted from being Brown Creeper-dominated to Tree Swallow-dominated (Fig. 2.5; Table 2.7). In addition to these two species, Black-capped Chickadee, Boreal Chickadee, and Yellow-bellied Sapsucker each accounted for >30% of site-variance along one or more axes. However, these species were not correlated with Axis 1 (r^2<0.3) and thus were not strongly associated with retention level (Table 2.7). Forest composition and structure differed among the three buffer treatments (Table 2.1), however no habitat features were correlated with any of the ordination axes (Table 2.7).

Indicator Species Analyses indicated that Northern Flicker (Indicator Value (IV)=35.1, Randomized Indicator Value (RIV)=17.0, p=0.01), House Wren (IV=30.2, RIV=15.9, p=0.04), and Tree Swallow (IV=38.5, RIV=12.6, p=0.004) used sites in the low retention treatment more frequently than other treatments.

2.3.1.2 *Assemblage-habitat Associations*

Local habitat features alone influenced the composition of bird assemblages, however this relationship was relatively weak (22% variance explained by three axes). Models using medium- and large-scale habitat features were not significant (Table 2.8). For the local-scale CCA, when all sites were analyzed (n=66), the first two axes accounted for 83% of the total variation explained and described two main habitat gradients across the sites (Fig 2.6.) The first axis (eigenvalue=0.38, 9.8% of variance explained) represented a gradient from high to low forest retention (r=0.912), and from high to low conifer tree density (*r*=0.586) (Fig. 2.6; Table 2.9). Axis 2 (eigenvalue=0.20, 5.1% of variance explained) was related to forest composition and represented a gradient from sites with high density of deciduous trees and large snags, suggestive of old deciduous forest, to those with a high conifer tree density (Fig. 2.6; Table 2.9).

Based on species site scores (as reflected in their position in multidimensional space), Brown Creeper and Red-breasted Nuthatch were highly and positively associated with increasing amount of forest retention and Tree Swallow was strongly and negatively associated with it (Fig. 2.6). No species were strongly associated with forest composition exclusively, but were influenced by a combination of retention and forest composition. Yellow-belled Sapsucker and Black-capped Chickadee used high retention buffers with a high density of old deciduous forest most however, this relationship was stronger for Yellow-bellied Sapsucker. Boreal Chickadee was associated with high retention sites and along with Downy Woodpecker and Northern Flicker, also with high conifer density. Pileated Woodpecker and Tree Swallow used low retention buffers more, the former with low conifer tree density and the latter with a low density of large snags. Hairy Woodpecker and House Wren showed no strong association to any habitat type.

2.3.2 *Analysis of Individual Species*

Regression models identified a suite of best predictor variables for cavity-nesters at each scale.

2.3.2.1 *Local Scale*

At the local scale, all habitat features had some influence on species site-use however retention, the density of large aspen trees with conks, conifer tree density and mean dbh of deciduous trees were the best predictors. Local habitat features accounted for a moderate amount of variation (15-71% deviance) in all individual species (Table 2.10). Tree Swallow and Brown Creeper were the only two species associated with forest retention. Site-use by Tree Swallow decreased, and Brown Creeper increased with increasing retention. Northern Flickers used sites with higher dbh of deciduous trees and lower density of large aspen trees with conks more, while Yellow-bellied Sapsuckers showed the reverse. The use of sites by Boreal Chickadee was positively related to conifer tree density.

2.3.2.2 *Medium Scale*

At the medium scale, the best habitat predictors of species site-use were the proportion of the following cover types: harvest, intact forest (including all deciduous- and coniferous-dominated), wetlands and conifer-dominated forest. Medium- scale habitat features accounted for a relatively high amount of variation in the abundance of only two species: Boreal Chickadee (27-36% deviance) and Tree Swallow (42-53% deviance) (Table 2.10). Boreal Chickadees used sites with lower proportions of harvest and wetland and higher proportions of intact and conifer-dominated forest more (Table 2.10). Tree Swallows used sites with higher proportions of harvest, intact forest and wetlands and lower proportions of conifer-dominated forest more (Table 2.10).

2.3.2.3 *Large Scale*

All large-scale variables influenced species site-use, however, the proportion of landscape in harvest, wetland and conifer-dominated forest were the best predictors. All species except Brown Creeper had a moderate to high amount of variation (7-44% deviance) in their abundance accounted for by large-scale habitat features (Table 2.10). Tree Swallows used sites with higher proportions of harvest more. No other species was related to the proportion of harvest. Yellow-bellied Sapsuckers had higher use, and Northern Flicker and Boreal Chickadee had lower use, of sites with higher proportions of wetlands. Northern Flickers and Yellow-bellied Sapsuckers had lower use, and Boreal Chickadees had higher use of sites with higher proportions of conifer-dominated forest.

2.3.3. *Importance of Each Scale in Defining Species Site-use*

Multi-scale models accounted for a moderate to high, although variable, amount of variation (17-86% deviance) in all species abundances (Table 2.10). Relative to medium- and large-scale habitat, the influence of local habitat on site-use by Yellow-bellied Sapsuckers and Tree Swallows was much higher (Table 2.10). Northern Flickers were influenced exclusively by large-scale habitat (Table 2.10). Likewise, relative to local habitat, site-use by Boreal Chickadee was more strongly influenced by large-scale habitat features. Brown Creepers were influenced exclusively by local habitat (Table 2.10).

2.4 Discussion

2.4.1 *Effect of Harvesting on Bird Assemblages in Buffer Strips*

Retained forest patches within recently harvested landscapes, such as riparian buffers, may provide habitat for forest-associated bird species (Darveau et al. 1995, Merrill et al. 1998, Pearson and Manuwal 2001). My results suggest that high amounts of timber removal could compromise this function. The combined results of the NMDS and MRPP indicated that partial-harvesting within buffers altered the composition of bird assemblages, but only at low levels of retention (below 33%).

Differences in assemblages at lower retention levels were driven by higher site-use by Tree Swallow, Northern Flicker, and House Wren and lower site-use by Brown Creeper. As forest retention decreased, the amount of open habitat increased, providing suitable nesting and foraging habitat for Tree Swallow, Northern Flicker, and House Wren (Conner and Adkisson 1977, Rendell and Robertson 1990, Johnson 1998, Elchuk and Wiebe 2002). At higher retention levels, buffers consisted of relatively contiguous mature forest, and had high canopy cover, providing suitable habitat for Brown Creeper (Robertson et al. 1992, Alberta Sustainable Resource Development 2003, Sallabanks et al. 2006).

My results are consistent with those of Hanowski et al. (2006) who compared passerine bird assemblages across a range (<2-10m^2/ha) of forest retention in deciduous-dominated (aspen and sugar maple (*Acer saccharum*)) riparian buffers in northern Minnesota, USA. Although my sites covered a narrower range of retention (basal area 0.25-6.4m^2/ha) than those of Hanowski et al. (2006) (basal area 0-10m^2/ha), in both studies, avian assemblages in low retention buffers (basal area <3m^2/ha) differed from those in higher retention buffers. Similar to my study, Hanowski et al. (2006) found more open-habitat species in low retention buffers. Furthermore, Kardynal (2007) compared riparian-using bird assemblages in partially-harvested buffers with low (5-35%), medium (35-75%), and high (>75%) forest retention in boreal mixed-wood forests. Abundance of many forest-associated species was lower in buffers with lower amounts of forest.

In upland boreal mixedwood forests, abundance of species using trees and shrubs for nesting was lower in cutblocks with <20% (Harrison et al. 2005) and <40% (Tittler et al. 2001) tree retention than uncut forests. Similarly, the review by Schieck and Song (2006) found that old-forest species increased and open-habitat species decreased as the number of large live trees retained in cutblocks increased. Finally, in cedar-hemlock forests of interior British Columbia, open-habitat bird species were more abundant in low retention (~40% forest volume) partially-harvested stands than higher retention stands (>70%) (Steventon et al. 1998). All these studies suggest that the structure of bird assemblages is altered at low levels of forest retention in buffers.

Although the amount of forest retention altered the composition of assemblages, this effect was relatively weak overall. Along with the relative lack of correlation between forest composition variables and the NMDS axes, this suggests assemblages were primarily structured by other factors. Conclusive relationships cannot be drawn however as the ordination was characterized by high stress and provided only a very general depiction of assemblage structure.

2.4.2 *Influence of Local and Landscape-scale Habitat, and Spatial Scale on Bird Assemblages*

Knowledge of species-habitat relationships is necessary to develop effective management guidelines. Until recently, many studies have ignored the effect of landscape context on community composition; this has been criticized (Saab 1999, Taylor and Krawchuk 2005, Warren et al. 2005). I examined bird assemblages at multiple spatial scales and found that the composition of assemblages was related to habitat at the local scale only. Previous assemblage-level studies have generally identified an influence of both local- and larger-scale habitat on species composition (Drapeau et al. 2000, Grand and Cushman 2003, Melles et al. 2003). Landscape-scale habitat influences may not have been identified in my study for several reasons. First, I examined relatively few species, and three of the most common (Brown Creepers, Yellow-bellied Sapsuckers, Tree Swallows) were strongly related to local-scale variables. These relationships may have overridden possible larger-scale habitat relationships of less common species. Second, compared to previous studies, my analyses included fewer landscape-scale variables and none described landscape configuration, which can influence the composition of some bird assemblages (Grand and Cushman 2003). Finally, other landscape-scale variables relevant to cavity-nesters may not have been included in my study.

The amount of forest retained within sites was the main variable accounting for variation in species composition. Tree Swallows were negatively and Brown Creepers, Red-breasted Nuthatches, Yellow-bellied Sapsuckers and Boreal Chickadees were positively associated with forest retention. Similar to Brown Creepers, Red-breasted Nuthatches and Boreal Chickadees commonly use areas of contiguous, undisturbed mature boreal forest (Hobson and Schieck 1999, Schieck and Hobson 2000). To a lesser degree, variation in species composition was described by tree species and level of decay. Yellow-bellied Sapsuckers are not commonly influenced by the amount of forest retention per se (Hobson and Schieck 1999, Schieck and Hobson 2000, Harrison et al. 2005) and fewer sapsuckers in low retention sites was likely due to a loss of decaying aspen and live birch trees for nesting and foraging (Savignac and Machtans 2006). Results suggest that in terms of habitat, management for entire bird assemblages should consider the amount of forest retained within a buffer. Meanwhile, the composition of residual forest appears less important.

2.4.3 *Influence of Local and Landscape-scale Habitat on Individual Species Site-use*

Although entire bird assemblages did not respond to landscape-scale features, my study confirms the utility of a multi-scale approach in determining habitat associations for individual species. At the local scale, the amount of forest retained, the density of large aspen trees with conks, conifer tree density and mean dbh of deciduous trees were the best predictors of species site-use. Results suggest Brown Creepers are the most vulnerable to local forest loss, while Tree Swallows may benefit from harvesting within buffers. Site-use by Yellow-bellied Sapsuckers, Northern Flickers, and Boreal Chickadees did not appear to be influenced by the overall amount of forest retention *per se* but by the composition of remaining forest patches.

Overall, observed relationships between species and local habitat were consistent with previous studies. The use of large aspen trees with fungal conks for nesting by Yellow-bellied Sapsuckers has been well documented (Kilham 1971, Harestad and Keisker 1989, Loose and Anderson 1995, Giese and Cuthbert 2005, Savignac and

Machtans 2006). However, sapsuckers do not always select the largest trees available as they may lack fungal conks or have thicker sapwood, making excavation difficult (Savignac and Machtans 2006). This may explain why Yellow-bellied Sapsuckers were negatively related to the mean dbh of deciduous trees in my study. Notably, I may have sampled in the upper ranges of trees size (only deciduous trees >12cm dbh were measured and the minimum dbh observed was 18cm). Had I measured a broader range of tree sizes, this relationship may have disappeared, given that sapsuckers generally select larger trees for nesting (Savignac and Machtans 2006). Northern Flickers appeared to use large deciduous trees in various states of decay, similar to other studies (Harestad and Keisker 1989, Aitken and Martin 2004, Cooke *personal communication*). Snag density was a poorer predictor of Northern Flicker site-use than mean dbh of deciduous trees, suggesting that tree size may be more important than tree condition for nest sites. The positive relationship between Boreal Chickadee site-use and conifer tree density is consistent with other studies (Hobson and Bayne 2000, Schieck and Hobson 2000, Morissette et al. 2002). Conifer trees are important foraging substrates for chickadees, which commonly glean arthropods from branches or cones (McLaren 1975, Ficken et al. 1996). In this study, Boreal Chickadees may have used conifer trees for foraging, as they tend to select nest trees based on softness of heartwood rather than species (Ficken et al. 1996).

At larger spatial scales, primary habitat features influencing species site-use included the proportion of harvest, intact forest, wetlands and conifer-dominated forest in the landscape. Habitat associations varied among species and spatial scales, making it difficult to identify a single type of landscape that may be more appropriate to harvest for all five cavity-nesters based on existing landscape features. However, variation in species-habitat relationships indicates the need for a management approach that maintains heterogeneity of habitat features measured across the landscape.

Yellow-bellied Sapsuckers and Tree Swallows had higher use of sites with more harvest in the surrounding landscape, consistent with other studies (Holt and Martin 1997, Harrison et al. 2005, Schieck and Song 2006). Yellow-bellied Sapsuckers and Tree Swallows have small territories (1.3ha and 0.008ha, respectively; Table 2.4) that could have been situated entirely within the local sample area. As such, their relationship to harvest at larger scales suggests they may select territories based in part on a high amount of harvest in the surrounding landscape. Alternatively, Brown Creepers, Boreal Chickadees and Northern Flickers have larger territories (>4ha, >5ha and 7ha, respectively; Table 2.4) that extend beyond the local sample area. For these species, forest loss (as indicated by area harvested) at the medium-scale likely reflects a change in the amount of suitable within-territory habitat. The negative association of Brown Creepers to the proportion of harvest measured at the large-scale suggests that cutblocks may represent movement barriers for this species.

2.4.4 *Influence of Spatial Scale on Individual Species Site-use*

The predictor values of habitat measured at each spatial scale varied among species, thus a buffer-centric management view may not be appropriate for all species. The majority of species responded most strongly to habitat features measured at a scale no larger than the area of their territories. For example, Tree Swallows and Yellow-bellied Sapsuckers, species with territories smaller than the local sample area, were primarily associated with local-scale habitat. Alternatively, Northern Flicker and Boreal Chickadee were most strongly influenced by large-scale habitat and their territories likely extended into the large-scale buffer. An exception to this trend was Brown Creepers which were most strongly influenced by local-scale habitat but had territories exceeding the local sample area. In this case, Brown Creepers may have selected more strongly for fine-scale nesting and/or foraging substrates (Poulin et al. 2008). Alternatively, they may have altered the dimensions of their territories in response to disturbance, and medium-scale buffers (which assume circular territories) may not have accurately described landscape features within their territories. Specifically, because Brown Creepers are highly old-growth dependent (Alberta Sustainable Resource Development 2003) and forest retention within buffers was typically arranged in narrow linear or castellated strips, they may have attempted to maximize the area of forest within their territories by establishing narrow linear territories. A similar shift in territory dimensions by Ovenbirds (*Seiurus aurocapillus*) in response to various forest widths in buffers has been observed (Lambert and Hannon 2000). Although this could occur with any species, it is more likely with Brown Creepers, which are highly sensitive to harvesting (Tittler et al. 2001).

2.4.5 *Study Limitations*

Because of the small survey areas I used, abundance of many species was low and some species present in the larger bird community may have been missed. Survey areas were constrained by the amount of cutblock along sampled wetlands, which in many sites was no greater than 400m. I therefore attempted to increase species detectability by maximizing the number of sites and visits per site. However, larger sample areas may have more accurately represented bird assemblages and increased statistical power to detect differences among buffer treatments. To address this limitation and increase statistical power, future studies should occur in regions where longer buffer strips are harvested, allowing for larger survey areas.

In addition, the composition of assemblages may continue to change for several years following disturbance (Schmiegelow et al. 1997, Hanowski et al. 2005) and my study occurred 1-2 years post-harvest. Therefore, the observed effects of riparian partial-harvesting on bird assemblages may not be indicative of relationships through time; longer-term studies are necessary to determine the value of retained habitat. Furthermore, the range in proportion of forest harvested at the large-landscape scales was limited (0%-39%). Had large-scale buffers encompassed a broader range of harvest amount, responses to harvest by some species at the large-scale may have been more evident (Schmiegelow et al. 1997). Moreover, species-specific habitat requirements can vary seasonally (Strong and Bock 1990). Therefore, because my study evaluated habitat relationships during the breeding season only, results may not include the full range of habitat associations.

2.4.6 *Conclusions and Management Implications*

Acknowledging the above limitations, my study suggests that the degree of riparian partial-harvesting influenced the composition of bird assemblages. However, this effect was relatively weak. A significant shift in composition occurred at low retention levels and was primarily attributed to four species: Tree Swallow, Northern Flicker, House Wren, and Brown Creeper. All other species appeared unaffected by forest loss or had sample sizes too low to effectively analyze their response. Among these four affected species, only the higher use of low retention buffers by Northern Flickers is expected to have cascading effects throughout the nest-web, as this is the only cavity-excavator. Specifically, the number of cavities excavated by Northern Flickers would likely increase, potentially increasing the abundance of species using their holes including Buffleheads (*Bucephala albeola*), American Kestrels (*Falco sparverius*), Mountain Bluebirds and Tree Swallows (Martin et al. 2004, *Cooke personal communication*). The level of retention where the composition in assemblages shifted was only broadly defined in my study (<33%), and future studies should aim to identify a more precise level. Until this level is identified, my study suggests that partially-harvested buffers should retain a minimum of 33% forest to maintain bird assemblages similar to those in higher retention and intact riparian buffers.

Bird assemblages were described by local habitat exclusively. However, local habitat explained a relatively small amount of variation in assemblage composition, suggesting assemblages may be structured by alternative factors. Future studies should aim to determine such factors, which may be of management interest. Specifically, functional interactions among primary nesters, weak excavators, and secondary nesters should be evaluated by identifying a cavity nest web (Martin and Eadie 1999) within partially-harvested buffers. The lack of association between assemblages and landscape-scale features indicates that consideration of the landscape features I measured is likely inappropriate for the management of entire bird assemblages in buffers. Assemblage-habitat relationships may have been more clearly identified if birds had been measured at larger scales.

Site-use by common, keystone and old-growth obligate cavity-nesting species was relatively well explained by habitat across multiple spatial scales. The influence of large landscape-scale features on local site-use indicates the need for multi-scale approaches in the management of cavity-nesting birds. However, managing for all species at all spatial scales is neither a practical nor feasible approach for forest managers. Alternatively, management may focus on a specific scale (i.e. buffers) whereby the goal may be to maximize habitat for a group of species (i.e. cavity-nesters) at that scale. In this case, an assessment of a suite of habitat features deemed important for all species at the scale of interest should be conducted. In my study, differences among species in their habitat associations within partially-harvested buffers suggest that a range in the amount of forest retained, the density of large aspen tree with conks, the density of conifer trees and the mean dbh of deciduous trees should be maintained in managed buffers. Furthermore, a range in the amount of harvest should be maintained across larger landscape scales.

An alternative management approach is to focus on species that may be of particular conservation interest. In this case, riparian management should consider the importance of both scale and habitat for individual species as managing habitat within buffers may be suitable for some species (i.e. Yellow-bellied Sapsuckers, Tree Swallows and Brown Creepers), however for others (i.e. Northern Flickers and Boreal Chickadees) larger-scale habitat features may need to be considered. Species of management concern are typically those that respond negatively to harvest and may have declining regional abundances or serve a keystone role in forest ecosystems. In my study, these species include Brown Creepers, Yellow-bellied Sapsuckers and Boreal Chickadees. Brown Creepers and Yellow-bellied Sapsuckers can likely be managed by retaining suitable within-buffer habitat including a high level of forest retention and a high density of large aspen trees with conks. To conserve additional habitat for Brown Creeper, some riparian forest should remain unharvested. Boreal Chickadee habitat can be conserved by retaining unharvested reserves >211ha (the area encompassed by the large-scale buffer) with a high proportion of intact, conifer-dominated forest and a low proportion of wetlands. Since wetlands are composed primarily of conifer trees, this suggests that upland conifer-dominated forests are of particular importance.

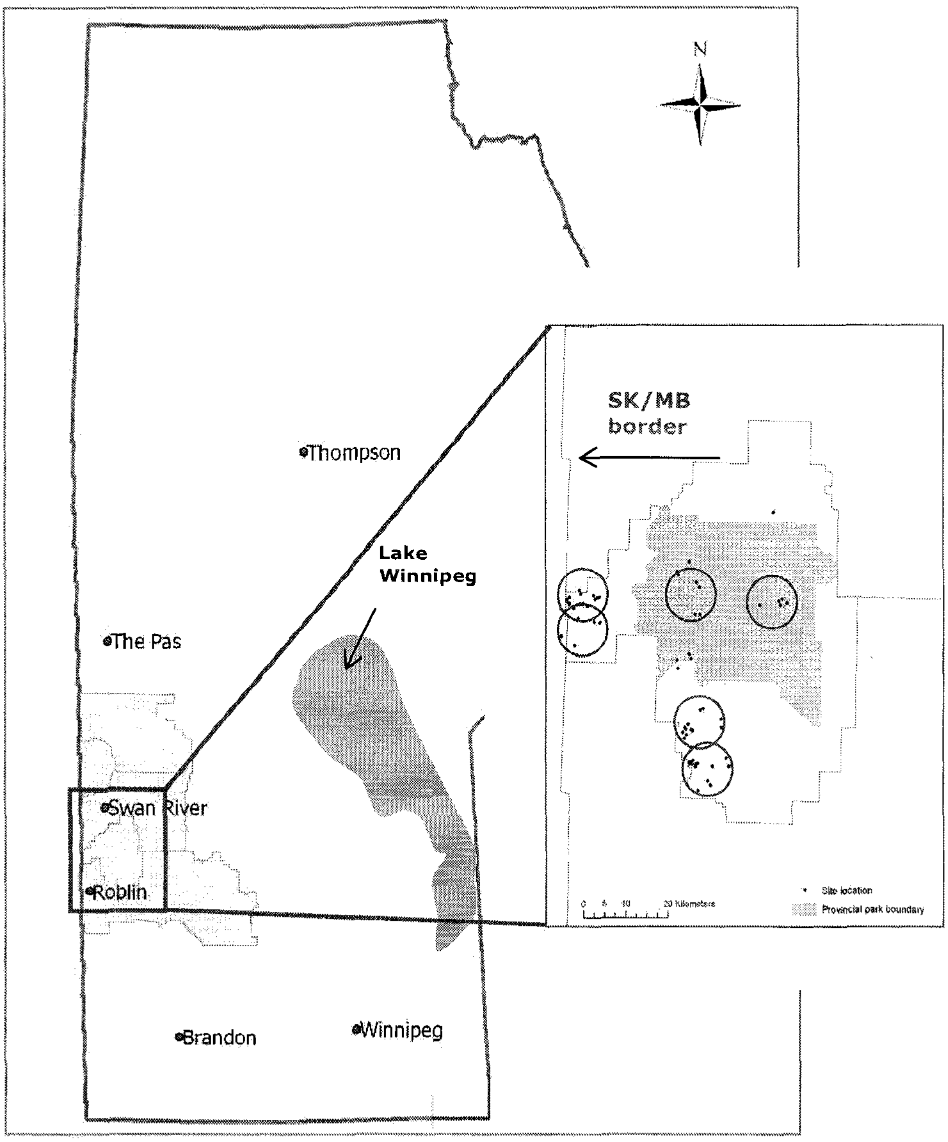

Figure 2.1. Location of the study area on and around the Louisiana Pacific Canada Ltd. (LP) Forest Management Unit #13 (FMU 13) in Duck Mountain Provincial Forest, MB. Inset shows the distribution of sample sites. The outline indicates the FMU boundary, the shaded area represents Duck Mountain Provincial Park and the circles encompass general harvest regions.

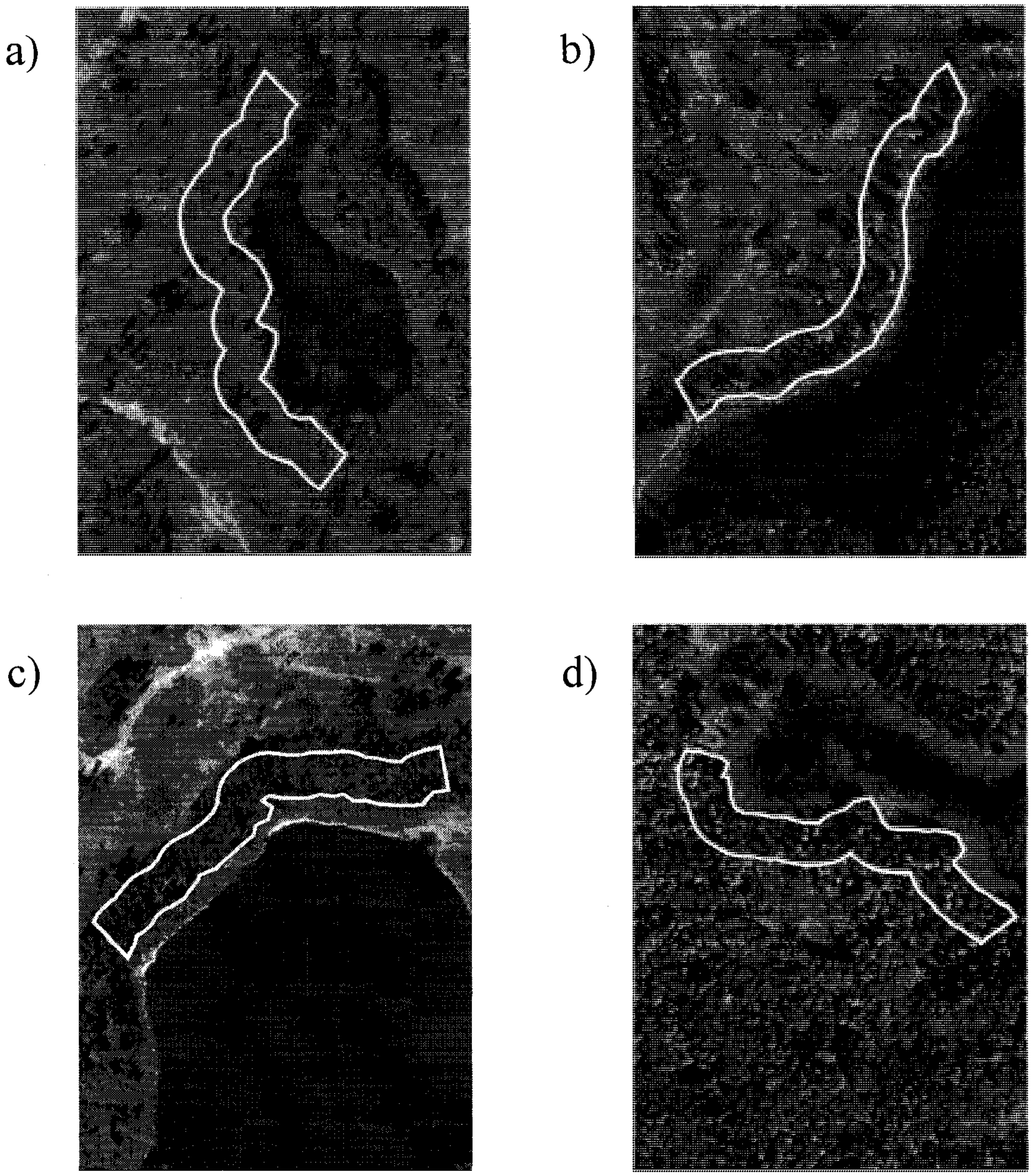

Figure 2.2. Aerial images of harvested landscapes representing the four riparian treatment types. a) low retention (0-33%) buffer, b) medium retention (34-66%) buffer, c) high retention (>66%) buffer, d) unharvested riparian forest. Sample areas are outlined on each image, and are 400m-long x 40m-wide. Edge of watercourse is defined by the tree(s) ≥4cm dbh that is (are) closest to the water's edge. Images courtesy of Louisiana Pacific (2006).

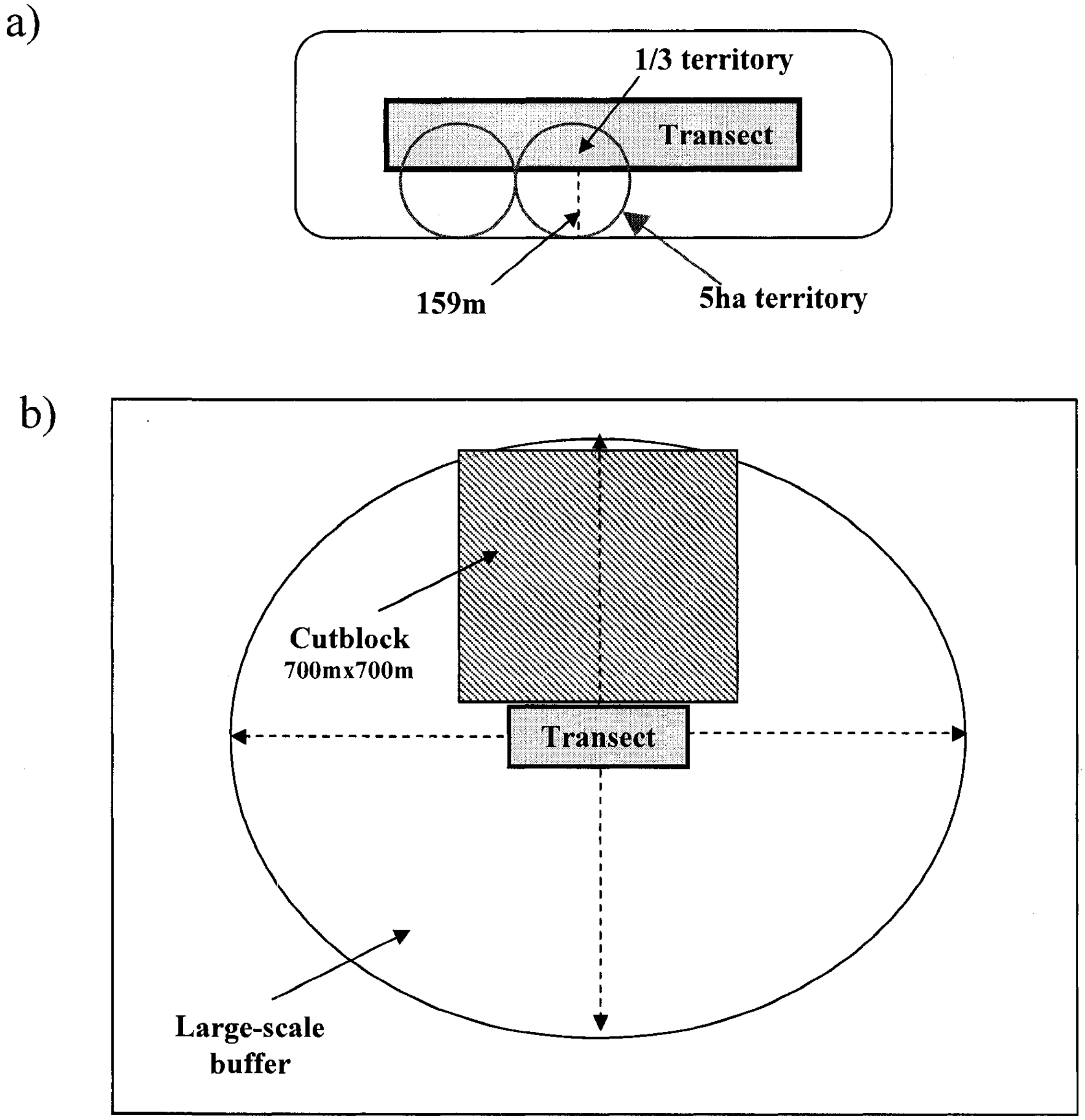

Figure 2.3. Schematic of a) a medium-scale and b) a large-scale landscape buffer. The transect area is 400m x 40m. In a) the large rectangle indicates medium-scale buffer boundary and the small circles indicate the assumed 5ha territories (circular bird territories are assumed). In b) the hatched square indicates a 700mx700m cutblock, the dotted arrows indicate a 700m distance from the edge of the transect, the circle indicates the large-scale buffer boundary and the large square indicates landscape extending beyond the large-scale buffer. Note: not to scale.

Table 2.1. Local habitat variable codes, descriptions, and descriptive statistics. Statistical values are shown for each variable in each treatment and in all sites. For a description of standing and downed wood decay classes, see Appendix 2.1.

Variable: *CODE*	**Description**	**Value**	**Low retention (0-33%) (n=11)**	**Medium retention (34-66%) (n=14)**	**High retention (>66%) (n=22)**	**Unharv-ested (n=19)**	**All sites (n=66)**
1. Density of large aspen trees with conks (#/ha): *ASPEN*	Number of trembling aspen trees ≥ 25cm dbh, fungal conk(s) present per hectare	Mean	5.03	12.14	53.91	42.90	33.73
		(±SE)	2.09	2.91	11.01	7.63	4.93
		Min	0.00	0.00	0.00	0.00	0.00
		Max	19.08	34.97	215.00	125.00	215.00
2. Density of large snags (#/ha): *SNAGS*	Number of trees ≥ 25cm dbh and decay class D1-D6 per hectare	Mean	8.49	19.64	45.12	48.16	34.49
		(±SE)	2.75	3.33	6.45	7.75	3.72
		Min	0.00	2.79	4.11	10.00	0.00
		Max	28.96	38.66	110.00	140.00	140.00
3. Density of conifer trees (#/ha): *CONIFER*	Number of conifer trees (white spruce, black spruce, jack pine, tamarack, balsam fir) ≥ 12cm dbh per hectare	Mean	65.67	93.15	241.76	309.74	200.46
		(±SE)	24.41	18.64	66.02	80.60	34.10
		Min	0.00	2.65	0.00	0.00	0.00
		Max	222.01	215.30	1337.56	1450.00	1450.00
4. Density of live birch trees (#/ha): *BIRCH*	Number of white birch trees ≥ 4cm dbh and decay class L1-L3 per hectare	Mean	14.21	88.66	85.93	96.84	77.70
		(±SE)	7.30	30.83	26.35	30.40	14.24
		Min	0.00	0.00	0.00	0.00	0.00
		Max	78.61	372.46	475.94	480.00	480.00
5. Mean DBH of deciduous trees (cm): *DBH*	Deciduous trees (trembling aspen, balsam poplar, paper birch) ≥12cm dbh	Mean	24.9	21.8	24.6	24.2	23.9
		(±SE)	0.9	0.4	0.7	1.1	0.4
		Min	20.6	18.8	19.7	18.3	18.3
		Max	29.3	24.8	30.9	36.5	36.5

Table 2.1. continued.

6. Number of decayed DWM/m: *DWM*	Number of DWM ≥ 12cm diameter where intersecting the sample transect and decay class >1 per meter	Mean	0.16	0.17	0.14	0.16	0.15
		(±SE)	0.02	0.02	0.02	0.02	0.01
		Min	0.03	0.08	0.04	0.05	0.03
		Max	0.26	0.29	0.37	0.33	0.37
7. Percent Forested: *RETENTION*	Area of unharvested forest (patches ≥10m diameter)/local sample area	Mean	13.0	49.0	88.0	100.0	71.0
		(±SE)	3.0	3.0	2.0	0.0	4.0
		Min	4.0	34.0	70.0	100.0	4.0
		Max	27.0	64.0	100.0	100.0	100.0
8. Local sample area (ha): *AREA OF SITE*	Total transect area as determined by 0m and 400m GPS coordinates and GIS	Mean	1.64	1.61	1.58	1.64	1.61
		(±SE)	0.03	0.03	0.02	0.02	0.01
		Min	1.49	1.35	1.33	1.45	1.33
		Max	1.75	1.82	1.77	1.84	1.84

Table 2.2. Medium- and large-scale habitat variable codes, descriptions, and descriptive statistics. Values were calculated by dividing the total area covered by each habitat type within the medium- or large-scale buffers by the total medium- or large-scale buffer area. For all forest variables (indicated by "*"), only stands that were >30% forested (i.e. defined as a forested stand by the land inventory) were included in calculations. NA indicates variables that were not used in the analysis.

		Medium-scale (n=61)				**Large-scale (n=46)**			
Variable: CODE	**Description**	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**
1. Proportion covered by cutblock: *HARVEST*	Harvested within the previous 10 years	0.24	0.03	0	0.67	0.14	0.02	0.00	0.39
2. Proportion intact forest: *INTACT*	*Forest >10 yrs	0.31	0.03	0.04	0.80	0.45	0.02	0.17	0.81
3. Proportion open water: *WATER*	Lakes, streams, standing water, wetlands with <6% forest cover	0.31	0.01	0.12	0.55	0.22	0.01	0.08	0.37
4. Proportion closed wetland: *WETLAND*	Treed bogs, fens, wetlands with >6% forest cover	0.02	0.00	0.00	0.15	0.02	0.01	0.00	0.18
5. Proportion deciduous-dominated forest: *DECIDUOUS*	*Forest >10 years, >50% deciduous tree species (trembling aspen, balsam poplar, paper birch)	NA	NA	NA	NA	0.37	0.03	0.00	0.76
6. Proportion conifer-dominated forest: *CONIFER*	*Forest >10 yrs with >50% conifer tree species (white spruce, black spruce, jack pine, tamarack, balsam fir)	0.06	0.02	0.00	0.63	0.08	0.02	0.00	0.63
7. Proportion young forest: *YOUNG*	*Forest 10-70 yrs	0.03	0.01	0.00	0.35	0.04	0.01	0.00	0.27
8. Local sample area: *BUFFER*	Extent of local bird and habitat sampling	1.62	0.01	1.35	1.84	1.61	0.01	1.35	1.84

Table 2.3. Variables selected for species-specific local-scale habitat models. Species-habitat relationships, as described in the literature and Chapter 1, are indicated by "+" if positive, and by "-" if negative. Blank cells indicate no known relationship. For species codes, see Table 2.4.

Species	Large aspen tree w/ conks density (#/ha)	Large snag density (#/ha)	Conifer tree density (#/ha)	Live birch tree density (#/ha)	Mean dbh of deciduous trees (cm)	Decaying DWM #/m	Reference
YBSA	+			+	+		Savignac & Machtans 2006 Conner et al. 1976 Eberhardt 2000 Giese & Cuthbert 2003 Harestad & Keisker 1989
NOFL	+	+			+	+	Harestad & Keisker 1989 Martin et al. 2004 Clarke M.Sc thesis chpt 3 Ingold 1994
BOCH		+	+				Warren et al. 2005 Hobson & Bayne 2000 McLaren 1975
TRSW[1]	-	+		-	+		Rendell & Robertson 1989 Holt & Martin 1997 Martin et al. 2004 (re-use) Clarke M.Sc thesis chpt 3
BRCR		+	+	+[2]	+		AB Sus. Res. Dev. 2003 Schieck & Nietfeld 1995 Banks et al. 1999

[1] TRSW is a secondary nester and thus variables represent both natural cavity substrates and substrates associated with NOFL, which, among all species studied, excavates cavities most commonly re-used by TRSW (Martin and Eadie 1999, Martin et al. 2004, *Cooke personal communication*). In this case, variables were additionally selected from NOFL model results.

[2] Brown Creepers are positively related to shrub density; in this case, birch density is used as a surrogate for shrub density as many live birch trees were small.

Table 2.4. All bird species detected in buffers and intact forest, including their 4-letter species code (American Ornithological Union), migratory status (LD=long-distance migrant, SD=short-distance migrant, R=resident/non-migrant; Partners in Flight 1991) territory size, nesting guild (PN=primary nester, WE=weak excavator, SN=secondary nester, BN=bark nester) (Martin and Eadie 1999), and the proportion of sites they occupied in each of the three buffer treatments (low (0-33%), medium (34-66%), and high (>66%) retention), in unharvested riparian forest, and across all sites. Species are listed from most to least common overall.

Species	**Species Code**	**Migratory status**	**Territory size (ha)**[1]	**Nesting Guild**	**Total number of birds detected**	**Proportion of sites sampled (n) with at least one observation:**				
						All sites (n=66)	**Low retention (n=11)**	**Medium retention (n=14)**	**High retention (n=22)**	**Unharvested (n=19)**
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	YBSA	SD	1.32	PN	47	0.42	0.27	0.5	0.55	0.31
Brown Creeper (*Certhia Americana*)	BRCR	SD	4.35	BN	49	0.36	0.09*	0.29	0.41	0.53
Black-capped Chickadee (*Poecile atricapilla*)	BCCH	R	3.40	WE	51	0.33	0.27	0.43	0.41	0.21
Boreal Chickadee (*Poecile hudsonica*)	BOCH	R	>5.00 (precise information lacking)	WE	34	0.29	0.00	0.36	0.27	0.42
Northern Flicker (*Colaptes auratus*)	NOFL	SD	7.00	PN	19	0.23	0.45	0.21	0.14	0.21
House Wren (*Troglodytes aedon*)	HOWR	LD	0.93	SN	16	0.15	0.27	0.07*	0.23	0.05*
Hairy Woodpecker (*Picoides villosus*)	HAWO	R	1.05	PN	12	0.15	0.27	0.14	0.14	0.11
Downy Woodpecker (*Picoides pubescens*)	DOWO	R	5.00	PN	8	0.09	0.09	0.00	0.14	0.11

Table 2.4. continued.

Tree Swallow (*Tachycineta bicolor*)	TRSW	SD	0.0079	SN	13	0.09	0.45	0.07*	0.00	0.00
Red-breasted Nuthatch (*Sitta Canadensis*)	RBNU	R	2.00	WE	5	0.08	0.00	0.07*	0.14	0.05*
Pileated Woodpecker (*Dryocopus pileatus*)	PIWO	R	2000	PN	3	0.05	0.09*	0.07*	0.05*	0.00
Black-backed Woodpecker (*Picoides arcticus*)	BBWO	R	Unknown	PN	2	0.03	0.00	0.00	0.05*	0.05*
White-breasted Nuthatch (*Sitta carolinensis*)	WBNU	R	15.00	WE	5	0.03	0.00	0.00	0.00	0.11
Three-toed Woodpecker (*Picoides tridactylus*)	TTWO	R	15.00	PN	1	0.02*	0.09*	0.00	0.00	0.00

[1] Territory sizes are from Poole (2007) for all species except for PIWO (from Bonar 1999) and NOFL (from Elchuk and Wiebe 2003). Sizes represent the median area from all studies in forest type as similar to study area as possible. An exception is NOFL, where mean *core foraging area* was used (territory sizes lacking in literature).

* Species present in a single site.

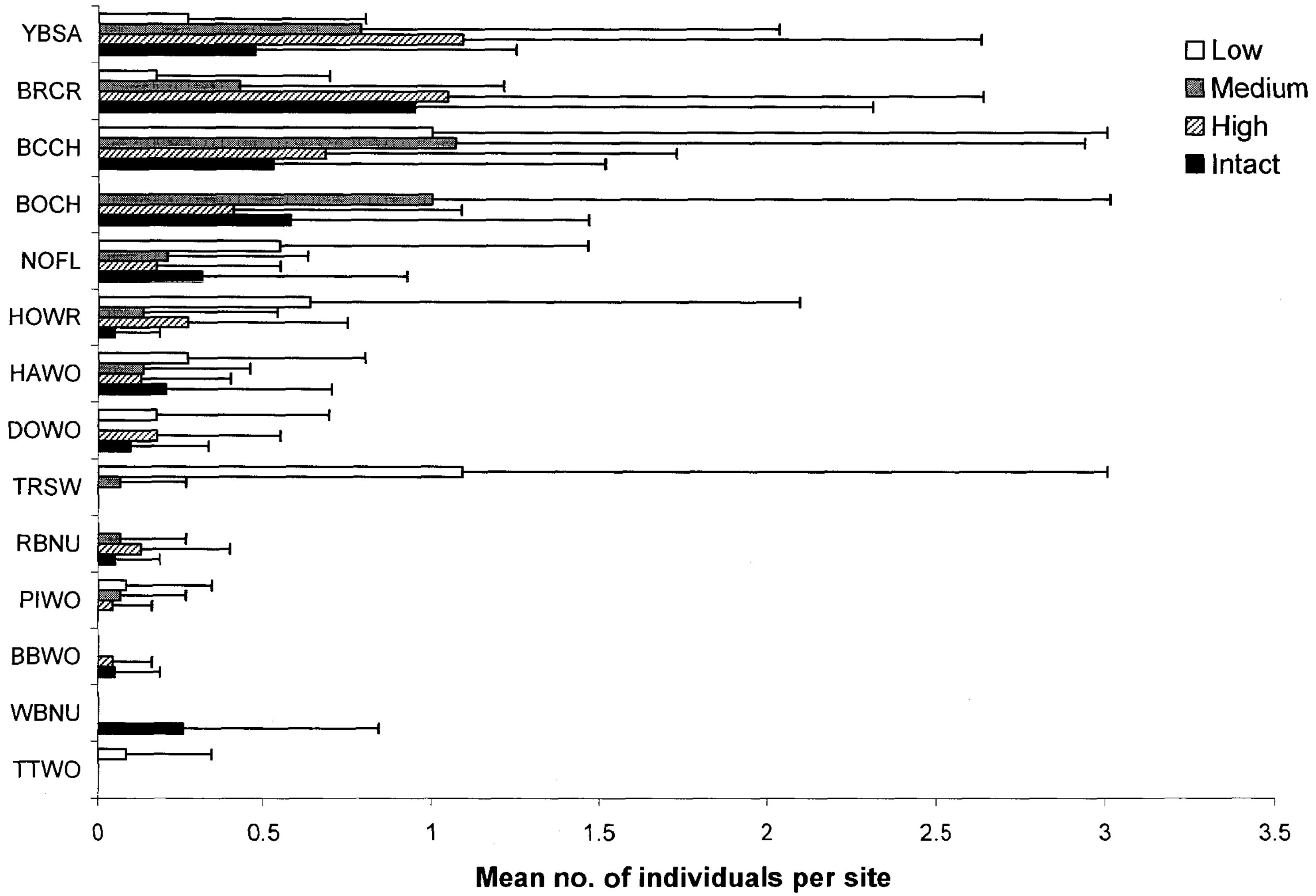

Figure 2.4. Mean (±90% CI) abundance of 14 cavity-nesting bird species in low (0-33%; n=11), medium (34-66%; n= 14) and high (>66%; n=22) retention buffers, and unharvested riparian forest (n=19). For species code descriptions, see Table 2.4.

Table 2.5. Results of the NMDS analysis investigating bird species composition within low, medium, and high retention buffers. Randomization *p*-value indicates the probability that a similar final stress value for the stated number of axes could have resulted by chance. The final number of iterations indicates the number of runs required to achieve an instability measure less than the cutoff value of 0.00001 (standard deviations in stress over the previous 15 iterations). Stress indicates the solutions departure from monotonicity and represents its overall fit. The proportion of variance explained (r^2) is that from the original site dissimilarity distance matrix.

Data Type	**No. sites**	**No. species**	**No. axes**	**Randomization *p*-value**	**Final no. iterations**	**Final stress**	**Final instability**	r^2
Harvest sites	44	11	3	0.04	56	15.786	0.00001	0.78

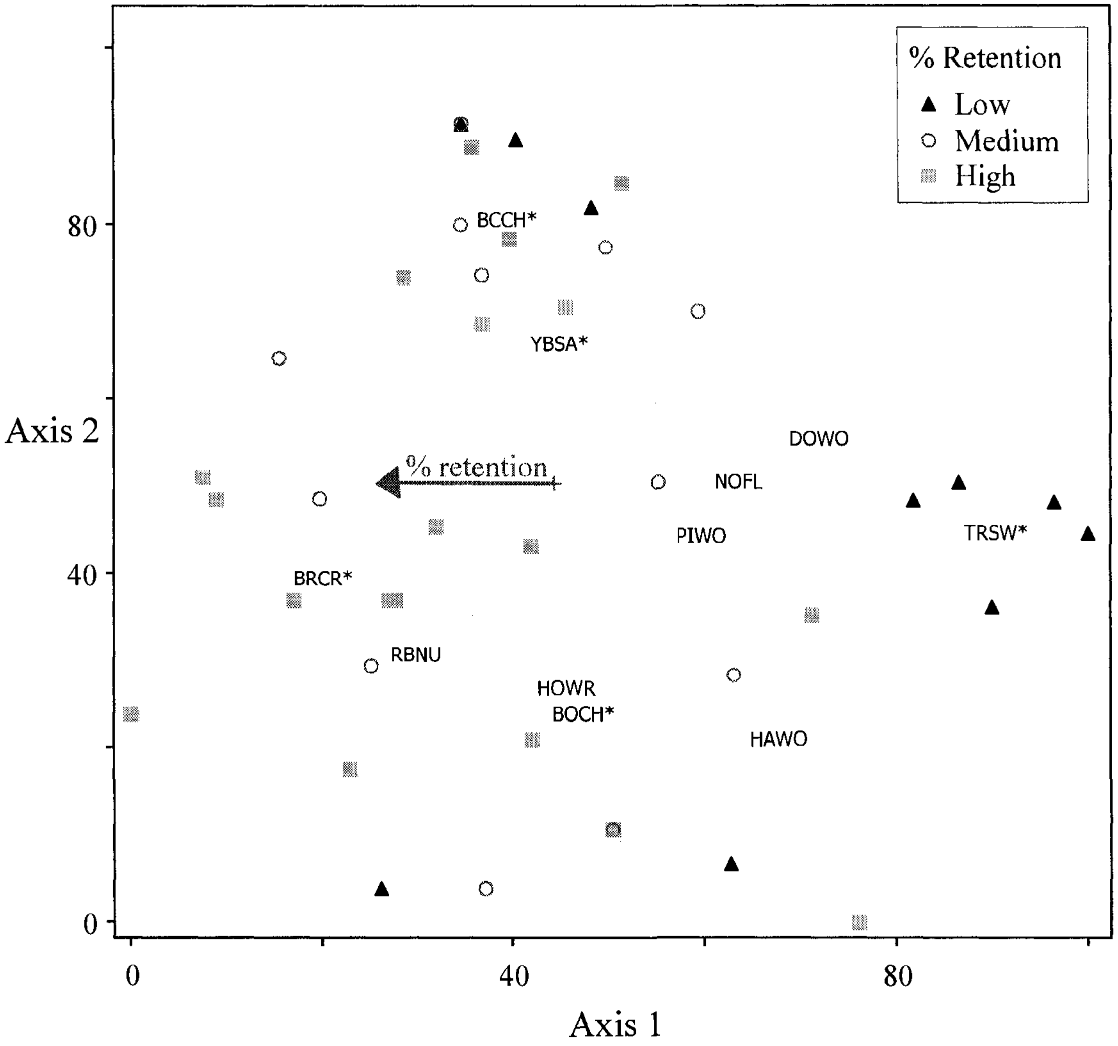

Figure 2.5. NMDS solution comparing bird species composition among low (0-33%), medium (34-66%), and high (>66%) retention buffers (PC-Ord 1999) (n=44). Sites closer together have bird assemblages that are more similar than those farther apart. The solution was 3-dimensional and accounted for 78% of the variation in the original distance matrix. Axes 1 and 2 are shown, accounting for 20% and 27% of the total variation, respectively. Species accounting for greater than 30% of site variation along any single axis (r^2>0.3) are indicated by (*). For species codes, see Table 2.4. Axes have been scaled in proportion to the longest axis.

Table 2.6. Results of MRPP analyses testing the null hypothesis of no difference in species composition among low, medium, and high retention buffers. The *A*-value is the chance-corrected within-group agreement test statistic and describes within-group homogeneity, compared to random expectation. It has a maximum value of 1 (all items within groups are identical) and a value >0.3 is considered high (McCune and Mefford, 1999). Differences between treatments were determined using pair-wise comparisons.

Buffer type	**Average distance**	N	**MRPP statistics**
Low retention	0.785	10	Observed delta = 0.768 Expected delta = 0.794 T = -2.598, A = 0.032, p=0.015
Medium retention	0.773	13	**Pair-wise comparisons** Low vs. medium: T=-2.28, A=0.04, p=0.03 Low vs. high: T=-4.88, A=0.06, p=0.0005 Medium vs. high: T=1.16, A=-0.01, p=0.93
High retention	0.757	21	

Table 2.7. Relationships between a) 11 bird species and b) 7 local habitat variables and each axis of the NMDS solution for 44 partially-harvested buffer sites. Habitat variables were related indirectly to the solution using overlays. Pearson correlation coefficients (*r*) indicate the relationship between a variable or species and an axis. Coefficients of determination (r^2) indicate the proportion of variance along each axis that is accounted for by a given variable or species. Species or habitat variables with r^2-values >0.3 on any axis are bolded along with the value on the relevant axis. For species codes, see Table 2.4. For habitat variable codes, see Table 2.1.

a) Species	Axis 1		Axis 2		Axis 3	
	r	r^2	*r*	r^2	*r*	R^2
YBSA	-.078	.006	.428	.183	-.757	**.574**
BCCH	-.280	.079	.709	**.503**	.358	.135
BOCH	-.005	.000	-.456	.208	.575	**.331**
TRSW	.641	**.411**	-.088	.008	-.066	.004
BRCR	-.705	**.497**	-.304	.092	.071	.005
NOFL	.379	.144	-.019	.000	.243	.059
HAWO	.298	.089	-.371	.138	-.157	.025
DOWO	.308	.095	.042	.002	.287	.082
PIWO	.148	.022	-.071	.005	-.128	.016
HOWR	-.025	.001	-.420	.176	-.334	.111
RBNU	-.175	.031	-.182	.033	.304	.092
b) Habitat variable						
RETENTION	-.568	**.322**	.042	.002	-.003	.000
ASPEN	-.250	.062	.127	.016	-.245	.060
SNAGS	-.341	.116	.178	.032	-.281	.079
CONIFER	.058	.003	-.209	.044	.332	.110
BIRCH	-.303	.092	.276	.076	-.145	.021
DBH	.098	.010	-.060	.004	-.151	.023
DWM	.134	.018	.177	.031	.064	.004

Table 2.8. Results from Canonical Correspondence Analyses of assemblage-habitat associations at three spatial scales. Total variance in the original species data set was 3.56. Species:environment correlations show Pearson correlation coefficients and indicate the relationship between scores for an axis derived from the species data (WA scores) and those that are linear combinations of the environmental variables (LC scores). Monte Carlo p-values indicate the proportion of randomized runs with an eigenvalue ≥ the observed eigenvalue. Only axes indicated by (*) are significantly different from random.

Spatial scale	**Local (n=39)** ***10 species; 8 habitat variables***		**Medium (n=39)** ***10 species; 7 habitat variables***		**Large (n=39)** ***10 species; 8 habitat variables***	
	Axis 1*	**Axis 2**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Eigenvalue	0.410	0.193	0.269	0.157	0.237	0.235
% Variance explained	11.5	5.4	7.6	4.4	6.7	6.6
Species:environment correlation	0.841	0.579	0.687	0.566	0.661	0.622
Monte Carlo p-value	0.007	0.424	0.371	0.623	0.778	0.128

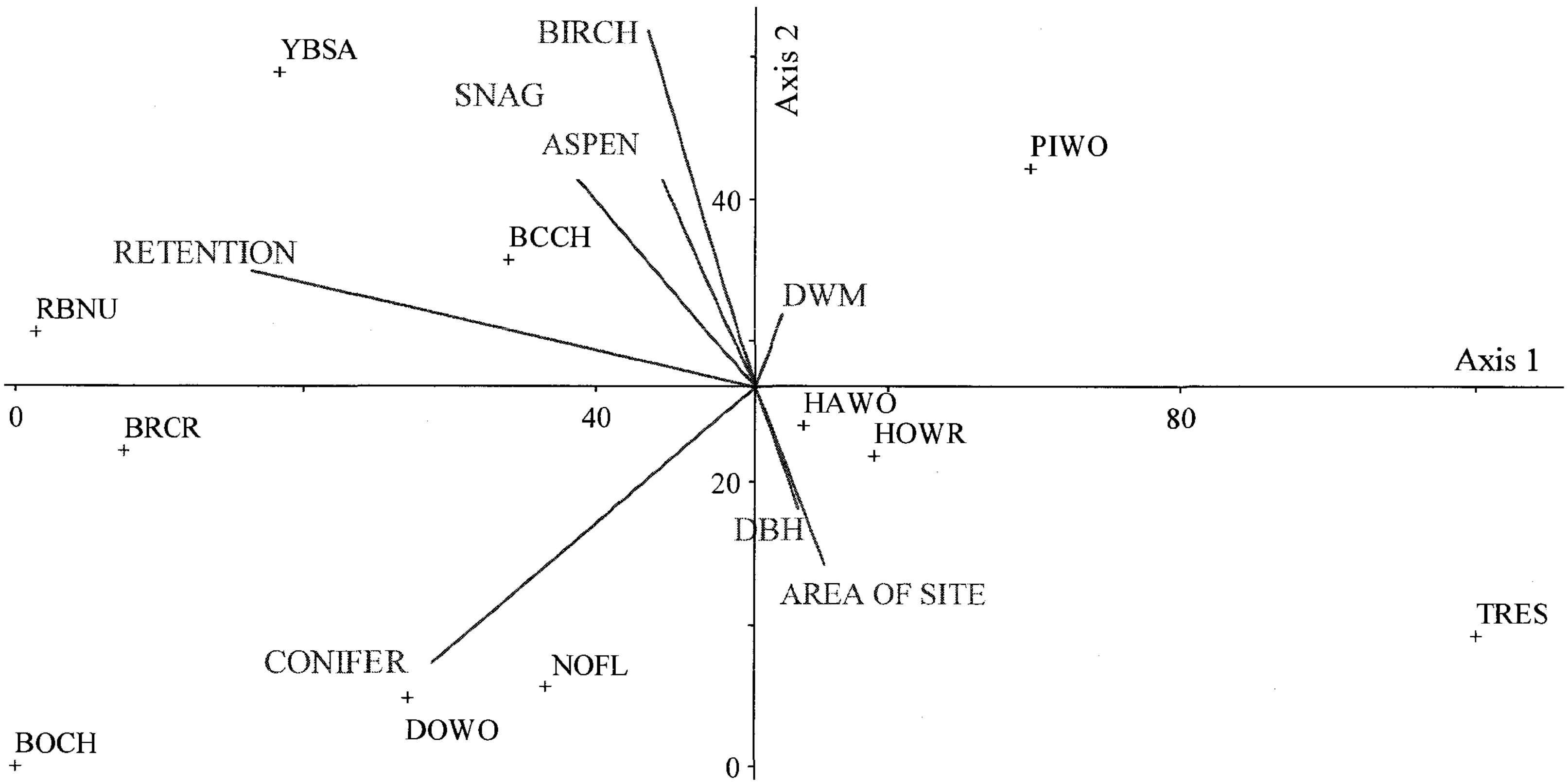

Figure 2.6. Canonical Correspondence Analysis biplot for 56 site assemblages of 11 species and 8 local-scale habitat variables. The solution was 3-dimensional; only Axes 1 and 2 are shown. Axes are linear combinations of habitat variables and cumulatively account for 14.9% of the variance in the species-site matrix. Site scores were centered and standardized to a mean=0 and variance=1 and were weighted by mean species scores to optimize species representation. For species codes, see Table 2.4. For habitat variable codes, see Table 2.1. Note: Axes have been scaled in proportion to the longest axis. Biplot was created using the complete local-scale data set (n=66; after CCA data reduction, n=56).

Table 2.9. Correlations between local habitat variables and axes 1 and 2 of the local-scale Canonical Correspondence Analysis. Values are "intraset correlation" coefficients (ter Braak 1986) and indicate relationships between environmental variables and site scores along axes derived from linear combinations of the environmental variables (LC scores). For a description of habitat variables, see Table 2.1. Note: Values were calculated using the complete local-scale data set (n=66; after CCA data reduction, n=56).

Variable	**Axis-1**	**Axis-2**
Density large aspen trees with conks (#/ha)	0.197	0.437
Density large snags (#/ha)	0.420	0.491
Density conifer trees (#/ha)	0.586	-0.501
Density live birch trees (#/ha)	0.197	0.648
Mean dbh of deciduous trees (cm)	-0.076	-0.221
Density decaying DWM (#/m)	-0.048	0.131
Retention	0.912	0.211
Buffer area (ha)	-0.131	-0.339

Table 2.10. Summary of species-habitat relationships at local, medium, large, and multiple spatial scales. Grey areas indicate no relationship. Relationships were determined by comparing a set of competing models for each species at each scale using AICc. For each species, the predictive value (PV) of each variable was determined by summing the Akaike weights (w_i) over all models in which a variable appeared. This value ranges from 0 (no predictive value) to 1 (a predictor) and is meaningful only in relation to the other model variables. Variables with a predictor value of 1.0 were either present in all models or were the only variable present. Standardized regression coefficient values (β) for each variable were determined using weighted averaging. The range of % deviance explained by all competing models for each species is indicated. For multi-scale variables, (m) and (l) indicate a medium- and large-scale variable, respectively. Variables deemed the best predictors are in bold. For habitat variable codes, see Tables 2.1 and 2.2. For species codes see Table 2.4.

		YBSA		**NOFL**		**BOCH**		**TRSW**		**BRCR**	
		PV	**β**	**PV**	**β**	**PV**	**β**	**PV**	**β**	**PV**	**β**
Local (n=66)	***Range of % deviance explained by models***	18-19		19-27		16-17		71		15	
RETENTION								**1.00**	**-3.40**	**1.00**	**2.83**
ASPEN		**1.00**	**4.10**	**0.63**	**-1.67**						
SNAGS				0.15	-1.45	0.29	0.79				
CONIFER						**1.00**	**3.52**				
BIRCH		0.21	0.81								
DBH		**0.29**	**-1.09**	**1.00**	**3.82**						
DWM				0.27	1.42						
Medium (n=61)	***Range of % deviance explained by models***	4-8		2-8		27-36		42-53		1-4	
HARVESTED		**0.09**	**0.65**	**1.00**	**0.04**	**0.49**	**-1.68**	**1.00**	**3.30**	**0.24**	**-1.17**
INTACT		**0.24**	**-0.99**	**0.24**	**-0.85**	**0.17**	**1.42**	**1.00**	**2.46**	**0.39**	**1.58**
WATER		0.20	0.82			0.11	-0.89				
WETLAND		**0.16**	**1.38**	**0.38**	**-1.22**	**1.00**	**-2.77**	**1.00**	**2.62**		
CONIFER		**0.56**	**-1.37**	**0.21**	**-1.10**	**1.00**	**3.36**	**0.73**	**-1.63**	**0.20**	**1.09**
YOUNG		0.10	-0.71			0.23	1.09	0.50	-1.31	0.16	0.63

Table 2.10. continued.

Large (n=46)	*Range of % deviance explained by models*	7-17		14-19		34-44		24-35		2-5	
HARVESTED								**0.85**	**2.51**	**0.18**	**-0.87**
INTACT		0.43	-1.89			0.17	2.36	0.35	-1.78	0.22	1.26
WATER		0.25	1.39	0.17	-0.95	0.17	1.04	0.72	-1.79	0.11	0.002
WETLAND		**0.63**	**2.14**	**0.72**	**-1.36**	**1.00**	**-2.32**			**0.11**	**0.09**
DECIDUOUS		0.28	1.37			0.17	-2.22			0.15	0.88
CONIFER		**0.47**	**-1.95**	**0.44**	**-1.17**	**0.83**	**2.26**			**0.11**	**0.15**
YOUNG		0.31	-1.25			0.73	2.06			0.12	0.44
Multi-scale (n=45)	*Range of % deviance explained by models*	18-24		17		36-46		73-86		18	
RETENTION								1.00	-2.03	1.00	2.46
ASPEN		1.0	3.27								
SNAGS											
CONIFER						0.46	1.53				
BIRCH											
DBH											
DWM											
HARVESTED(m)											
INTACT(m)											
WATER(m)											
WETLAND(m)											
CONIFER(m)		0.23	-0.87								
YOUNG(m)											
HARVESTED(l)								0.52	1.80		
INTACT(l)											
WATER(l)								0.52	0.57		
WETLAND(l)		0.26	1.73	1.00	-1.47	1.00	-2.17				
DECIDUOUS(l)											
CONIFER(l)		0.26	-1.73			1.00	1.32				
YOUNG(l)						1.00	1.19				

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CHAPTER 3

COMPOSITION OF CAVITY-NESTING BIRD ASSEMBLAGES AND SPECIES SITE-USE AMONG BURNED, PARTIALLY-HARVESTED AND INTACT BOREAL MIXEDWOOD FOREST ALONG LAKES

3.1 Introduction

Across the Boreal Plains ecozone of western Canada, industrial development has placed increasing pressure on forest ecosystems (Schneider and Walsh 2005, Government of Saskatchewan 2007). Conventional boreal mixedwood harvesting has primarily followed a "sustained-yield" approach with a two-pass clearcutting system and a short rotation age (~70 years) (Bergeron et al. 2002, Schneider 2002). This not only leads to wide-spread habitat loss and fragmentation across the landscape, but also limits the natural trajectory of forest succession and reduces the number of old (>100 years), structurally heterogeneous stands across the landscape (Schmiegelow and Mönkkonen 2002, Burton et al. 2006, Macdonald and Fenniak 2007). These habitat alterations may have detrimental effects on some boreal bird species (Schmiegelow et al. 1997, Imbeau and Desrochers 2002, Schmiegelow and Mönkkönen 2002). To alleviate negative ecological effects of conventional harvesting, Hunter (1993) proposed that forests should be harvested in a way that emulates patterns of natural disturbance. This natural disturbance model (NDM) is a coarse-filter approach that assumes organisms are adapted to natural disturbances and thus should be affected less by harvesting if it approximates natural disturbance events. Across the boreal landscape, fire is the dominant form of natural disturbance (Rowe and Scotter 1973, Weir et al. 2000) and is thus appropriate as a harvest model (Hunter 1993).

Riparian forests, defined as the treed interface between aquatic and terrestrial ecosystems (Gregory et al. 1991), are highly productive, structurally diverse, and support a high diversity of bird species (Stauffer and Best 1980, Stevens et al. 1995, Naiman and Decamps 1997, Harper and Macdonald 2001). Flooding and tree-felling by beavers create standing snags and downed woody material in some forests adjacent to riparian areas (Rosell and Parker 1996, Martell et al. 2006). Tree fall caused by high winds in riparian forests further increases the abundance of downed woody material (Stevens et al. 1995) and high levels of humidity promote fungal growth and tree decay (Jackson and Jackson 2004). These features provide nesting and foraging opportunities for many species of primary and secondary cavity-nesting birds (Harestad and Keisker 1989, Weikel and Hayes 1999, Gunn and Hagan 2000, Aitken and Martin 2004, Martin et al. 2004, Savignac and Machtans 2006). Riparian forests can have a dense understory of deciduous shrubs and saplings (Harper and Macdonald 2001, Mosley et al. 2006) providing foraging opportunities for arthropod gleaning and sap-sucking species (Johnson 1998, Savignac and Machtans 2006). Finally, riparian forests can provide abundant insect prey for aerially foraging species (Whitaker et al. 2000).

In riparian forests in Canada, harvesting policy has dictated retention of variable-width, uncut buffer strips along watercourse edges to conserve water quality (Lee and Smyth 2002) and fish stocks (Wesche et al. 1987). Uncut buffer strips may provide habitat for some bird species in intact riparian forests (Whitaker and Montevecchi 1999, Lambert and Hannon 2000, Pearson and Manuwal 2001). This is referred to as a "lifeboat function" whereby buffers (i.e. lifeboats) maintain species present prior to harvesting over the forest regeneration phase (Matveinen-Huju et al. 2006). Several studies have compared intact forest to buffer strips to determine whether harvest reduces species presence and abundance (Darveau et al. 1995, Whitaker and Montevecchi 1997, Hannon et al. 2002). However, the retention of intact buffer strips is not consistent with a natural disturbance model because wildfire can disturb riparian areas (Andison and McCleary 2002, Everett et al. 2003). Recently, some forest companies have attempted to emulate riparian forest structure following fire by partially harvesting riparian buffers. The effects of partial-harvesting in boreal riparian buffers and whether it emulates fire in its effects on biodiversity is relatively unknown (but see Kardynal 2007).

In this study, I investigated the effect of partial harvesting in riparian forest on cavity-nesting birds in boreal mixedwood forest in Saskatchewan. I focused on cavity-nesting birds because many cavity-nesting species rely on mature and old-growth forest, the age classes targeted for harvest (Schmiegelow and Mönkkonen 2002). Functional interactions among cavity nesters are described using nest webs (Martin and Eadie 1999): cavities created by primary nesters are then used by secondary-nesting species. Thus, negative effects on excavators will exert a strong influence on the entire cavity-nesting community. In the Boreal Plains ecozone, Yellow-bellied Sapsucker (*Sphyrapicus varius*) is the dominant primary nester and Pileated Woodpecker (*Dryocopus pileatus*), Hairy Woodpecker (*Picoides villosus*) and Northern Flicker (*Colaptes auratus*) are major keystone excavators (Cooke, *personal communication*).

In my study I assessed differences in the composition of cavity-nesting bird assemblages and site-use by individual species among burned, harvested, and intact riparian forests. Burned and harvested sites were compared to determine whether partial-harvest emulates the effects of fire for cavity-nesting birds. Harvested and intact sites were compared to determine whether partially-harvested buffers provide lifeboats for cavity-nesting birds in harvested landscapes. Additionally, I determined assemblage and species relationships with local habitat features. My research objectives were to: 1) determine if bird assemblages were similar in partially-harvested and burned riparian forests; 2) assess whether partial harvesting in riparian forest maintained bird assemblages present in intact riparian forests; 3) identify the habitat features that structure bird assemblages in burned, harvested, and intact habitats; and, 4) identify proximate factors affecting the use of sites by individual species among these three habitat types.

3.2 Methods

3.2.1 *Study Area*

The study occurred during the spring and summer of 2005 in Weyerhaeuser Canada Ltd.'s Prince Albert FMA, located in the mid-boreal upland sub-region of the Boreal Plains ecozone of Saskatchewan (Saskatchewan Environment and Resource Management 1995) (Fig. 3.1). This sub-region is characterized by mixed-wood forest and is dominated by trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). Less abundant tree species include white spruce (*Picea glauca*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*). Dominant understory shrubs include river alder (*Alnus rugosa*), beaked hazelnut (*Corylus cornuta*) and willow (*Salix* sp.), with various other species present.

Currently, the primary anthropogenic disturbance in the mid-boreal upland of Saskatchewan is logging: most occurring over the past 30 years. Across the FMA, mean cutblock size for the 2004/2005 operating season was ~65ha (Weyerhaeuser Canada Ltd. 2006). Experimental partial-harvesting in riparian buffers was conducted in select harvest blocks across the FMA for four years prior to my study. Partial-harvest involved the retention of a lakeside 10-m-wide no-harvest strip, adjacent to a 30m-wide variable-retention strip. The 30m strip contained a representative 5% to 25% of the original tree species and sizes, distributed as both individuals and residual patches. Cutblocks adjacent to buffers were also partially-harvested, using a mean target retention level of 3% (range=0-10%; Weyerhaeuser Canada Ltd. 2006). The main regional natural disturbance in the FMA is wildfire (Weir et al. 2000), and fires were abundant across the FMA during 2002 and 2003, creating several recently-burned riparian forest stands.

3.2.2 *Site Selection*

Thirty-two sites in three riparian treatments were sampled: eight in forests burned two to three years prior to my study; 12 in partially-harvested buffers cut one to two years prior to my study; and 12 in intact forests. Fewer burn sites were sampled because burned riparian forest of an age and composition suitable for comparison among other treatments was relatively scarce. All sites were located in mature (>70 years old) mixed-wood forest along lakes that ranged in size from 11 to 12,610ha, and were at least 1km apart to reduce the chance of double-counting birds with large territories. Sites were chosen to minimize variability in vegetation composition across sites prior to disturbance. Intact sites did not have any recent burn or harvesting within a 1km radius. Burn sites covered a broad range of burn severity and were composed of standing wood with frequent small forest gaps. In harvested sites, forest retention over the 40m buffer width ranged from 50% to 80% and was arranged in a few large patches surrounded by individual residual trees. The non-random location of riparian harvest activity and the mosaic nature of the boreal region made it difficult to standardize landscape variables around sites, although attempts were made to maximize similarity between sites. Sites were distributed non-randomly within the FMA due to the non-random location of both fire and harvest disturbance (Fig. 3.2).

3.2.3 *Bird Sampling*

Each site consisted of a 400m X 40m strip: the long axis ran parallel to the edge of riparian zone of the watercourse. Within the centre of the strip, I established a 400m-long transect line. Line surveys were used rather than point counts because line surveys may better detect species with large territory sizes (Toms et al. 2006), and a long, narrow, sampling area is better surveyed by maximizing the linear distance traveled. Each site was sampled three times between 24 April and 18 June, 2005. This period represented peaks in territorial and breeding activities for many cavity-nesting species. Cavity excavation and territory establishment was highest from mid-April to early-May, and the feeding of chicks peaked from late-May to early-June (Poole 2005). Because the number of sites was limited, the number of surveys per site was maximized to increase bird detections and the ability to detect differences among treatments. Three surveys per site were conducted, each between 0600 and 1200 hrs, lasting an average of 49 minutes, and following a modified version of the line transect method (Bibby et al. 1992). A single trained observer (one of two) traveled at a slow and even pace along the transect, stopping and listening for three minutes at 50m intervals. This increased detectability of birds that may have stopped vocalizing due to observer movements. Because high shrub density in some sites reduced detectability, observers also stopped briefly (one minute) at 25m intervals in all sites to record individuals that might have gone undetected between 50m intervals. All birds seen or heard within 20m on either side of the transect were recorded.

To prevent sampling bias, treatment type sampled (i.e. burned, harvested, intact) was alternated among days and the order of sites surveyed was the same among sample rounds. To decrease the risk of observer bias, prior to data collection trained observers conducted 10 practice surveys simultaneously. Inconsistencies between their results were identified and behaviours leading to those differences were corrected. Further practice surveys were conducted until results between observers were minimized to the extent possible. Furthermore, during sampling, observers were alternated among sites and treatments. Because there were three sample rounds and only two observers, each observer surveyed certain sites twice and others only once. To reduce potential sampling bias, both observers sampled approximately the same proportion of sites from each treatment class. Surveys were not conducted in windy (Beaufort >6), rainy, or snowy conditions. A higher Beaufort cut-off level than conventional studies (e.g. Schmiegelow et al. 1997) was selected because riparian forests tend to be windier overall compared to upland forests and because sampling radius was small.

Since the transect width was narrow, I assumed that the detectability of birds was similar among treatments. For each species, maximum abundance over the three sampling rounds was used in all subsequent analyses. This measure was better suited than mean abundance as it was applied to sampling areas that may have encompassed only a portion of a bird's territory (Toms et al. 2006). Species with large territories may have only been present for one or two sampling sessions, and maximum abundance would more accurately indicate their site abundance. Overall however, species abundances were low (generally 0-3 individuals per site) and results are more indicative of differences in species use rather than abundance among sites. Furthermore, because habitat use may vary depending on behaviour (e.g. nesting, foraging, roosting), which I did not record, results should be interpreted only as general site-use, and not as evidence of a breeding territory.

3.2.4 *Habitat Sampling*

To measure vegetation composition, each site was divided widthwise into three 133m-long, 40m-wide sections. Within each section, a point was randomly selected and a 0.04ha circular plot was established. In each plot the species, diameter at breast height (dbh) class (1 of 4 classes; Appendix 3.1), decay class (1 of 9 classes; Appendix 3.1), and burn class (1 of 6 classes; Appendix 3.1) of all trees were measured. Along a randomly-oriented axis running across the 22.6m diameter of the circular plot, all downed woody material (DWM) greater than 12cm where intersecting the axis (the minimum size deemed appropriate as potential foraging substrate for birds), were counted. Data from all three plots were pooled and used to calculate mean site values for six habitat variables: the density (#/ha) of: conifer trees ≥12cm dbh, light to moderately burned conifer trees (burn class 1-5) ≥12cm dbh, large (≥25cm dbh) live (decay class L1-L3) aspen trees with fungal conks (*Phellinus tremulae*), large (≥25cm dbh) snags (decay class D1-D6), and live birch trees (≥4cm dbh; decay class L1-L3); and the number of downed woody material pieces/m. These six variables were chosen to represent important nesting and foraging structures used by cavity-nesting bird species based on a review of recent literature in boreal forests (Villard 1994, Savignac et al. 2000, Hoyt and Hannon 2002, Alberta Sustainable Resource Development 2003, Savignac and Machtans 2006, Koivula and Schmiegelow 2007, Venier and Pearce 2007).

Two additional habitat variables were measured for each site: the proportion of the surrounding landscape that was covered by the lake (i.e. relative lake size) and the proportion of unharvested forest in the transect. I hypothesized that larger lakes (i.e. greater proportion of landscape) could reduce site-use by creating a barrier for bird movement into the site (St. Clair 2003). Sites with less forest could offer less habitat and decrease habitat connectivity within the site (Taylor et al. 1993). Using the maximum perpendicular distance over all sites' riparian edge and the far edge of the adjacent waterbody (4065m) as a radius, I delineated a 5191ha circular buffer around each site. Using land inventory data provided by Weyerhaeuser Canada Ltd and the GIS program ArcView 9.0 (ESRI Inc. 2004) I subsequently calculated the proportion of each buffer covered by the lake adjacent to each site. Land inventory data were in vector format and were projected in UTM zone 13N using the geographic coordinate system of North American Datum 1983. Forest patches within the transect area were mapped on the ground using a Trimble Pathfinder GPS unit (Trimble Navigation, Ltd. 1995). A patch was defined as a group of five or more trees, separated by at least 10m from the next nearest patch. ArcView 9.0 was used to calculate the area of these patches and this value was divided by total transect area to determine the proportion of unharvested forest in each transect.

3.2.5 *Data Analyses*

3.2.5.1 *Non-metric Multidimensional Scaling*

I used Non-metric Multidimensional Scaling (NMDS) (Kenkel and Orloci 1986, Clarke 1993) to determine how bird assemblages related to the three treatments and to all habitat variables measured except two: the density of light-to-moderately burned conifer trees and the proportion of site remaining unharvested. These two variables were each uniquely associated with a single habitat class, and could therefore have undermined the effects of more proximate habitat features. The remaining six variables used described nesting and foraging habitat required for all study species (Stauffer and Best 1980; Harestad and Keisker 1989; Villard 1994; Johnson 1998; Weikel and Hayes 1999; Gunn and Hagan 2000; Savignac et al. 2000; Hoyt and Hannon 2002; Alberta Sustainable Resource Development 2003; Aitken and Martin 2004; Martin et al. 2004; Warren et al. 2005; Savignac and Machtans 2006; Koivula and Schmiegelow 2007). Assemblages were assessed using the abundance of both individual species and members of different nesting guilds (primary nesters, weak excavators and secondary nesters). I also used NMDS to explore habitat composition of burned, harvested and intact riparian forests to test if they were distinct habitat types. All habitat variables were applied to this ordination because they were important descriptors of site differences.

NMDS is a non-parametric, multivariate method based on distance-rankings of assemblage dissimilarities, derived from species abundance, between sample units. It is well-suited to community data because it avoids assumptions of linear relationships among variables and works well with non-normally distributed data (Clarke 1993, McCune and Grace 2002). NMDS involves creating a distance matrix (here on sites) and subsequently projecting it in a reduced metric space such that the distances are as closely monotonic as possible to the dissimilarities in the original unreduced space (Kenkel and Orloci 1986). Monotonicity simply refers to the preservation of the actual order of site dissimilarities in species composition, as portrayed in the NMDS bi-plot. Departure from monotonicity is termed "stress" and the final ordination solution is one that minimizes stress while using the fewest possible dimensions. For ecological data, final stress tends to fall between 10 and 20, and a value in the lower end of this range indicates a reliable solution (McCune and Grace 2002). However, as sample size approaches 4k (k= the number of solution dimensions), the interpretation of high stress values (i.e. >10) becomes more stringent (McCune and Grace 2002). A measure of "stability" indicates how often different runs result in a similar final solution, and thus represents the reliability of the ordination. Stability is calculated as the number of standard deviations in stress over the previous 15 solution iterations, and generally has a desired value of <0.001. A minimum sample size of 20 sites per environmental gradient described is considered sufficient to accurately portray assemblage responses along each gradient (McCune and Grace 2002). In this study, sample size was low, suggesting a moderate level of accuracy in NMDS results and the need for a relatively strict evaluation of final stress.

Using the program PC-Ord 4.2 (McCune and Mefford 1999), and the Sorenson (Bray-Curtis) distance measure, the data were relativized by each habitat variable in the habitat-site matrix, and by sites in the species- and guild-site matrices, using a general relativization (McCune and Grace 2002). Each data set was subsequently analyzed using the "slow and thorough" autopilot mode in PC-Ord with default settings. This mode ran

40 iterations with real data, and 50 with randomized data, for each of one to six dimension solutions. The randomized data run assessed the probability that a similar final stress for a given dimensionality could have been obtained by chance. After selecting the optimal number of dimensions, the data were re-run using the starting configuration of the previous 40 runs for the dimensionality that resulted in the lowest stress value, and a final solution was determined. To assess the strength of the final solution, the Pearson correlation coefficient of determination (r^2) for each ordination axis was calculated. This value indicates the proportion of variation in the original data matrix that is explained by the reduced matrix. To elucidate relationships between site scores and species abundances, guild abundances, or habitat traits, r^2-values between the latter and each ordination axis were calculated. When r^2-values were deemed sufficiently high (>0.3), specific correlations were assessed using Pearson correlation coefficients (r). To determine relationships among species or guild composition and habitat variables, r^2-values between each axis of the species or guild ordination and the unreduced habitat matrix were obtained Again, when r^2-values were>0.3, specific habitat correlations were assessed using r-values.

3.2.5.2 *Multiple Response Permutation Procedures*

To test for differences in species, guild and habitat representation among the three treatments, a Multiple Response Permutation Procedures (MRPP) (Mielke 1984, Zimmerman et al. 1985) was used for each comparison. While NMDS provides a visual representation of site data among treatments, MRPP statistically determines differences among treatments. MRPP is a non-parametric equivalent of Discriminant Function

Analysis (DFA) and is used to test a null hypothesis that no significant multivariate difference exists among pre-defined groups. MRPP lacks assumptions of data normality or homogeneity of variance, making it suitable for use in ecological community analyses where these assumptions are often violated. Furthermore, it is robust to uneven sample size among groups (Zimmerman et al. 1985)

Using a Sorenson distance measure and a natural group weighting factor $n_i/\Sigma\, n_i$ (where n_i is the number of sample plots in each group), differences were analyzed among the three treatments for each of the three data sets using the relativized data. When a significant treatment effect was found, pair-wise comparisons were conducted to determine where the differences occurred (McCune and Mefford 1999). Statistical significance was assessed using the p-value and a full Bonferroni-corrected alpha value. Effect size was evaluated using the chance-corrected within-group agreement test statistic (A). This describes within-group homogeneity, compared to random expectation, and has a maximum value of one (all items within groups are identical). A value >0.3 is considered high (McCune and Mefford, 1999).

3.2.5.3 *Indicator Species Analysis*

For each of the species and guild data sets, Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) was used to determine whether single dependent variables within each data set differed significantly among treatments. ISA does not require even sample size among treatments and was well-suited to my sample size (Dufrêne and Legendre 1997). The analysis considers both relative abundance and frequency of occurrence by a given variable in a single treatment class to determine its indicator value

(INDVAL). This value ranges from 0 to 100 where 100 indicates perfect indication (i.e. a dependent variable indicates a particular class without error). The significance of INDVAL was evaluated using a Monte Carlo simulation of 10,000 runs and by randomly assigning samples to groups and recalculating INDVALs. The unrelativized data were analyzed and results considered significant only when $p<0.1$ and INDVAL was greater than 25 (Dufrêne and Legendre 1997).

Prior to all multivariate analyses, the original species-site and guild-site data sets were reduced by removing sites with zero values, sites greater than 2 standard deviations from the mean Sorensen distance among sites, and rare species (i.e. those present in fewer than 5% of sites), as suggested by McCune and Grace (2002). Guild abundance was calculated using all species, regardless of their rarity. Unidentified woodpecker observations were included in the guild analysis. Brown Creeper observations were excluded from this analysis because it was the only species in its guild (bark-nester). For all significance tests, an error-wise alpha rate of 0.1 was used. This reduced the chance of committing Type II errors, which can have greater consequences for conservation outcomes than Type I errors (Smith 1995).

3.2.5.4 *General Linear Modeling*

I modeled habitat associations using general linear models for five indicator species (see above): Northern Flicker, Tree Swallow, House Wren, Hairy Woodpecker and Red-breasted Nuthatch. Using S-plus 7.0 (Insightful Corp. 2005), species abundance was related to all habitat variables, except the density of light to moderately burned conifer trees and the proportion of site remaining unharvested. As previously noted, these two variables were associated with only a single treatment each, and thus were more descriptive of overall treatment effects than proximate factors. Species abundance data followed a Poisson distribution (Kolmogorov-Smirnov Test, $p>0.1$) and were not overdispersed; therefore, multiple Poisson regression analyses were used. Multiple Poisson regression can be used to model discrete count data in relation to continuous predictor variables to determine the frequency of an event (i.e. species presence) occurring over time (Pradham and Leung 2006). Final models were determined using stepwise selection and *Cp* values (Crawley 2002). The *Cp* statistic measures the amount of variation explained by a model in relation to the number of variables it contains (Mallows 1973). The final model selected was that with the fewest explanatory variables whose explanatory power (i.e. variation in data set explained) was not significantly lower than that of the full model ($p>0.05$ ANOVA). The significance of final model terms was assessed using ANOVA and Chi-squared values and overall model fit was assessed by the percent of deviance (a measure of difference between observed and fitted values) it explained. Again, an error-wise alpha rate of 0.1 was employed. An *a priori* analysis indicated no correlation among predictor variables (Spearman's rank correlation, $R<0.7$) and all were entered as model covariates.

3.3 Results

In total, 14 species of cavity or bark-nesting birds from three nesting guilds were observed (Table 3.1; for summary statistics see Appendices 3.2, 3.3, and 3.4). The most common species, present in 59% of sites, was the Brown Creeper, followed by the Northern Flicker (38%), and Yellow-bellied Sapsucker (34%). All other species occurred in fewer than 20% of sites with Black-backed Woodpecker, Mountain Bluebird, and Northern Hawk Owl being the rarest species (<5%) (Table 3.1; Fig. 3.3). There were no secondary cavity-nesters detected in intact forest (Fig. 3.4).

3.3.1 *Composition of Bird Assemblages*

Species composition differed significantly between burned and intact forests (MRPP; Table 3.2) but did not differ between either burned and harvested, or harvested and intact forests. Although this difference in species composition was significant ($p<0.1$), it was fairly weak, with high heterogeneity within each forest class (i.e. low *A*-value in the MRPP analysis, Table 3.2). Differences in species composition were reflected by the NMDS solution, where burned and intact sites separated in ordination space and assemblages in harvested forest were scattered among the two treatments (Fig. 3.5). An exception to this pattern was a single intact site situated among burned sites (Fig. 3.5). This site was composed of only two species, Northern Flicker (which was associated with burn sites) and Black-capped Chickadee (which was observed in this site only), explaining its position in multidimensional space. For these reasons, this site is not indicative of overall patterns in assemblages. The species-site NMDS solution was 3-dimensional, significantly different from a random solution ($p<0.1$), explained 87% of the variance in the initial distance matrix and provided a fair representation of the true differences in species composition among sites (stress=12.83; Table 3.3). Axis 1 and 3 represented a gradient from intact to harvested to burned forest, while axis 2 indicated the opposite pattern (Fig. 3.5). Overall, based on the amount of site variance accounted for by each species on each axis (i.e. $r^2 > 0.3$) and the direction of the relationship (i.e. r), assemblages in burned sites were dominated by Northern Flicker and Tree Swallow and assemblages in intact sites were dominated by Hairy Woodpecker, Yellow-bellied Sapsucker, Boreal Chickadee, and Brown Creeper (Table 3.4). Assemblages in harvested sites appeared to be characterized by species occurring in both intact and burned forests (Fig 3.6a and 3.6b), except for Hairy Woodpecker and Black-capped Chickadee which were not observed in harvested sites (Table 3.1). Species assemblages were not related to any habitat features measured. All r^2-values between species-ordination axes and the unreduced habitat matrix were less than 0.3 (Table 3.4).

3.3.2 *Guild Composition*

MRPP indicated differences in guild composition between burned and intact sites, and between harvested and intact sites, although differences in the former were weak (value of A was relatively low; Table 3.2). Burned and harvested sites did not differ significantly in guild composition (Table 3.2). The NMDS guild analysis did not reach a stable solution, and thus did not provide a clear representation of patterns in guild composition among sites. ISA indicated that the weak-excavator guild used intact sites more frequently and the secondary-nester guild used burned sites more frequently (Fig. 3.4; Table 3.5).

3.3.3 *Species-habitat Relationships* Northern Flicker, Tree Swallow, and House Wren were indicators for burned sites and Hairy Woodpecker and Red-breasted Nuthatch were indicators for intact sites (Table 3.5). There were no indicator species for partially-harvested sites.

The use of sites by Northern Flicker was positively related to large snag density and downed woody material abundance (Table 3.6). Tree Swallow site-use also increased with snag density, but decreased with increasing density of live birch trees (Table 3.6). House Wren site-use was positively related to large snag density only (Table 3.6). The positive relationship with snag abundance for these three species was relatively strong for all species ($\beta > 1.6$), particularly for Northern Flicker (Table 3.6). Hairy Woodpecker site-use was positively related to the density of live birch trees (Table 3.6). Red-breasted Nuthatch site-use was not significantly related to any local habitat variables (Table 3.6). Of the five models, that of the Northern Flicker explained the most deviance (44%), followed by Tree Swallow, (40%), Hairy Woodpecker (34%), Red-breasted Nuthatch (20%) and House Wren (13%) (Table 3.6).

3.3.4 *Habitat Composition Across Sites and Treatments*

Using multivariate methods, I confirmed that burned, partially-harvested and intact sites represented compositionally and structurally distinct habitat types based on the habitat variables I measured. When described by habitat, sites from the three treatments were relatively well-clustered and separated from each other in ordination space (Fig 3.6). The habitat-site NMDS solution was 3-dimensional, significantly different from a random solution ($p<0.1$), explained 89% of the variance in the initial distance matrix and provided a fair representation of the true differences in habitat composition among sites (stress=11.03; Table 3.3). Axis 1 represented a gradient from highly forested burned and intact sites, the latter situated on larger lakes, to harvested sites abundant in downed woody material, as determined by habitat-axis correlation coefficients (r) (Table 3.4; Fig. 3.6a). Axis 2 indicated a gradient from unburned sites with a high density of large aspen trees with conks, to sites with a high burned conifer density (Table 3.4; Fig. 3.6a and 3.6b). Axis 3 represented a gradient from sites with high live birch density to those with a high snag and burned tree density (Table 3.4; Fig. 3.6b).

Habitat differences among treatments were significant and moderately strong (i.e. relatively high observed *A*-values for pair-wise comparisons; Table 3.2.) indicating that habitat variation was greater among sites than within sites. Burned sites had higher large snag density (ANOVA, F=8.84 (2,29) p=0.001), harvested sites had and more downed woody material (ANOVA, F=12.81 (2,29) p<0.001) and intact sites had higher density of live birch (ANOVA, F=6.57 (2,29) p=0.004) than other treatments.

3.4 Discussion

3.4.1 *Bird Assemblages in Burned and Partially-Harvested Forests*

Hunter (1993) hypothesized that organisms are adapted to environmental variation caused by natural disturbances, thus anthropogenic disturbances that emulate natural disturbance should have minimal impacts on populations and communities. In my study, bird assemblages in burned and partially-harvested sites did not differ significantly, however, sample sizes were small (especially in burn sites) and the heterogeneity of species composition was high within treatments, reducing my ability to detect differences. In addition species known to be associated with burns, and found only in burns in my study (e.g. Black-Backed Woodpecker, Mountain Bluebird, and Northern Hawk Owl (Hoyt and Hannon 2002, Hannah and Hoyt 2004, Hutto and Gallow 2006), were rare and were thus not included in the ordinations. Because of these potential problems, I cannot definitively conclude that assemblages in burns and partial-harvest sites are the same.

At the species-level, however, Northern Flicker, Tree Swallow, House Wren, and the secondary-nester guild were indicators of burned forest and Black-Backed Woodpecker, Mountain Bluebird, and Northern Hawk Owl were only detected in burned forest. These species have been found at higher abundances in burned boreal forests in several other studies (Bock and Lynch 1970, Hutto 1995, Hoyt and Hannon 2002, Morissette et al. 2002, Hannah and Hoyt 2004, Saab et al. 2004, Hutto and Gallow 2006, Koivula and Schmiegelow 2007). Although there were no species that were strong indicators of the harvested forest condition, Pileated Woodpecker, Boreal Chickadee, and Red-breasted Nuthatch were present in harvested sites but not burns. This was not unexpected as none of these three species is commonly associated with burned forest (Raphael and White 1984, Bull and Jackson 1995, Ficken et al. 1996, Hannon and Drapeau 2005). Thus, while these data suggest some species differences between burns and partial-harvest sites, more research with larger sample sizes is required to make definitive conclusions.

3.4.2 *Bird Assemblages in Partially-Harvested and Intact Forests*

Intact buffer strips can act as lifeboats in harvested landscapes by retaining some bird species found in the riparian forest prior to harvest (Whitaker and Montevecchi 1999, Lambert and Hannon 2000, Pearson and Manuwal 2001). In my study, bird assemblages in partially-harvested buffers and intact forest were similar, and both were used by Yellow-bellied Sapsucker, Boreal Chickadee, and Brown Creeper. Sampling issues, as noted above, preclude definitive conclusions, but investigations of single species suggest some differences between the treatments. For example, Hairy Woodpecker, Red-breasted Nuthatch, and the weak-excavator guild used sites in intact forest more frequently, consistent with other studies in the boreal forest (Norton and Hannon 1997, Hobson and Bayne 2000, Schieck and Hobson 2000, Schieck et al. 2000). Furthermore, Black-capped Chickadee, although rare, was not observed in partially-harvested buffers. Intact forests may contain a higher abundance of trees with pre-existing cavities, which some weak-excavating species may use (Martin and Eadie 1999). I also observed Tree Swallows and House Wrens in partially-harvested buffers but not intact forest. Harvested buffers provide a higher abundance of forest gaps and edge-habitat than intact forest, and Tree Swallows and House Wrens may use these areas for aerial foraging (Robertson et al. 1992) and insect gleaning (Johnson 1998), respectively.

3.4.3 *Species-Habitat Associations* Northern Flicker, Tree Swallow, and House Wren, indicators of burned forest, all had a strong positive relationship to large snag density. Due to fire-kill, large snags were denser in burned forests than intact forest or harvested buffers. Northern Flickers commonly excavate cavities in large snags (Harestad and Keisker 1989), while Tree Swallows and House Wrens may use old Northern Flicker cavities (Martin et al. 2004) or natural cavities in broken limbs or the tops of broken snags that were created by fire (Newton 1994). Whether Tree Swallows and House Wrens reused Flicker cavities after the burn is unclear as most cavities used by Tree Swallows and House Wrens were charred around the edges (*personal observation*), suggesting they were excavated prior to burning. Open habitat in burned forest may have been favored by Northern Flicker and Tree Swallow, as they are species that forage in open areas (Robertson et al. 1992, Elchuck and Wiebe 2002). It is unlikely that snags were used for foraging by Northern Flicker, Tree Swallow or House Wren, which are predominantly ground probers (Moore 1995, Elchuck and Wiebe 2002), aerial foragers, (Robertson et al. 1992), and shrub or ground gleaners (Johnson, 1998), respectively. Although Northern Flickers commonly forage for ants on the ground (Elchuck and Wiebe 2002), ant colonies were not observed in burned forests and flickers may have been foraging for insects upon downed woody material; this has been observed elsewhere (Bull et al. 1986, Bull 2002).

Hairy Woodpecker site-use was positively related to the density of live birch trees, which was highest in intact forest. Hairy Woodpeckers prefer hardwood trees for cavity sites (Schepps et al. 1999) and may have used some of the larger birch trees for nesting. Site-use by Tree Swallow was negatively associated with the density of live birch trees. Most live birch trees were relatively small (~4 cm dbh), and occurred in dense clumps (*personal observation*), creating a relatively closed habitat. A low density of birch in burns reduced the number of birch clumps, and created a more open habitat, providing foraging space for this aerial insectivore.

3.4.4 *Study Limitations*

The power to detect differences in the composition of bird assemblages among treatments was compromised by low sample size and small survey area. Sample size was low because there were few partially-harvested and recently-burned forests of suitable age and canopy composition. As a result, only relatively large differences among treatments could be statistically detected, as the probability of revealing smaller differences increases with sample size (Gerrodette 1987). By surveying more sites, variation across treatments may have been reduced. Assuming that within-site variation is lower than among site variation, this would increase the chance of detecting smaller differences in the composition of assemblages among treatments. The effect of this on elucidating responses to burned forest may have been particularly evident as the range of burn severity sampled varied considerably. Moreover, if additional sites had been sampled, rare species may have been observed more often, providing better overall assemblage descriptions. Survey area was limited by the extent of burned or harvested forest along a riparian edge. As a result, transect area was smaller than the size of some species' territories, and, assuming their territory overlapped the site, reduced the probability they would be present during a single survey. Therefore, by increasing survey area, species may have been observed more frequently, again, providing a clearer depiction of the composition of bird assemblages.

Furthermore, I was unable to determine whether some of the observed habitat differences among treatments existed prior to, or were an effect of, the treatment (i.e. fire or harvest). I attempted to select sites to minimize habitat differences across treatments, but the scale of available inventory data was too coarse to compare pre-treatment habitat of sites.

Results should be interpreted with caution. Species-habitat associations may change seasonally (Strong and Bock 1990), and my results are from the breeding season only. Furthermore, the pattern of partial-harvest applied may not accurately represent a post-fire riparian forest. Specifically, the retention of a 10m-wide intact strip adjacent to the water's edge is inconsistent with natural burn patterns, as wildfire can occur to the forest edge (Andison and McCleary 2002). Future research investigating the emulation of burned riparian forest on bird communities should be conducted using buffers partially-harvested to the edge of a watercourse.

3.4.5 *Conclusions and Management Implications*

Because of the limitations noted above, conclusions are tentative. For most species, partial-harvesting does not appear to emulate recently burned riparian forest, despite an overall similarity between treatment assemblages. Pileated Woodpecker, Boreal Chickadee, and Red-breasted Nuthatch used harvested buffers and intact forest more than burns, however, for Northern Flicker, Tree Swallow, House Wren, Black-backed Woodpecker, Mountain Bluebird and Northern Hawk Owl, burned forest appeared more suitable. Differences among bird species using recently burned forest and forest harvested to emulate recent burns have been observed in both upland and riparian forests (Hobson and Schieck 1999, Imbeau et al. 1999, Simon et al. 2002, Schieck and Song 2006, Kardynal 2007). Similar to management recommendations from previous studies, I suggest that burned riparian forest should be retained on the landscape to conserve habitat for burn-associated species.

Compared with intact forest, partial-harvesting appears to represent a less suitable habitat for some cavity-nesters. Specifically, Hairy Woodpecker and Black-capped Chickadee were not observed in harvested sites, suggesting partially-harvested buffers do not serve as lifeboats in harvested landscapes for these species. It is possible that intact buffer strips provide habitat for these species (Darveau et al. 1995, Whitaker and

Montevecchi 1997), however this conclusion is beyond the scope of my study as unharvested buffer strips were not sampled. To conserve habitat for Hairy Woodpecker and weak-excavators (Red-breasted Nuthatch, Boreal Chickadee, Black-capped Chickadee), some mature (>70 years old) intact riparian forest (i.e. no recent harvest or fire activity within a 1km radius) should remain on the landscape.

The composition of bird assemblages was not related to the habitat features measured. This suggests that alternative factors, such as interspecific competition (Martin et al. 2004) or predation (King et al. 1998) may affect the composition of bird assemblages more than local habitat. Future studies should aim to determine such factors, which may be of management interest. To this end, a longer-term study of cavity use and re-use by cavity-nesting species in partially-harvested buffers should be conducted and functional interactions among primary nesters, weak excavators, and secondary nesters should be evaluated by assembling a cavity nest web (Martin and Eadie 1999).

Individual species-habitat associations suggest that habitat for Northern Flicker, Tree Swallow and House Wren can be conserved in part by retaining large snags (>25cm dbh), including those containing natural cavities, within managed riparian stands. Lee et al. (1997) emphasize the importance of deadwood retention in terms of accurately emulating post-disturbance conditions in mixed-wood boreal forests. Downed woody material may also provide habitat for Northern Flicker and as such, should be retained in harvested buffers. Specifically, it should be dispersed evenly throughout the buffer rather than being placed in piles which may reduce habitat for some tree and mammal species (Kipra and Fyles 2005).

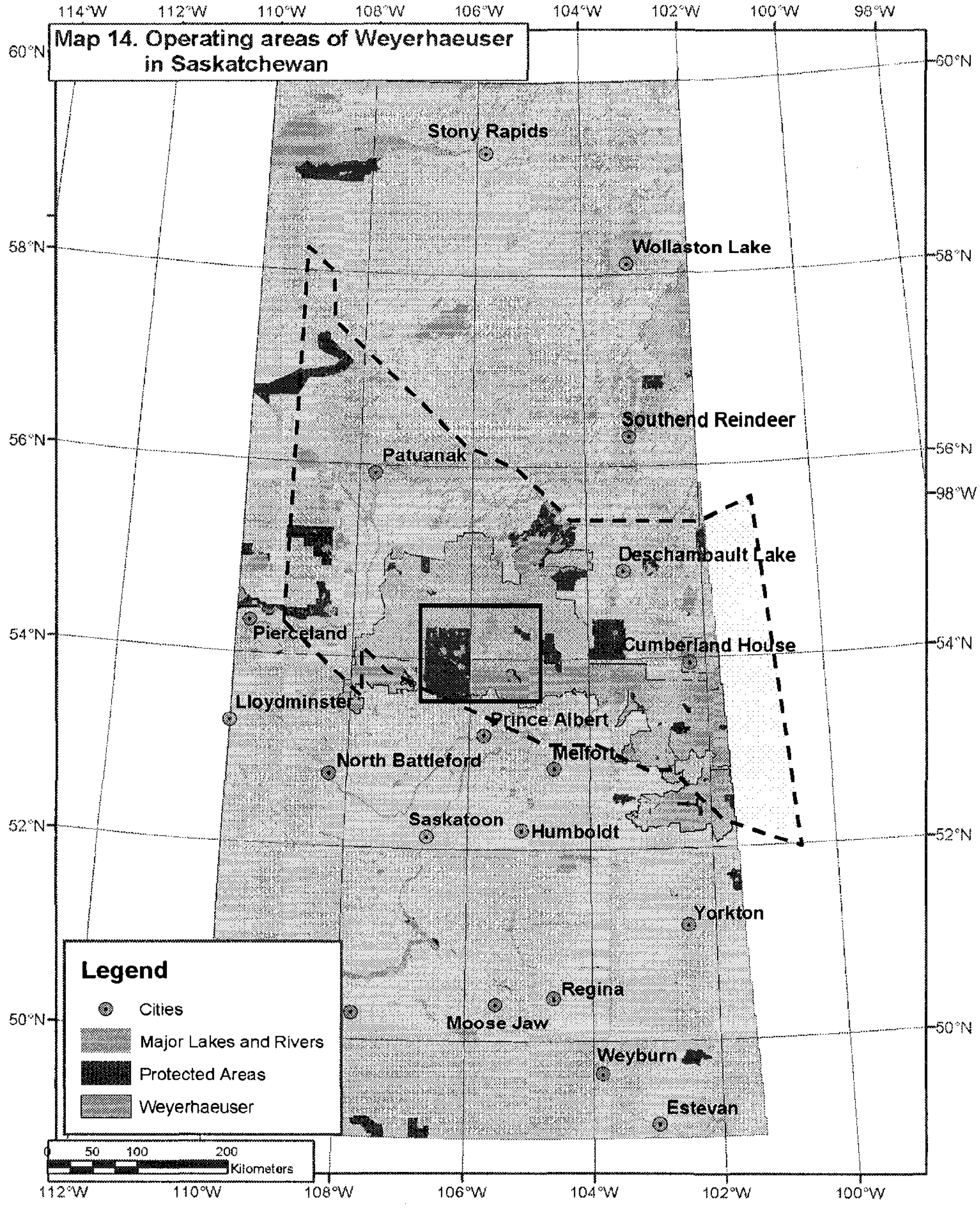


Figure 3.1. Location of the study area on the Weyerhaeuser Prince Albert Forest Management Area (FMA) in Saskatchewan, Canada. The provincial extent of the Boreal Plains ecozone is shaded in brown, the area covered by the FMA is shaded in pink, and the study area is enclosed within the black box (excluding the protected area indicated). Base map courtesy of Weyerhaeuser Canada Ltd. (2004).

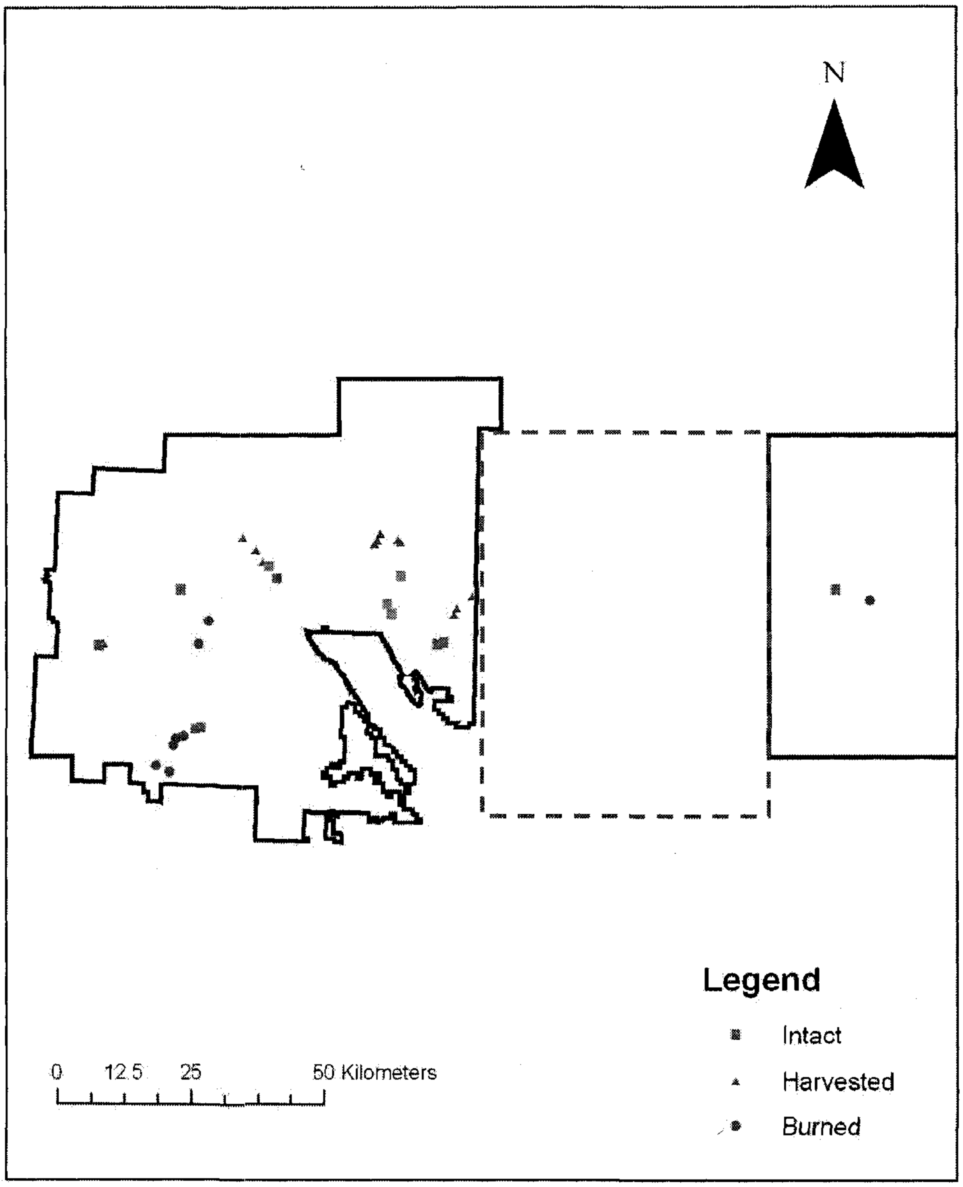


Figure 3.2. Location of intact (n=12), harvested (n=12) and burned (n=8) sample sites across the study area. The solid line indicates the boundaries of the Weyerhaeuser FMA. The dashed line indicates the boundaries of Prince Albert National Park, SK.

Table 3.1. Observed species indicated with their species code and cavity nesting guild (PN=primary nester, WE=weak excavator, SN=secondary nester, NB=bark nester) (Martin and Eadie 1999) and the proportion of sites they were observed in within each treatment and across all sites. Species are listed from most to least common overall.

Species	AOU[1] Species Code	Nesting Guild	Proportion of sites			
			Burn n=8	Harvest n=12	Intact n=12	All sites n=32
Brown Creeper (*Certhia americana*)	BRCR	BN	0.50	0.58	0.67	0.59
Northern Flicker (*Colaptes auratus*)	NOFL	PN	0.63	0.50	0.08	0.38
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	YBSA	PN	0.13	0.33	0.5	0.34
Boreal Chickadee (*Poecile hudsonica*)	BOCH	WE	0.00	0.17	0.33	0.19
Red-breasted Nuthatch (*Sitta Canadensis*)	RBNU	WE	0.00	0.08	0.33	0.16
Tree Swallow (*Tachycineta bicolor*)	TRSW	SN	0.38	0.17	0.00	0.16
House Wren (*Troglodytes aedon*)	HOWR	SN	0.38	0.08	0.00	0.13
Hairy Woodpecker (*Picoides villosus*)	HAWO	PN	0.00	0.00	0.25	0.09
Three-toed Woodpecker (*Picoides tridactylus*)	TTWO	PN	0.13	0.08	0.08	0.09
Black-capped Chickadee (*Poecile atricapilla*)	BCCH	WE	0.13	0.00	0.08	0.06
Pileated Woodpecker (*Dryocopus pileatus*)	PIWO	PN	0.00	0.08	0.08	0.06
Black-backed Woodpecker (*Picoides arcticus*)	BBWO	PN	0.13	0.00	0.00	0.03
Mountain Bluebird (*Sialia currucoides*)	MOBL	SN	0.13	0.00	0.00	0.03
Northern Hawk Owl (*Surnia ulula*)	NHOW	SN	0.13	0.00	0.00	0.03

[1] AOU= American Ornithological Union

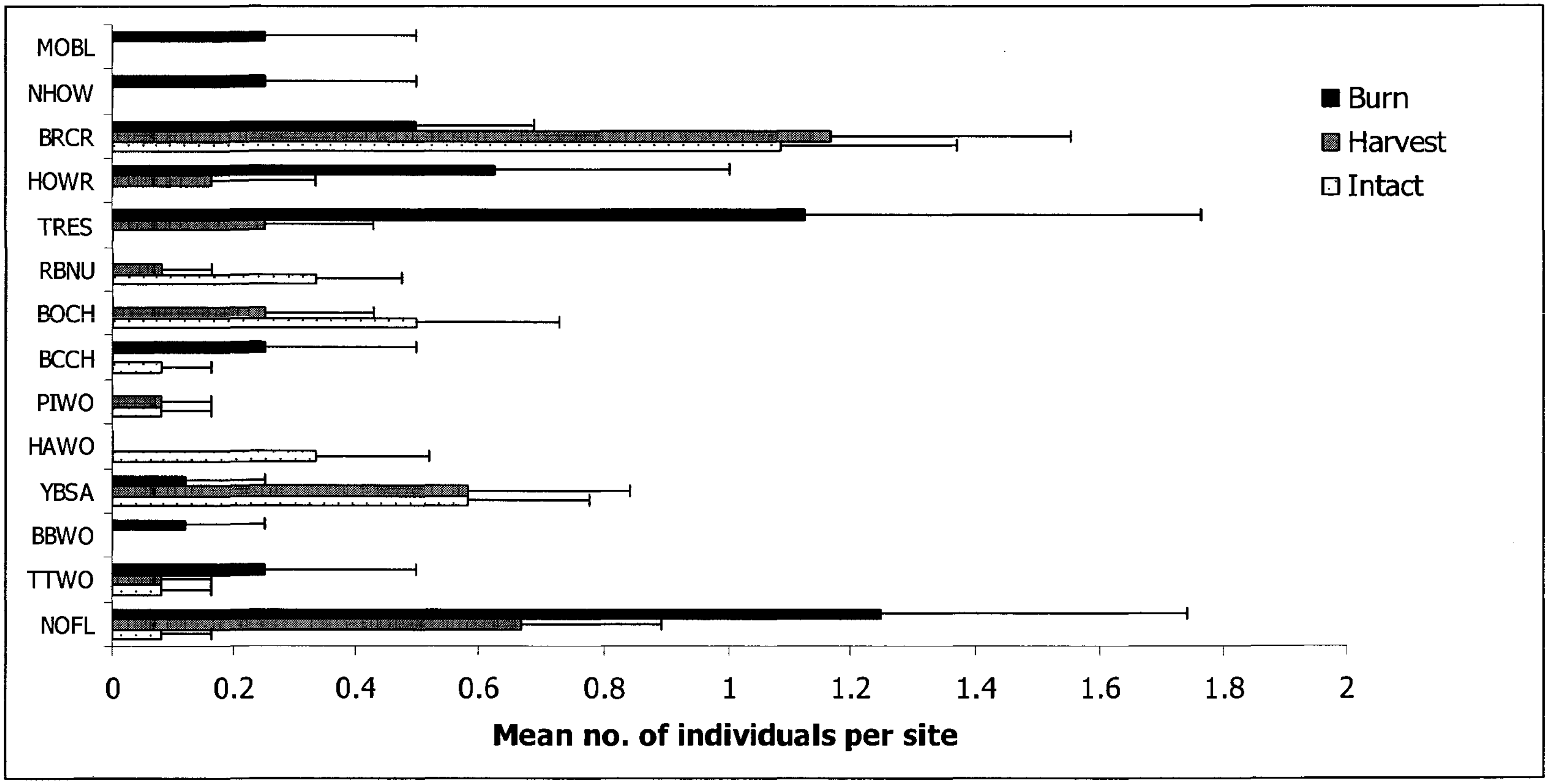


Figure 3.3. Mean (± SE) abundance of 14 cavity or bark-nesting bird species in burned (n=8), harvested (n=12), and intact (n=12) riparian forests. House Wren (HOWR), Tree Swallow (TRES), and Northern Flicker (NOFL) all used burned sites more frequently than harvested or intact sites (Indicator Species Analysis, INDVAL>25, p<0.1; see Table 3.5). For species code descriptions, see Table 3.1.

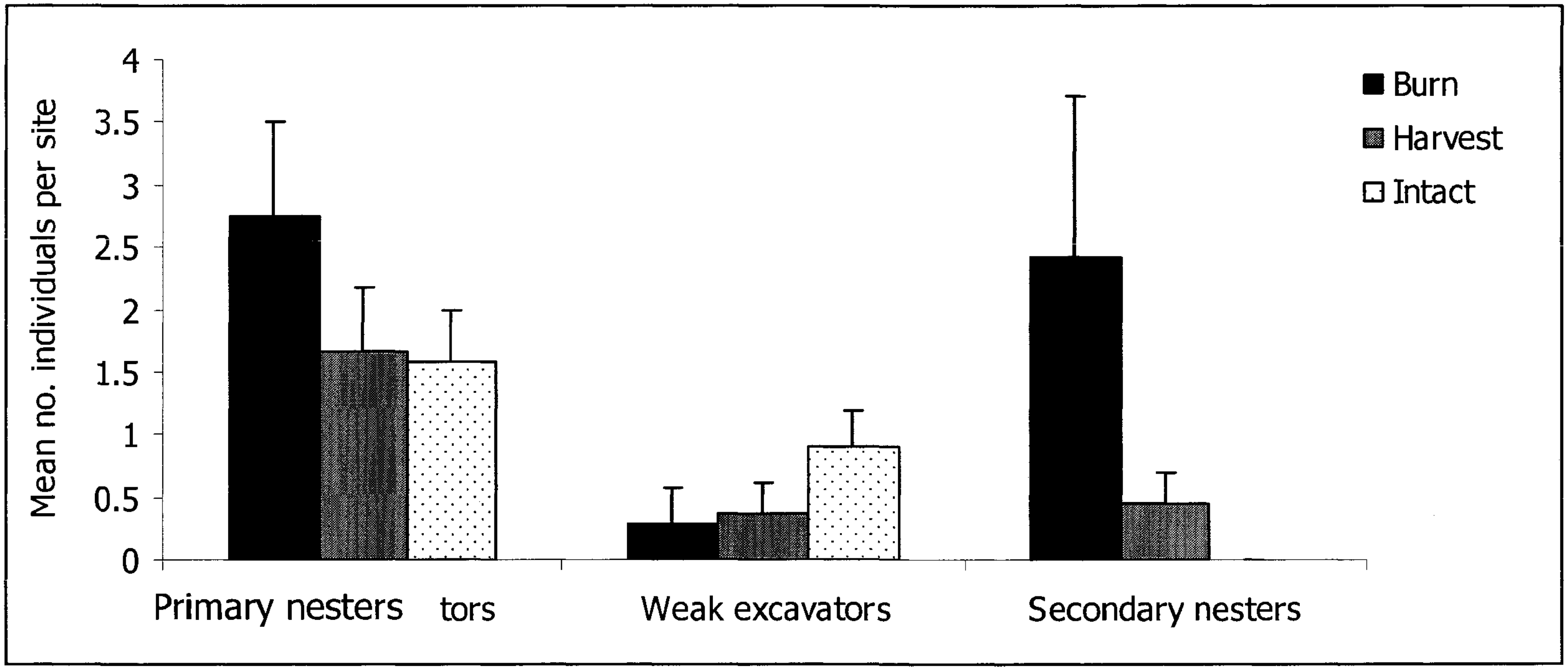
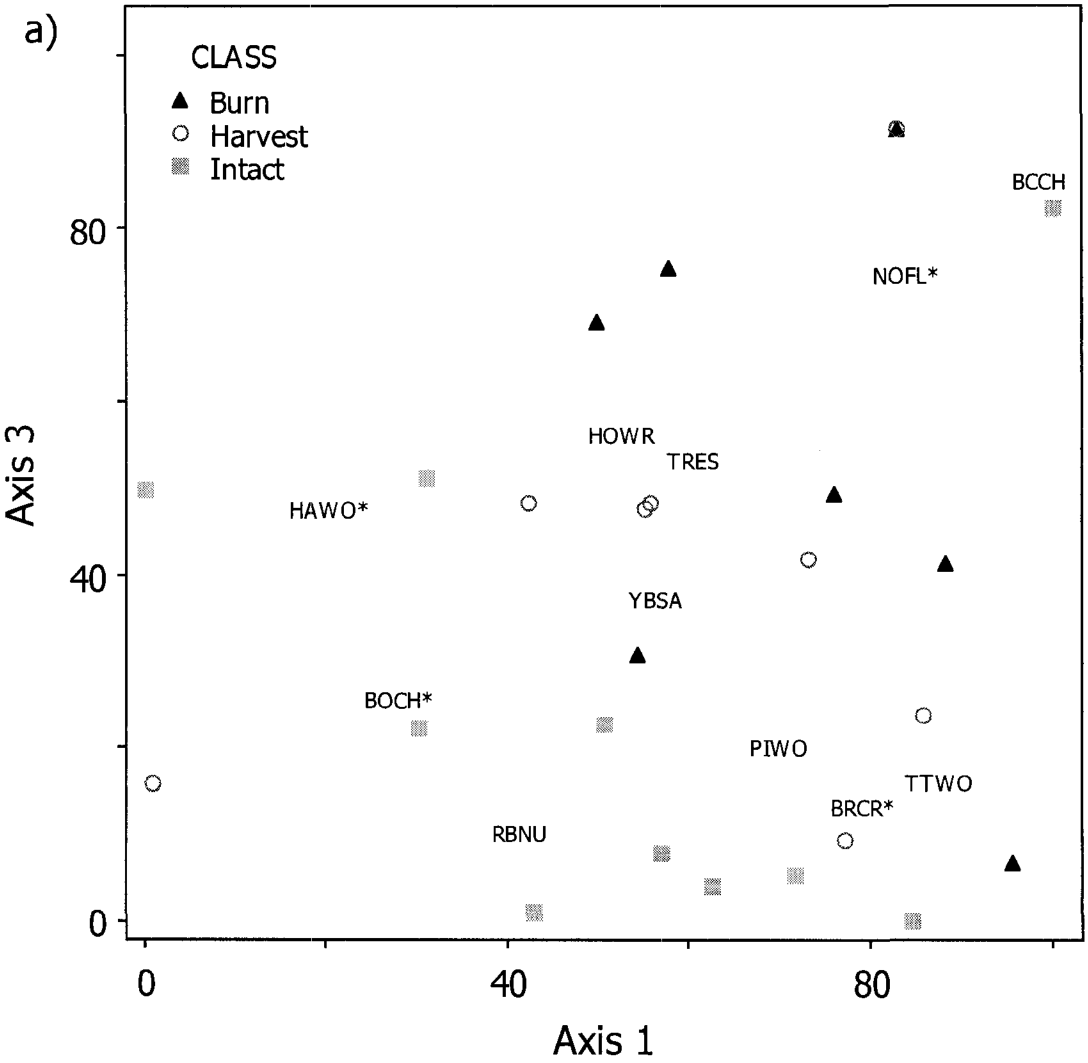


Figure 3.4. Mean (± SE) abundance of individuals from three nesting guilds in burned (n=8), harvested (n=12), and intact (n=12) riparian forests. Weak excavators used intact sites more frequently than burned or harvested sites, and secondary nesters used burned sites more frequently than intact or harvested sites (Indicator Species Analysis, INDVAL>25, p<0.1; see Table 3.5). For a description of guild membership, see Table 3.1.

Table 3.2. Results of MRPP analyses testing the null hypothesis of no difference in species, guild or habitat composition among burned, harvested, and intact boreal riparian forests

Difference among site species composition	**Average distance**	**N**	**MRPP statistics** Observed delta = 0.7235 Expected delta = 0.7525 T = -1.823, A = 0.0386, p = 0.05
Burn	0.6956	7	
Harvest	0.7647	11	**Significant pair-wise comparisons** Burn vs. intact: T=-3.78, A=0.09, p=0.003
Intact	0.7000	11	
Difference among site guild composition	**Average distance**	**N**	**MRPP statistics** Observed delta = 0.3071 Expected delta = 0.3515 T = -2.6205, A = 0.1264, p = 0.02
Burn	0.4083	6	
Harvest	0.2639	9	**Significant pair-wise comparisons** Burn vs. intact: T=-1.82, A=0.09, p=0.06 Harvest vs. intact: T=-3.79, A=0.18, p=0.01
Intact	0.2852	10	
Difference among site habitat composition	**Average Distance**	**N**	**MRPP statistics** Observed delta = 0.3815 Expected delta = 0.4829 T = -10.904, A = 0.2100, p<0.001
Burn	0.463	8	
Harvest	0.340	12	**Significant pair-wise comparisons** Burn vs. harvest: T=-8.08, A=0.20, p<0.0001 Burn vs. intact: T=-6.90, A=0.16,
Intact	0.369	12	


a)
CLASS
Burn
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Axis 3
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40
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BCCH
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HAWO*
YBSA
BOCH*
PIWO
TTWO
BRCR*
RBNU

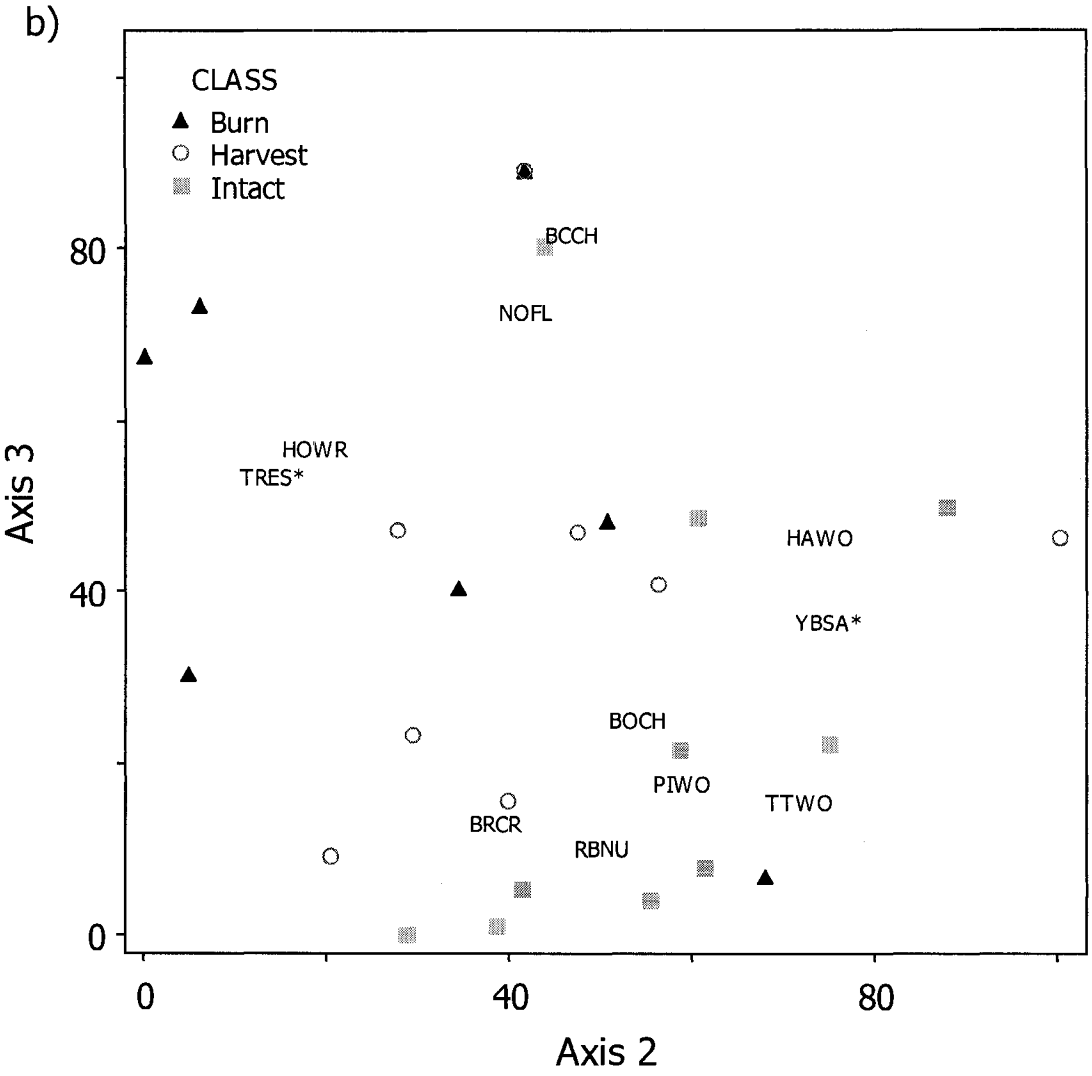


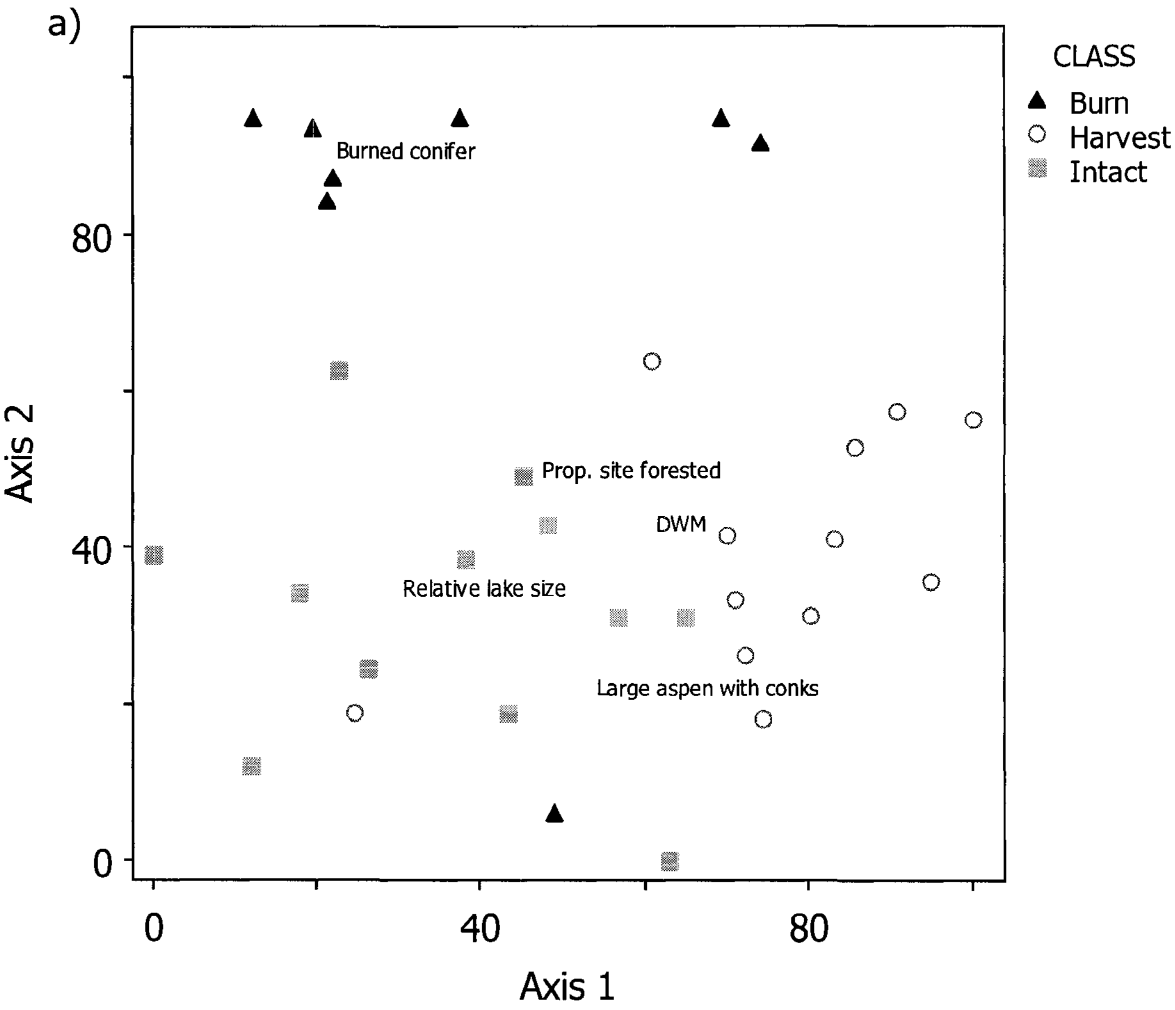
Figure 3.5. NMDS solution comparing bird species composition among sites in burned, partially-harvested and intact boreal riparian forests (PC-Ord 1999). Sites that are closer together have more similar bird assemblages than those that are farther apart. The 3-dimensional solution accounted for 87% of the variation in the original distance matrix. a) Axis 1 and 3, accounting for 23% and 45% of variation, respectively; b) Axis 2 and 3, accounting for 19% and 45% of variation, respectively. Species representing greater than 30% of site variation along any single axis ($r^2>0.3$) gradient are indicated with an (*). For species codes, see Table 3.1. Note: Axes have been scaled in proportion to the longest axis.

Table 3.3. Results from the NMDS analyses investigating the bird species composition and the habitat composition among burned, harvested and intact sites. Randomization *p*-values indicate the probability that a similar final stress value for the stated number of axis could have resulted by chance. Final number of iterations indicate the number of runs required for the instability measure to be less than the cutoff value of 0.00001 (standard deviations in stress over the previous 15 iterations). The proportion of variance explained (r^2) is that of the original site dissimilarity distance matrix.

Data Type	**No. sites**	**No. dependent variables**	**No. axes**	**Randomization *p*-value**	**Final no. iterations**	**Final stress**	**Final instability**	r^2
Sites by species	29	11	3	0.02	400	12.83	0.00006	0.87
Sites by habitat	32	8	3	0.02	112	11.03	0.00001	0.89

Table 3.4. Relationships between dependent variables where r^2>0.3 for at least one axis and each axis of the NMDS solution for species-site and habitat-site ordinations. Pearson correlation coefficients (r) indicate the relationship between each variable and axis, and coefficients of determination (r^2) indicate the proportion of variance along each axis that is accounted for by a given variable. Values on the axis relevant to each variable are bolded. For species codes, see Table 3.1.

Dependent variable	**Axis 1**		**Axis 2**		**Axis 3**	
Species composition	r	r^2	r	r^2	r	r^2
NOFL	0.418	0.175	-0.117	0.014	0.783	**0.614**
BOCH	-0.758	**0.574**	0.168	0.028	-0.180	0.032
BRCR	0.456	0.208	-0.318	0.101	-0.754	**0.568**
YBSA	-0.244	0.059	0.751	**0.564**	0.008	0.000
TRSW	-0.111	0.012	-0.632	**0.400**	0.257	0.066
HAWO	-0.587	**0.345**	0.375	0.14	0.110	0.012
Habitat composition	r	r^2	r	r^2	r	r^2
Density large snags (ha)	-0.52	0.27	0.35	0.12	0.80	**0.62**
Density large aspen trees with conks (ha)	0.07	0.00	-0.70	**0.49**	0.30	0.09
No. DWM/m	0.70	**0.49**	-0.41	0.17	0.05	0.00
Prop. site unharvested	-0.69	**0.48**	0.21	0.04	0.27	0.07
Density burned conifer trees (ha)	-0.45	0.21	0.67	**0.45**	0.66	**0.44**
Density live birch trees (ha)	-0.37	0.14	-0.24	0.06	-0.62	**0.38**
Relative lake size	-0.56	**0.31**	-0.31	0.09	0.01	0.00


a)
CLASS
▲ Burn
○ Harvest
▨ Intact
Burned conifer
Prop. site forested
DWM
Relative lake size
Large aspen with conks
Axis 2
Axis 1
80
40
0
0
40
80

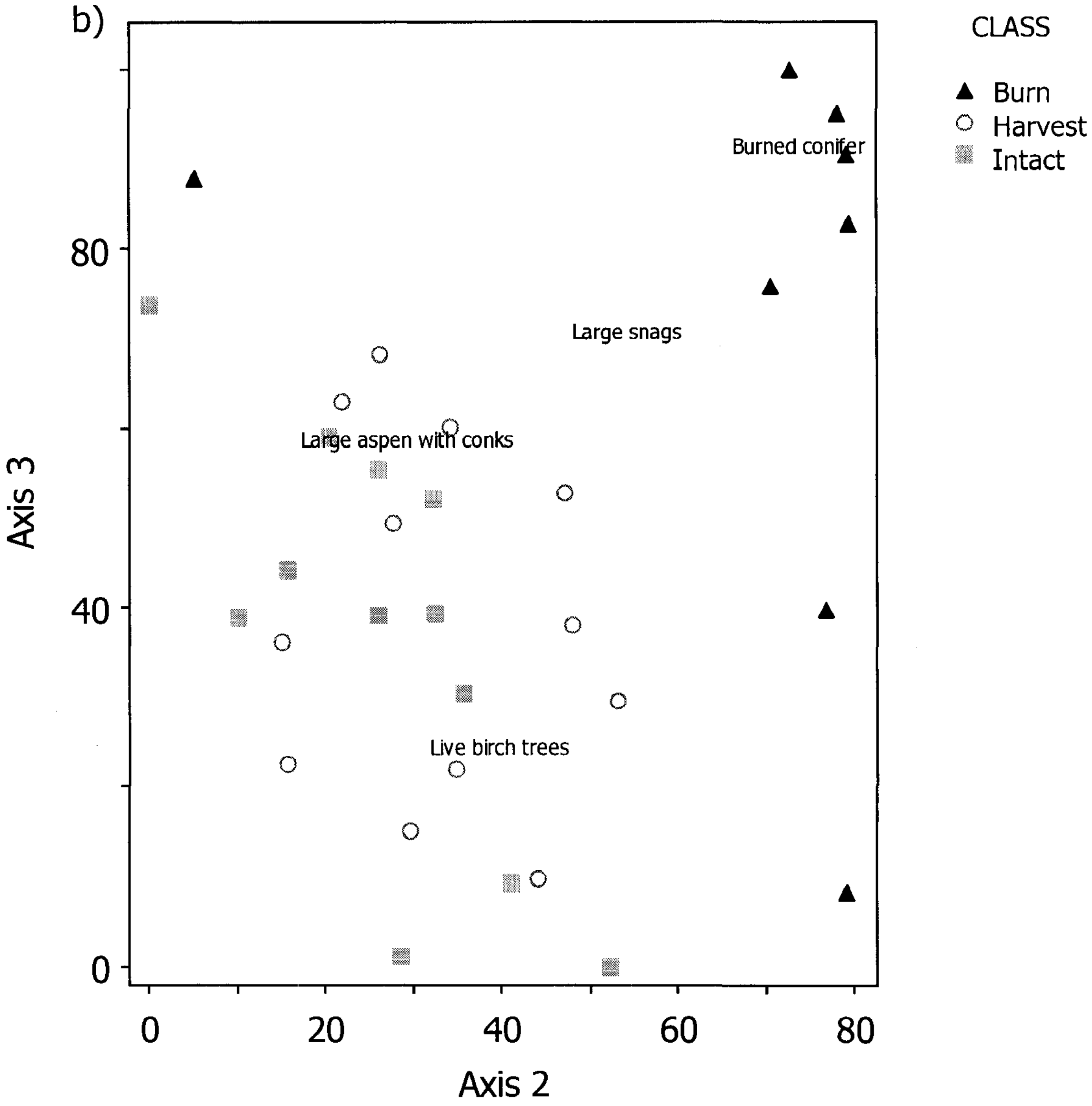


Figure 3.6. NMDS solution comparing habitat composition among sites in burned, partially-harvested and intact boreal riparian forests (PC-Ord 1999). Sites that are closer together have more similar habitats than those that are farther apart. The 3-dimensional solution accounted for 89% of the variation in the original distance matrix. a) Axes 1 and 2, accounting for 23% and 37% of variation, respectively; b) Axes 2 and 3, accounting for 37% and 30% of variation, respectively. Only variables representing greater than 30% of site variation along any single axis gradient ($r^2 > 0.3$) are indicated. For a description of habitat variables, see Table 3.7. Note: Axes have been scaled in proportion to the longest axis.

Table 3.5. Indicator and mean randomized indicator values for nesting guilds and species that used sites in one of the three treatments (i.e. burned, partially-harvested, intact) significantly more often (p<0.1). Results with indicator values >25 are shown. For species codes, see Table 3.1.

Forest class	**Variable**	**Indicator value**	**Randomized indicator value**	***P*-value**
Guild				
Burn	Secondary nesters	51.6	22.4	0.01
Intact	Weak excavators	50.3	25.0	<0.01
Species				
Burn	HOWR	29.0	14.5	0.06
Burn	NOFL	37.8	25.0	0.09
Burn	TRSW	30.2	16.3	0.09
Intact	HAWO	27.3	12.6	0.09
Intact	RBNU	29.1	15.8	0.07

Table 3.6. Results from Multiple Poisson Regression Analysis on Northern Flicker, Tree Swallow, House Wren, Hairy Woodpecker and Red-breasted Nuthatch abundance. Final model variables are presented. Significant model terms are bold marked and significant p-values indicated with an (*). For species codes, see Table 3.1.

Spp.	**Variable**	**Standardized β (β/se)**	**p-value**	**Total % deviance explained by model**
NOFL	Intercept	-2.347		44.0
	Density of conifer trees (ha)	-2.094	0.279	
	Density of large aspen trees with conks (ha)	-1.712	0.398	
	Density of large snags	4.112	0.002*	
	No. DWM/m	2.741	0.007*	
TRSW	Intercept	-1.273		40.0
	Density of large snags (ha)	1.629	0.003*	
	Density of live birch trees (ha)	-1.753	0.001*	
HOWR	Intercept	-3.771		13.0
	Density of large snags (ha)	2.206	0.047*	
HAWO	Intercept	-3.838		34.0
	Density of live birch trees (ha)	2.903	0.01*	
RBNU	Intercept	-3.368		20.4
	Density of large aspen trees with conks (ha)	1.921	0.144	
	Density of live birch trees (ha)	1.451	0.194	

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CHAPTER 4

THESIS SUMMARY, MANAGEMENT RECOMMENDATIONS AND FUTURE RESEARCH

4.1 Background

In the Boreal Plains ecozone of western Canada, riparian forests are commonly managed through retention of treed buffers adjacent to waterbodies (Lee et al. 2004). In addition to reducing the effects of upland run-off on aquatic systems, buffers can also provide habitat for forest-associated bird species in harvested landscapes (Hannon et al. 2002). For cavity-nesting birds, riparian buffers may provide appropriate nesting and foraging habitat as these buffers contain a large proportion of old-growth forest, relative to the rest of the landscape (Lee and Barker 2005), and an abundance of decaying trees, standing snags and downed woody material (Stevens et al. 1995, Jackson and Jackson 2004, Martell et al. 2006).

Increasing demands for forest resources in the Boreal Plains ecozone and concerns over the effect of industrial development on wildlife have prompted the use of alternative harvesting techniques (Schneider and Walsh 2005). Predominant among these are practices that follow a natural disturbance model (Hunter 1993). Typically, this involves harvesting in an attempt to emulate the effects of natural wildfire. In riparian forests, this involves partial harvesting of buffers: retaining individual trees and forest patches of various sizes to represent natural fire-skips. However, whether this partial harvest affects bird communities in similar ways to wildfire is not well understood (but see Kardynal 2007). Specific knowledge gaps regarding cavity-nesters include: 1) the effect of harvesting within treed buffers on the composition of bird assemblages; 2) whether species site-use is affected by habitat in the landscape surrounding the buffer; and 3) whether bird assemblages differ between harvested buffers and burned riparian forest. The purpose of my thesis was to address these knowledge gaps and provide recommendations to forest managers to ensure the maintenance of cavity-nesting bird assemblages. Cavity-using species were chosen as a focal group because many species rely on mature and old-growth forest, the age classes targeted for harvest (Schmiegelow and Mönkkonen 2002), and certain species are keystones (Martin et al. 2004, Savignac and Machtans 2006, Cooke *personal communication*) and indicators, because their nesting and foraging activities influence the abundance of other forest birds (Drever et al. 2008). My research objectives were to:

1. Determine how increasing levels of harvest in buffers affected the composition of cavity-using bird assemblages.
2. Identify local and landscape-level habitat features that influenced the composition of bird assemblages and the scale at which habitat features had the strongest influence on assemblage composition.
3. Identify local and landscape-level habitat features that influenced site-use by five species: Yellow-bellied Sapsucker (*Sphyrapicus varius*), Northern Flicker (*Colaptes auratus*), Boreal Chickadee (*Poecile hudsonica*), Tree Swallow (*Tachycineta bicolor*) and Brown Creeper (*Certhia Americana*) and for each, determine the scale at which habitat features had the strongest influence on their use of sites.
4. Determine whether partial harvesting in buffers emulated the effects of fire for cavity-nesting birds.

My study occurred in the Boreal Plains ecozone of Saskatchewan and Manitoba from April to June in 2005 and 2006, respectively. I surveyed cavity-nesting birds using 400m-long line transects situated 20m upland from the treed edge of the riparian forest. Birds detected within 20m on either side of the transect were recorded and the maximum abundance of each species over three visits per site was used in subsequent analyses. Abundance values were low and therefore results were interpreted generally as species site-use. Habitat features relevant to cavity nesters were measured both on the ground and using forest inventory data. I measured habitat at three scales: local (within buffer: ~1.6ha), medium (an area related to most species' territory size: ~23ha) and large (an area related to median cutblock size – a known dispersal barrier to some birds: ~211ha). All sites sampled were composed of mature (>70 years old), aspen-dominated mixedwood (>50% aspen) forest, and were situated adjacent to wetlands of various size (2005: 11-12610ha; 2006: 2-67ha).

I addressed objectives 1-3 using data collected in 2006 from 47 partially-harvested buffers (harvested 1-2 years prior) and 19 intact riparian forests. Harvested buffers varied in the amount of forest retained and were divided into 3 retention classes: low (<33% retention; 11 sites), medium (34-66% retention; 14 sites) and high (66-100% retention; 22 sites). I addressed objective 4 using data collected in 2005 from 8 sites in burned (2-3 years post-fire) riparian forests, 12 sites in partially-harvested buffers (harvested 1-4 years prior), and 12 sites in intact riparian forests. Multivariate methods and general linear models were used for assemblage-level and species-habitat analyses, respectively.

4.2 Results

Assemblages of cavity-nesting birds in sites with <33% forest retention differed from medium and high retention sites. Tree Swallows, Northern Flickers and House Wrens, all species characteristic of more open habitats, had higher site-use, and Brown Creepers, an old-forest species, had lower site-use in lower retention sites. Changes in site-use by other species were not statistically significant. Within the buffer, the amount of forest retained had the strongest influence on the bird composition, while tree species and level of decay had a weaker influence. Site-use by Yellow-bellied Sapsuckers was higher in sites with a high density of large decaying aspen trees and live birch trees. Habitat measured over medium and large scales had no influence on the composition of bird assemblages.

Among the five species, relationships to spatial scale varied and the majority were most strongly related to habitat features measured at a scale no larger than the area of their territories. Relative to larger scales, habitat features within the buffer had a stronger influence on site-use by Yellow-bellied Sapsuckers, Tree Swallows and Brown Creepers. Habitat elements with high predictive value were the amount of forest retained, mean dbh of deciduous trees ≥12cm dbh, the density of large (≥25cm dbh) aspen (*Populus tremuloides*) trees with fungal conks (*Phellinus tremulae*) and the density of conifer trees. The use of sites by Northern Flickers and Boreal Chickadees was most strongly influenced by habitat measured at the large-scale. Habitat features with the strongest influence on species site-use were the proportion of landscape harvested, composed of wetland and composed of conifer-dominated forest.

The bird assemblages in partially-harvested buffers were similar to those in burned riparian forest, with some exceptions. Northern Flickers, Tree Swallows and House Wrens were indicators of burned forest while Pileated Woodpeckers, Boreal Chickadees and Red-breasted Nuthatches were observed in harvested buffers but not burns. Black-backed Woodpeckers, Northern Hawk Owls and Mountain Bluebirds were rare, but only observed in burns. Compared to intact forest and harvested buffers, burned sites had a higher density of large (≥25cm dbh) snags.

4.3 Management Implications

4.3.1 *Management for bird assemblages*

A coarse-filter management approach attempts to maintain a range of environmental conditions at multiple scales to provide habitat for most species (Noss 1987, Hunter et al. 1988). In my study, the fact that assemblages were not related to habitat at larger spatial scales suggests that effort to manage bird assemblages is best focused at the scale of the buffer. Differences in the composition of bird assemblages at low levels of forest retention suggest that within buffers a minimum of 33% of forest should be retained to maintain the composition of assemblages in higher retention and intact riparian buffers. Relative to the amount of retained forest, forest composition appeared less important.

4.3.2 *Management for individual species*

A fine-scale management approach tries to maintain specific habitat elements to conserve one or a few species of primary interest (Noss 1987, Hunter et al. 1988). For forest managers, species of interest are typically those negatively affected by harvesting that meet one or more of the following three criteria: 1) they rely on old-growth or early post-fire habitat, 2) they have declining regional abundances or 3) their activities strongly affect other species in forest ecosystems (i.e. keystone species).

Short rotation intervals, wildfire suppression and salvage logging have reduced the proportion of old-growth and early post-fire forest stands on the landscape (Schneider and Walsh 2005). As such, species relying on these habitat types for nesting or foraging have become a conservation priority for forest managers. Harvesting in boreal mixedwood has negative impacts on several old forest-associated cavity-nesting species including Three-toed Woodpeckers, Pileated Woodpeckers, Boreal Chickadees, Barred Owls, Red-breasted Nuthatches, White-breasted Nuthatches, Hairy Woodpeckers and Brown Creepers (Schieck et al. 2000, Schmiegelow and Mönkkonen 2002, Schieck and Song 2006). Consistent with this, I found that site use by Boreal Chickadees and Brown Creepers, the two species with sufficient data to analyse, was negatively affected by partial harvest.

Northern Flickers, Tree Swallows, Black-backed Woodpeckers, Mountain Bluebirds and Northern Hawk Owls are species associated with early post-fire habitat (Bock and Lynch 1970, Hutto 1995, Hoyt and Hannon 2002, Morissette et al. 2002, Hannah and Hoyt 2004, Saab et al. 2004, Hutto and Gallow 2006, Koivula and Schmiegelow 2007. Consistent with these studies, I observed higher use of burned forest relative to other forest types by Northern Flickers and Tree Swallows, and observed Black-backed Woodpeckers, Mountain Bluebirds and Northern Hawk Owls in burns only.

Yellow-bellied Sapsucker, Boreal Chickadee, Brown Creeper and Tree Swallow are either declining or at risk of decline in western Canada. In Saskatchewan, Yellow-bellied Sapsucker populations have declined over the past 20 years (Downes and Collins 2007). The abundance of Boreal Chickadees has decreased across Canada over the past 40 years (Downes and Collins 2007) and the species is among the five bird species in greatest decline across North America (73% population decline in 40 years; National Audubon Society 2008). An assessment of population size, habitat availability, and breeding potential for birds inhabiting the Boreal Plains suggests that Boreal Chickadees are of conservation priority while Yellow-bellied Sapsuckers are potentially at risk of decline and require close monitoring (Schonewille et al. 2007). Brown Creeper populations in western Canada appear stable, however data are limited and their dependence on old-growth forests suggests the potential for populations to decline as harvest activity increases and old-growth habitat availability decreases (Alberta Sustainable Resource Development 2003). Tree Swallows are among aerial insectivorous species whose abundances are declining across Canada (McCraken 2008).

Of my study species, only Yellow-bellied Sapsuckers and Northern Flickers are likely keystone species in the Boreal Plains ecozone as their cavities provide habitat for secondary-nesters (*Cooke personal communication*).

I identified a range of habitat conditions necessary to maintain habitat for species considered of conservation interest in harvested landscapes (Table 4.1). This was done using only variables that statistical models identified as having the greatest influence on these species' site-use. Yellow-bellied Sapsuckers, Boreal Chickadees, Brown Creepers, Northern Flickers, and Tree Swallows all meet the critera as species of conservation interest. However, Northern Flickers and Tree Swallows were positively affected by harvesting within buffers and thus will not be further discussed. To maintain habitat for Yellow-bellied Sapsuckers, Boreal Chickadees and Brown Creepers, the range in habitat conditions I identified suggests that within partially-harvested buffers:

1. At least 33% of forest should be retained.
2. In deciduous-dominated forest, a high density of large (≥ 25cm dbh) aspen trees with conks (>20 trees/ha) should be retained. In conifer-dominated stands, a high density of conifer trees (>20 trees/ha) should be retained.
3. Retained deciduous trees should be at least 21cm dbh with some reaching 36 cm dbh.

Furthermore, within a 211ha area of partially-harvested buffers, the proportion of landscape harvested should not exceed 20%.

The natural disturbance model is a hypothesis tested under active adaptive management approaches. Adaptive management allows managers to assess the effectiveness of different partial-harvest scenarios by monitoring ecological responses to them and contrasting these responses with ecological benchmarks (Gregory et al. 2006, McCarthy and Possingham 2007). To facilitate this approach, some conventional intact riparian buffer strips should be maintained on a portion of the landscape. Moreover, intact buffers will help alleviate potential risks faced by sensitive species in the application of management initiatives with uncertain outcomes.

4.3.3 *Management for burn-associated species*

Bird assemblages in partially-harvested buffers and burned forest were similar in this study however use of the two forest types differed among species, suggesting that the partial-harvest approach used in this study did not emulate recently burned riparian forest for cavity-nesting birds. Differences among species using recently burned forest and forest harvested to emulate recent burns has been observed in both upland and riparian forests (Hobson and Schieck 1999, Imbeau et al. 1999, Simon et al. 2002, Schieck and Song 2006, Kardynal 2007). Similar to these studies, my results indicate that burned forest represents a distinct habitat for some birds, in part due to an abundance of large standing snags. These conclusions are tentative however, as my sample size was low and some species were rare. Until additional studies with a higher sample size are conducted, I recommend that to conserve habitat for Black-backed Woodpeckers, Mountain Bluebirds, Northern Hawk Owls, all species I identified as burn-associates, and other post-fire specialists not observed in my study, recently burned riparian forest should be retained on the landscape. Because large snags were more abundant in burns and provide both nesting and foraging habitat for burn-associated species (Hutto 1995, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002), they should be left standing whenever possible. If not, the value of burned habitat for these species may be diminished and the abundance of species restricted to large snags for nesting and/or foraging sites may decline (Imbeau et al. 1999, Morissette et al. 2002)

4.4 Caveats

My results are relevant to riparian forest management in the Boreal Plains ecozone. However, some of my conclusions are preliminary because my statistical power to detect differences was low. This was due to low sample size, low density of birds and high variation among sites. Furthermore, I only examined assemblages up to four years post-harvesting, and responses by assemblages to harvesting may change for more than four years following disturbance (Schmiegelow et al. 1997). My study examined species habitat use only, and to better assess the value of harvested buffers to cavity-nesters, breeding success and survival rates should be evaluated for each study species. Finally, my study was conducted in the breeding season only and species-habitat associations may change seasonally (Strong and Bock 1990). Management implications are based on the range of habitat conditions I measured and conditions occurring outside that range were not considered.

4.5 Suggestions for Future Research

In my study, the level of buffer retention where the composition of assemblages shifted was only broadly defined as 33%. Future studies should determine a more precise level by relating species composition to a continuous range of retention. Specifically, the critical threshold level of retention where community structure shifts should be identified to help managers assess species "trade-offs" under different management scenarios and effectively manage for species of high conservation priority (Sallabanks et al. 2006).

Bird assemblages were not strongly related to habitat features measured at any scale suggesting they were structured by alternative factors. Martin and Eadie (1999) suggest that cavity-nesting bird communities are structured in part by the dependency of non-excavating species on excavating species for suitable nest sites, termed a nest-web. A research priority should be to investigate these functional relationships in riparian-using communities and to determine how they vary in response to different harvest prescriptions. This will help managers predict the response of bird communities to different management approaches and will elucidate species and habitat elements of key management interest to conserve the integrity of communities in partially-harvested buffers.

Finally, riparian partial-harvesting is not unique to wetlands, and is also applied in stream-side buffers (Lee et al. 2004). The response of cavity-nesting birds to the partial-harvesting of buffers adjacent to streams has not been assessed in the Boreal Plains ecozone and thus, the relevance of my management recommendations to stream-side forest is unclear.

Studies that address the limitations in my study should be conducted to confirm my results. The ability to assess bird abundance was limited in my study by small survey area, which was constrained by a short distance of harvesting along a watercourse edge (maximum ~400m). In future studies, forest operators should harvest longer strips to allow for larger survey area. Furthermore, studies should involve a larger sample size and increased statistical power to detect differences among treatments. This can be facilitated by forest operators harvesting more buffers of suitable forest composition in the study area. The number of recently burned riparian forests was limited in my study area and future investigation should occur in a region with a higher abundance of suitable burned sites. Additionally, many species have territories that extend beyond my sample area, and a larger sample area in future studies may increase species detectability and encompass a larger range of habitat variation. Moreover, the power to determine species associations to landscape-scale habitat may be higher by sampling individuals at a landscape-scale and relating their abundance to the context of the landscape; this approach may allow for a greater sample size.

Table 4.1. Relationships between Yellow-bellied Sapsucker (YBSA), Boreal Chickadee (BOCH) and Brown Creeper (BRCR) abundance and habitat measured at a) local (i.e. within buffer) and b) landscape (~211ha buffer around site) scales in Manitoba, 2006. Landscape-scale variables indicate the percentage of buffer composed of each variable. Colors indicate the mean abundance for each species in sites of each habitat class relative to their mean abundance over all sites. Light grey=lower relative abundance (0.1-0.8), dark grey=approximately equal relative abundance (0.8-1.2) and black=higher relative abundance (>1.2) where a value of 1.0 indicated equal abundance (i.e. no effect of habitat for that class). Red boxes encompass the range of habitat variation that includes suitable conditions for all three species.

a)	YBSA	BOCH	BRCR
Retention (% forest)			
Low	░		░
Medium	▓	▓	░
High	█	▓	█
Intact	░	▓	█
# Conifer trees/ha			
0-20	▓		░
20-100	█	░	░
100-200	▓	█	▓
>200	░	█	█

	YBSA	BOCH	BRCR
# Large aspen trees w/ conks/ha			
0-5	░	▓	░
5-20	░	░	░
20-60	▓	▓	█
>60	█	░	█
Mean DBH of deciduous trees >12cm dbh			
18-21	░	▓	░
21-23	▓	█	░
23-26	▓	░	░
26-36	▓	▓	█

b)	YBSA	BOCH	BRCR
Harvest (over previous 10 yrs)			
0	░	▓	▓
3-20	█	█	█
20-40	▓	░	░

	YBSA	BOCH	BRCR
Wetlands >6% forested			
0	░	█	▓
1-5	█	░	█
5-18	░	░	░

	YBSA	BOCH	BRCR
Conifer (>50% spp) dominated forest >10yrs			
0-5	▓	░	░
5-20	█	█	▓
20-60	░	░	▓

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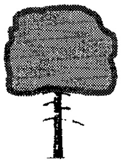
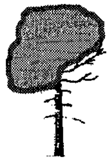
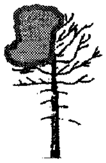
Appendix 2.1. Tree and downed woody material decay classes.

Class	Deciduous species	Coniferous species	Schematic
L1	Live/healthy; no decay in canopy branches or main trunk; note: it can have broken/dead limbs on lower part of trunk but all canopy should be alive	Live; no sign of death	
L2	Live with defects: may have dead or broken top, or dead limbs, >50% of canopy is live/green	Mostly live; some colour change in needles; <50% needles yellow/orange	
L3	Live with defects: may have dead or broken top, or dead limbs, <50% of canopy is live/green	Partly live; >50% of needles yellow/orange	
D1	Dead but recently killed; no live/green branches in canopy; twigs intact	Newly dead; needles still on tree	
D2	Dead; no live/green branches; twigs lost but most other branches intact, bark intact, wood hard	Dead; needles lost; all branches and twigs still on	
D3	Dead; snag with most branches intact; twigs and small branches lost; bark condition may be variable; wood hard	Dead; twigs lost; major branches intact	
D4	Dead; snag with only major branches remaining; wood condition variable	Dead; trunk mostly sound; only major branches present, if any	
D5	Dead; snag with no branches; often broken-top; wood condition variable; bark condition variable	Dead; broken top; few/no branches; wood condition variable but mostly sound	

D6	Dead; decomposing stump; wood very soft; bark peeling	Dead; stump; wood soft	
DWM decay classes (all species):			
1	Freshly fallen stem or little or no apparent decay; bark intact		
2	Some decay; wood remains relatively strong and intact; bark may or may not be present		
3	High decay; wood falls apart easily when kicked; usually very moist; moss may be present		

Appendix 2.2. Spearman rank correlation coefficients (rho) among local-, medium- and large-scale habitat variables. Data are from sites with non-overlapping buffers at both the medium- and large-scale (n=45). Significant correlations (rho >0.7) are bolded. For variable codes, see Table 2.1. Note: correlation coefficient values calculated from non-overlapping sites at each scale (local; n=66, medium; n=61, large; n=46) were similar to those shown.

LOCAL-SCALE	**DBH**	**RETEN-TION**	**ASPEN**	**SNAGS**	**CON-IFER**	**DWM**	**BIRCH**	
DBH	1							
Retention	.04	1						
ASPEN	.45	.54	1					
Snags	.10	.61	.65	1				
Conifer	-.06	.34	-.18	.13	1			
DWM	.00	-.01	.37	.22	-.18	1		
Birch	-.21	.32	.16	.45	.10	.25	1	
MEDIUM-SCALE	**HARVESTED**	**INTACT**	**WATER**	**WET-LAND**	**DECIDUOUS**	**CONIFER**	**MATURE**	**YOUNG**
Harvested	1							
Intact	-.59	1						
Water	-.24	-.25	1					
Wetland	-.11	.29	-.13	1				
Deciduous	-.43	**.74**	-.16	-.15	1			
Conifer	-.07	.33	-.13	.64	-.20	1		
Mature	-.60	**.94**	-.17	.23	.70	.31	1	
Young	.18	.06	-.18	.47	-.08	.20	-.18	1
LARGE-SCALE	**HARVESTED**	**INTACT**	**WATER**	**WET-LAND**	**DECIDUOUS**	**CONIFER**	**MATURE**	**YOUNG**
Harvested	1							
Intact	-.62	1						
Water	-.06	-.40	1					
Wetland	-.07	.08	-.20	1				
Deciduous	-.45	.68	-.21	-.41	1			
Conifer	-.16	.21	-.03	.68	-.34	1		
Mature	-.67	**.86**	-.27	.08	.60	.23	1	
Young	.27	-.01	.01	.19	-.20	.16	-.38	1

Appendix 2.3. Results of One-Sample Kolmogorov-Smirnoff (KS) analyses testing whether the abundance data of 5 bird species followed a Poisson distribution. P-value indicates the 2-tailed significance level. For species codes, see Table 2.4.

Scale	Parameter		YBSA	NOFL	BOCH	TRSW	BRCR
Local	N		64	64	63	64	64
	Mean		0.73	0.30	0.41	0.20	0.77
	Most extreme differences:	Absolute	0.08	0.02	0.06	0.09	0.16
		Positive	0.08	0.02	0.05	0.09	0.16
		Negative	-0.05	-0.01	-0.06	-0.05	-0.09
	KS Z-score		0.66	0.18	0.49	0.72	1.28
	P-value		0.77	1.00	0.97	0.68	0.08
Medium	N		61	61	60	61	61
	Mean		0.72	0.30	0.42	0.02	0.74
	Most extreme differences:	Absolute	0.09	0.03	0.07	0.09	0.15
		Positive	0.09	0.03	0.06	0.09	0.15
		Negative	-0.05	-0.01	-0.07	-0.05	-0.09
	KS Z-score		0.69	0.20	0.52	0.73	1.13
	P-value		0.74	1.00	0.95	0.70	0.16
Large	N		46	46	45	46	46
	Mean		0.74	0.20	0.38	0.17	0.70
	Most extreme differences:	Absolute	0.09	0.01	0.06	0.07	0.15
		Positive	0.09	0.00	0.05	0.07	0.15
		Negative	-0.07	-0.01	-0.06	-0.04	-0.12
	KS Z-score		0.60	0.03	0.37	0.49	1.04
	P-value		0.87	1.00	0.10	0.97	0.23

Appendix 2.4. Model coefficients for within-scale and multi-scale generalized linear models relating the abundance of Yellow-bellied Sapsucker (YBSA), Northern Flicker (NOFL), Boreal Chickadee (BOCH), Tree Swallow (TRSW), and Brown Creeper (BRCR) to habitat features at three spatial scales (local, medium, and large). Only models with significant support (ΔAICc<2.0), representing the final model subset, are shown. Within each subset, the model with the lowest ΔAICc value is bolded and was used in the among-scale model analyses. *B*= standardized regression coefficient, K= number of parameters estimated (including the intercept, regression coefficients, and residual variance), AICc= Akaike Information Criterion value corrected for small sample size (i.e. n/K<40), Δ AICc=measure of a models fit relative to the best model, w_i= probability that a model is the best among all candidate models (Burnham and Anderson 2002). All coefficients were calculated using the entire set of candidate models. For habitat codes, see Tables 2.1 and 2.2. For species codes see Table 2.4.

Species	Scale	Model #	% dev. Exp.	Terms	*B*	SE	n	K	AICc	Δ AICc	w_i
YBSA	Local	1	19	Intercept	0.82	2.48	66	5	84.15	1.07	0.26
				Area of site	-0.67	0.0001					
				Dbh	-1.09	0.05					
				Aspen	3.87	0.003					
		2	18	Intercept	0.44	2.48	66	5	84.81	1.73	0.19
				Area of site	-0.83	0.0001					
				Aspen	4.20	0.05					
				Birch	0.81	0.003					
		3	**18**	**Intercept**	**0.37**	**2.29**	**66**	**4**	**83.08**	**0.00**	**0.44**
				Area of site	**0.73**	**0.0001**					
				Aspen	**4.22**	**0.002**					
	Medium	1	6	Intercept	1.27	2.36	61	5	90.24	1.87	0.09
				Area of site	-1.26	0.0002					
				Intact	-0.70	0.88					
				Conifer	-1.05	2.05					
		2	6	Intercept	1.18	2.42	61	5	90.22	1.85	0.09
				Area of site	-1.41	0.0002					
				Water	0.73	1.40					
				Conifer	-1.23	1.98					
		3	8	Intercept	1.30	2.33	61	5	88.98	0.61	0.16
				Area of site	-1.39	0.0002					
				Wetland	1.38	7.00					
				Conifer	-1.73	2.88					
		4	5	Intercept	1.39	2.35	61	4	89.19	0.82	0.15
				Area of site	-1.38	0.0002					
				Intact	-1.16	0.86					
		5	4	Intercept	3.18	2.45	61	4	89.81	1.44	0.11
				Area of site	-1.62	0.0002					
				Water	0.90	1.42					
		6	**6**	**Intercept**	**1.13**	**2.37**	**61**	**4**	**88.37**	**0.00**	**0.22**
				Area of site	**-1.40**	**0.0002**					
				Conifer	**-1.30**	**1.97**					
		7	4	Intercept	1.50	2.35	61	4	90.01	1.64	0.10
				Area of site	-1.61	0.0002					
				Young	-0.71	3.01					
		8	4	Intercept	1.54	2.39	61	4	90.20	1.83	0.09
				Area of site	-1.70	0.0002					

				Harvested	0.65	0.84					
	Large	1	17	Intercept Area of site Intact Wetland Conifer	1.67 -1.45 -1.24 2.07 -1.96	2.98 0.0002 1.28 11.33 4.35	46	6	66.85	1.00	0.04
		2	17	Intercept Area of site Water Wetland Conifer	1.77 -2.04 1.41 2.16 -2.00	3.08 0.0002 2.17 11.02 4.29	46	6	66.50	0.65	0.05
		3	17	Intercept Area of site Wetland Conifer Young	2.01 -2.00 2.02 -2.02 -1.14	2.82 0.0002 10.96 4.29 3.76	46	6	66.91	1.06	0.04
		4	12	Intercept Area of site Intact Young	1.36 -1.07 -1.48 -1.33	2.90 0.0002 1.27 3.75	46	5	67.18	1.33	0.03
		5	11	Intercept Area of site Water Young	1.51 -1.76 1.33 -1.19	2.98 0.0002 2.19 3.72	46	5	67.77	1.92	0.02
		6	**14**	**Intercept** **Area of site** **Wetland** **Conifer**	**1.97** **-2.01** **2.07** **-2.08**	**2.93** **0.0002** **10.92** **4.17**	**46**	**5**	**65.85**	**0.00**	**0.06**
		7	8	Intercept Area of site Intact	1.30 -1.07 -1.48	3.01 0.0002 1.32	46	4	66.84	0.99	0.04
		8	8	Intercept Area of site Water	1.43 -1.76 1.50	3.10 0.0002 2.25	46	4	66.95	1.10	0.04
		9	7	Intercept Area of site Conifer	1.45 -1.48 -1.10	2.90 0.0002 2.19	46	4	67.57	1.72	0.03
		10	8	Intercept Area of site Young	1.70 -1.73 -1.32	2.83 0.0002 3.64	46	4	67.04	1.19	0.04
		11	20	Intercept Area of site Intact Water Wetland Deciduous	1.74 -1.77 -2.30 1.25 2.38 2.16	3.07 0.0002 4.54 2.53 11.74 4.52	46	7	67.51	1.66	0.03
		12	21	Intercept Area of site Intact Wetland Young Deciduous	1.79 -1.50 -2.38 2.24 -1.28 2.11	2.81 0.0002 4.59 11.48 3.97 4.51	46	7	67.01	1.16	0.04
		13	18	Intercept Area of site Intact	1.75 -1.54 -2.40	2.94 0.0002 4.37	46	6	66.26	0.41	0.05

				Wetland Deciduous	2.22 2.12	11.38 4.30					
		14	16	Intercept Area of site Wetland Conifer Deciduous	1.68 -1.47 2.04 -2.24 -1.15	3.00 0.0002 11.30 4.45 1.30	46	6	67.08	1.23	0.03
	Among	**1 (local)**	**18**	**Intercept** **Area of site** **Aspen**	**1.21** **-1.43** **3.47**	**3.27** **0.0002** **0.003**	**45**	**4**	**59.58**	**0.00**	**0.45**
		2 (local/med)	20	Intercept Area of site Aspen Conifer(m)	1.14 -1.33 3.14 -0.87	3.24 0.0002 0.003 2.45	45	5	61.17	1.59	0.20
		3 (local/lar)	24	Intercept Area of site Aspen Wetland(l) Conifer(l)	1.49 -1.67 3.01 1.73 -1.73	3.23 0.0002 0.003 11.94 4.51	45	6	60.91	1.33	0.23
NOFL	Local	1	27	Intercept Area of site Dbh Aspen Dwm	-1.82 0.33 4.07 -1.77 1.42	4.40 0.0002 0.05 0.01 3.11	66	6	56.54	0.55	0.19
		2	21	Intercept Area of site Dbh Snag	-1.53 0.33 3.55 -1.45	4.42 0.0002 0.05 0.01	66	5	57.77	1.78	0.10
		3	**24**	**Intercept** **Area of site** **Dbh** **Aspen**	**1.63** **0.37** **3.94** **-1.59**	**4.40** **0.0002** **0.05** **0.01**	**66**	**5**	**55.99**	**0.00**	**0.25**
		4	19	Intercept Area of site Dbh	-1.81 0.53 3.49	4.39 0.0002 0.053	66	4	56.99	1.00	0.15
	Medium	1	8	Intercept Area of site Harvested Intact Wetland	-1.36 1.17 -0.45 -0.74 -1.17	4.40 0.0002 1.67 1.78 15.23	61	6	57.03	1.94	0.11
		2	3	Intercept Area of site Harvested Intact	-1.24 1.04 -0.41 -0.94	4.29 0.0002 1.75 1.82	61	5	56.60	1.52	0.13
		3	7	Intercept Area of site Harvested Wetland	-1.26 0.98 0.07 -1.24	4.35 0.0002 1.30 15.17	61	5	55.11	0.03	0.28
		4	5	Intercept Area of site Harvested Conifer	-1.25 0.96 0.13 -1.10	4.26 0.0002 1.31 4.13	61	5	55.63	0.55	0.21
		5	**2**	**Intercept** **Area of site** **Harvested**	**-1.18** **0.77** **0.33**	**4.31** **0.0002** **1.33**	**61**	**4**	**55.08**	**0.00**	**0.28**

	Large	1	19	Intercept Area of site Water Wetland	-0.19 0.19 -0.95 -1.49	5.59 0.0004 4.72 42.61	46	5	37.66	1.59	0.06
		2	18	Intercept Area of site Wetland Conifer	-0.30 0.17 -0.99 -0.71	5.75 0.0004 45.55 14.17	46	5	37.94	1.87	0.06
		3	**16**	**Intercept** **Area of site** **Wetland**	**-0.30** **0.13** **-1.45**	**5.96** **0.0004** **41.13**	**46**	**4**	**36.07**	**0.00**	**0.14**
		4	14	Intercept Area of site Conifer	-0.16 -0.01 -1.41	5.34 0.0003 13.57	46	4	36.69	0.62	0.10
	Among	**1 (large)**	**17**	**Intercept** **Area of site** **Wetland(l)**	**-0.15** **-0.01** **-1.47**	**6.06** **0.0004** **41.27**	**45**	**4**	**35.50**	**0.00**	**1.00**
BOCH	Local	1	17	Intercept Area of site Conifer Snag	-1.50 1.10 3.53 0.79	3.65 0.0002 0.0004 0.007	65	5	69.10	1.77	0.23
		2	**16**	**Intercept** **Area of site** **Conifer**	**-1.36** **0.99** **3.52**	**3.57** **0.0002** **0.0004**	**65**	**4**	**67.33**	**0.00**	**0.55**
	Medium	1	36	Intercept Area of site Intact Wetland Conifer	-1.35 0.96 1.42 -2.79 3.33	3.65 0.0002 0.95 19.45 2.59	60	6	59.99	0.88	0.17
		2	28	Intercept Area of site Wetland Conifer Young	-1.52 1.25 -2.71 3.25 1.07	3.77 0.0002 22.09 2.67 2.69	60	6	60.91	1.80	0.11
		3	27	Intercept Area of site Wetland Conifer	-1.43 1.16 -2.84 3.68	3.64 0.0002 18.37 2.46	60	5	59.37	0.27	0.23
		4	32	Intercept Area of site Harvested Water Wetland Conifer	-1.37 1.40 -1.82 -0.89 -2.81 3.38	3.61 0.0002 1.04 2.12 20.71 2.71	60	7	60.87	1.77	0.11
		5	33	Intercept Area of site Harvested Wetland Conifer Young	-1.60 1.44 -1.65 -2.64 2.97 1.10	3.68 0.0002 1.07 24.42 2.87 2.75	60	7	60.69	1.59	0.12
		6	**31**	**Intercept** **Area of site** **Harvested** **Wetland** **Conifer**	**-1.55** **1.38** **-1.64** **-2.77** **3.38**	**3.59** **0.0002** **1.05** **19.96** **2.63**	**60**	**6**	**59.11**	**0.00**	**0.26**

	Large	1	44	Intercept Area of site Water Wetland Conifer Young	-2.71 2.71 1.04 -2.14 1.84 2.18	7.70 0.0004 5.05 24.12 3.47 3.28	45	7	43.39	1.66	0.06
		2	**41**	**Intercept** **Area of site** **Wetland** **Conifer** **Young**	**-2.96** **2.85** **-2.28** **2.14** **2.02**	**5.55** **0.0003** **24.17** **3.41** **2.74**	**45**	**6**	**41.73**	**0.00**	**0.14**
		3	34	Intercept Area of site Wetland Conifer	-2.74 2.62 -2.50 2.70	4.95 0.0003 20.74 3.16	45	5	42.45	0.72	0.10
		4	44	Intercept Area of site Intact Wetland Young Deciduous	-2.82 2.53 2.36 -2.30 2.05 -2.22	5.95 0.0004 3.56 26.27 2.73 3.66	45	7	43.38	1.65	0.06
	Among	**1 (large)**	**36**	**Intercept** **Area of site** **Wetland(l)** **Conifer(l)** **Young(l)**	**-2.87** **2.76** **-2.28** **2.14** **1.99**	**5.62** **0.0003** **24.06** **3.40** **2.75**	**44**	**6**	**41.63**	**0.00**	**0.54**
		2 (loc/lar)	46	Intercept Area of site Conifer Wetland(l) Conifer(l) Young(l)	-2.28 2.14 1.53 -2.05 0.39 0.26	5.90 0.0004 0.002 29.15 4.94 4.21	44	7	41.91	0.28	0.47
TRSW	Local	**1**	**71**	**Intercept** **Area of site** **Retention**	**-0.02** **0.20** **-3.40**	**5.61** **0.0003** **0.03**	**66**	**4**	**27.83**	**0.00**	**0.95**
	Medium	1	53	Intercept Area of site Harvested Intact Wetland Conifer Young	-0.29 -1.31 3.32 2.61 2.98 -1.70 -1.36	6.32 0.0005 5.92 5.72 18.94 8.00 15.03	61	8	49.35	0.03	0.36
		2	**49**	**Intercept** **Area of site** **Harvested** **Intact** **Wetland** **Conifer**	**-1.00** **-0.84** **3.42** **2.49** **2.56** **-1.56**	**5.53** **0.0004** **4.90** **4.95** **18.65** **9.34**	**61**	7	**49.32**	**0.00**	**0.37**
		3	45	Intercept Area of site Harvested Intact Wetland Young	0.34 -1.80 3.09 2.29 2.30 -1.19	5.91 0.0005 6.80 6.58 12.39 12.72	61	7	51.31	1.99	0.14
		4	42	Intercept	-0.28	5.08	61	6	51.27	1.94	0.14

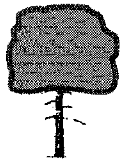
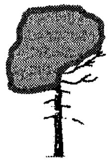
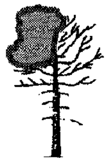
				Area of site Harvested Intact Wetland	-1.52 3.15 2.14 1.80	0.0004 5.78 5.77 12.04					
	Large	1	27	Intercept Area of site Intact Water	-0.22 0.85 -2.61 -2.20	6.62 0.0004 3.09 6.62	46	5	41.62	1.85	0.15
		2	35	Intercept Area of site Harvested Intact Water	-0.30 0.42 1.74 -1.17 -1.83	6.75 0.0004 4.94 3.80 7.68	46	6	41.00	1.23	0.20
		3	**31**	**Intercept** **Area of site** **Harvested** **Water**	**-0.20** **-0.09** **2.72** **-1.60**	**6.53** **0.0004** **4.17** **7.28**	**46**	**5**	**39.77**	**0.00**	**0.37**
		4	24	Intercept Area of site Harvested	-1.01 0.38 2.78	6.17 0.0004 3.77	46	4	40.33	0.56	0.28
	Among	1 (local)	73	Intercept Area of site Retention	0.26 -0.16 -2.65	9.13 0.0006 0.04	45	4	20.08	0.14	0.48
		2(loc/lar)	**86**	**Intercept** **Area of site** **Retention** **Harvested(l)** **Water(l)**	**-0.80** **0.68** **-1.46** **1.79** **0.57**	**26.87** **0.002** **0.11** **12.35** **15.15**	**45**	**6**	**19.94**	**0.00**	**0.52**
BRCR	Local	**1**	**15**	**Intercept** **Area of site** **Retention**	**-1.90** **1.33** **2.83**	**3.27** **0.0002** **0.008**	**66**	**4**	**155.48**	**0.00**	**0.49**
	Medium	**1**	**4**	**Intercept** **Area of site** **Intact**	**-0.46** **0.21** **1.58**	**3.35** **0.0002** **0.97**	**61**	**4**	**150.49**	**0.00**	**0.39**
		2	2	Intercept Area of site Conifer	-0.58 0.45 1.01	3.40 0.0002 1.54	61	4	151.80	1.31	0.20
		3	1	Intercept Area of site Young	-0.62 0.52 0.63	3.39 0.0002 2.78	61	4	152.29	1.80	0.16
		4	3	Intercept Area of site Harvested	-0.61 0.61 -1.17	3.33 0.0002 1.08	61	4	151.45	0.96	0.24
	Large	**1**	**5**	**Intercept** **Area of site** **Intact**	**-0.56** **0.25** **1.26**	**4.47** **0.0003** **1.61**	**46**	**4**	**111.98**	**0.00**	**0.22**
		2	2	Intercept Area of site Water	-0.91 0.85 0.002	4.66 0.0003 3.26	46	4	113.38	1.40	0.11
		3	2	Intercept Area of site Wetland	-0.92 0.84 0.09	4.59 0.0003 7.03	46	4	113.37	1.39	0.11
		4	2	Intercept Area of site Conifer	-0.93 0.85 0.15	4.55 0.0003 1.95	46	4	113.35	1.37	0.11

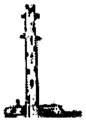
		5	2	Intercept Area of site Young	-1.00 0.91 0.44	4.59 0.0003 3.72	46	4	113.16	1.18	0.12
		6	4	Intercept Area of site Deciduous	-0.67 0.46 0.88	4.42 0.0003 1.46	46	4	112.66	0.68	0.15
		7	3	Intercept Area of site Harvested	-0.58 0.56 -0.87	4.66 0.0003 2.21	46	4	112.32	0.34	0.18
	Among	**1 (local)**	**18**	**Intercept** **Area of site** **Retention**	**-0.90** **0.34** **2.46**	**4.30** **0.0003** **0.01**	**45**	**4**	**105.55**	**0.00**	**0.53**

Appendix 2.5. Summary statistics for the number of each species detected per site during the study. Values are given for low (0-33%), medium (34-66%), and high (>66%) retention buffers, unharvested riparian forests, and all sites. For species codes, see Table 2.4.

Species	Low (n=11)				Medium (n=14)				High (n=22)				Unharvested (n=19)				All sites (n=66)			
	Mean	SE mean	Min	Max	Mean	SE mean	Min	Max	Mean	SE mean	Min	Max	Mean	SE mean	Min	Max	Mean	SE mean	Min	Max
YBSA	0.27	0.14	0	1	0.79	0.26	0	3	1.09	0.26	0	4	0.47	0.17	0	2	0.71	0.12	0	4
NOFL	0.55	0.20	0	2	0.21	0.11	0	1	0.18	0.10	0	2	0.32	0.17	0	3	0.29	0.07	0	3
HAWO	0.27	0.14	0	1	0.14	0.09	0	1	0.14	0.07	0	1	0.21	0.16	0	3	0.18	0.06	0	3
DOWO	0.18	0.18	0	2	0.00	0.00	0	0	0.18	0.10	0	2	0.11	0.07	0	1	0.12	0.05	0	2
PIWO	0.09	0.09	0	1	0.07	0.07	0	1	0.05	0.04	0	1	0.00	0.00	0	0	0.05	0.02	0	1
TTWO	0.09	0.09	0	1	0.00	0.00	0	0	0.00	0.00	0	0	0.00	0.00	0	0	0.02	0.01	0	1
BBWO	0.00	0.00	0	0	0.00	0.00	0	0	0.05	0.04	0	1	0.05	0.05	0	1	0.03	0.02	0	1
BCCH	1.00	0.55	0	5	1.07	0.45	0	5	0.68	0.21	0	3	0.53	0.26	0	4	0.77	0.16	0	5
BOCH	0.00	0.00	0	0	1.00	0.57	0	8	0.41	0.15	0	2	0.58	0.17	0	2	0.52	0.14	0	8
HOWR	0.64	0.45	0	5	0.14	0.14	0	2	0.27	0.11	0	2	0.05	0.05	0	1	0.24	0.09	0	5
TRSW	1.09	0.45	0	5	0.07	0.07	0	1	0.00	0.00	0	0	0.00	0.00	0	0	0.20	0.09	0	4
BRCR	0.18	0.18	0	2	0.43	0.20	0	2	1.05	0.31	0	4	0.95	0.23	0	3	0.74	0.14	0	4
RBNU	0.00	0.00	0	0	0.07	0.07	0	1	0.14	0.07	0	1	0.05	0.05	0	1	0.08	0.03	0	1
WBNU	0.00	0.00	0	0	0.00	0.00	0	0	0.00	0.00	0	0	0.26	0.18	0	3	0.08	0.05	0	3

Appendix 3.1. Tree decay, diameter at breast height (dbh), and burn classes.

Class	Deciduous species	Coniferous species	Schematic
L1	Live/healthy; no decay in canopy branches or main trunk; note: it can have broken/dead limbs on lower part of trunk but all canopy should be alive	Live; no sign of death	
L2	Live with defects: may have dead or broken top, or dead limbs, >50% of canopy is live/green	Mostly live; some colour change in needles; <50% needles yellow/orange	
L3	Live with defects: may have dead or broken top, or dead limbs, <50% of canopy is live/green	Partly live; >50% of needles yellow/orange	
D1	Dead but recently killed; no live/green branches in canopy; twigs intact	Newly dead; needles still on tree	
D2	Dead; no live/green branches; twigs lost but most other branches intact, bark intact, wood hard	Dead; needles lost; all branches and twigs still on	
D3	Dead; snag with most branches intact; twigs and small branches lost; bark condition may be variable; wood hard	Dead; twigs lost; major branches intact	
D4	Dead; snag with only major branches remaining; wood condition variable	Dead; trunk mostly sound; only major branches present, if any	
D5	Dead; snag with no branches; often broken-top; wood condition variable; bark condition variable	Dead; broken top; few/no branches; wood condition variable but mostly sound	

D6	Dead; decomposing stump; wood very soft; bark peeling	Dead; stump; wood soft	
DBH classes (all species):			
P	Pole: 4-12 cm		
S	Small: 12-18 cm		
M	Medium: 18-25 cm		
L	Large: >25 cm		
Burn severity classes (all species):			
0	No visible burn		
1	Burn visible <1m tall on trunk		
2	Burn on trunk only; no burned branches		
3	Burn visible on branches		
4	No branches intact; usually a standing snag		
5	Severely burned; usually a small stump		

Appendix 3.2.. Description, mean, minimum, and maximum values of habitat variables within each of three treatments and across all sites Variables that were significantly higher in a single treatment compared to all others are in bold (ANOVA, P<0.1). See Appendix 3.1 for burn and decay class descriptions.

Variable	**Description**	**Value**	**Treatment**			
			Burn (n=8)	**Harvest (n=12)**	**Intact (n=12)**	**All sites (n=32)**
1	Density of conifer trees (#/ha)	Mean	235.4	428.5	318.1	338.8
		(±SE)	(48.5)	(72.1)	(47.8)	(36.3)
		Minimum	0.0	116.7	41.7	0.0
		Maximum	391.7	991.7	600.0	991.7
2	Density of large live trembling aspen trees with fungal conks (*Phellinus tremulae*) (#/ha)	Mean	8.3	9.7	22.9	14.3
		(±SE)	(7.2)	(2.7)	(7.3)	(3.5)
		Minimum	0.0	0.0	0.0	0.0
		Maximum	58.3	25.0	91.7	91.7
3	Density of large snags (#/ha)	Mean	**108.3**	23.6	42.4	51.8
		(±SE)	(27.3)	(5.6)	(10.7)	(9.8)
		Minimum	0.0	0.0	0.0	0.0
		Maximum	241.7	50.0	125.0	241.7
4	Density of live birch trees (#/ha)	Mean	7.3	43.1	**130.6**	66.9
		(±SE)	(4.8)	(12.9)	(35.0)	(16.5)
		Minimum	0.0	0.0	0.0	0.0
		Maximum	33.3	141.7	433.3	433.3
5	Number of DWM/m	Mean	0.3	**0.6**	0.3	0.4
		(±SE)	(0.0)	(0.1)	(0.0)	(0.0)
		Minimum	0.2	0.3	0.1	0.1
		Maximum	0.5	0.9	0.5	0.9

Apprendix 3.2 cont…

Variable	Description	Value	Treatment			
			Burn (n=8)	**Harvest (n=12)**	**Intact (n=12)**	**All sites (n=32)**
6	Relative lake size	Mean (±SE) Minimum Maximum	0.04 (0.02) <0.01 0.12	0.06 (0.03) <0.01 0.31	0.14 (0.05) 0.01 0.47	0.09 (0.02) <0.01 0.47
7	Density of light to moderately burned conifer trees (#/ha)	Mean (±SE) Minimum Maximum	70.8 (21.4) 0.0 150.0	0.0 0.0 0.0	0.0 0.0 0.0	17.7 (7.5) 0.0 150.0
8	Proportion of site unharvested	Mean (±SE) Minimum Maximum	100.00 (0.00) 100.00 100.00	63.30 (3.17) 42.07 80.79	100.00 (0.00) 100.00 100.00	86.24 (3.39) 42.07 100.00

Appendix 3.3. Mean, standard error, minimum, maximum and sum of observations for 14 species and three nesting guilds of cavity-nesting birds in burned riparian forest sites.

Species	Mean #/site	SE mean	Min #/site	Max #/site	Sum
BBWO	0.13	0.125	0	1	1
BCCH	0.25	0.250	0	2	2
BOCH	0.00	0.000	0	0	0
BRCR	0.50	0.189	0	1	4
HAWO	0.00	0.000	0	0	0
HOWR	0.63	0.375	0	3	5
MOBL	0.25	0.250	0	2	2
NHOW	0.25	0.250	0	2	2
NOFL	1.25	0.491	0	4	10
PIWO	0.00	0.000	0	0	0
RBNU	0.00	0.000	0	0	0
TRSW	1.13	0.639	0	4	9
TTWO	0.25	0.250	0	2	2
YBSA	0.13	0.125	0	1	1
Primary nesters	2.75	0.750	0	6	22
Weak excavators	0.25	0.250	0	2	2
Secondary nesters	2.25	1.146	0	9	18

Appendix 3.4. Mean, standard error, minimum, maximum and sum of observations for 14 species and three nesting guilds of cavity-nesting birds in partially-harvested riparian forest sites.

Species	Mean #/site	SE mean	Min #/site	Max #/site	Sum
BBWO	0.00	0.000	0	0	0
BCCH	0.00	0.000	0	0	0
BOCH	0.25	0.179	0	2	3
BRCR	1.17	0.386	0	4	14
HAWO	0.00	0.000	0	0	0
HOWR	0.17	0.167	0	2	2
MOBL	0.00	0.000	0	0	0
NHOW	0.00	0.000	0	0	0
NOFL	0.67	0.225	0	2	8
PIWO	0.08	0.083	0	1	1
RBNU	0.08	0.083	0	1	1
TRSW	0.25	0.179	0	2	3
TTWO	0.08	0.083	0	1	1
YBSA	0.58	0.260	0	2	7
Primary nesters	1.67	0.497	0	6	20

Weak excavators	0.33	0.225	0	2	4
Secondary nesters	0.42	0.229	0	2	5

Appendix 3.5. Mean, standard error, minimum, maximum and sum of observations for 14 species and three nesting guilds of cavity-nesting birds in intact riparian forest sites.

Species	**Mean #/site**	**SE mean**	**Min #/site**	**Max #/site**	**Sum**
BBWO	0.00	0.000	0	0	0
BCCH	0.08	0.083	0	1	1
BOCH	0.50	0.230	0	2	6
BRCR	1.08	0.288	0	3	13
HAWO	0.33	0.188	0	2	4
HOWR	0.00	0.000	0	0	0
MOBL	0.00	0.000	0	0	0
NHOW	0.00	0.000	0	0	0
NOFL	0.08	0.083	0	1	1
PIWO	0.08	0.083	0	1	1
RBNU	0.33	0.142	0	1	4
TRSW	0.00	0.000	0	0	0
TTWO	0.08	0.083	0	1	1
YBSA	0.58	0.193	0	2	7
Primary nesters	1.58	0.398	0	5	19
Weak excavators	0.92	0.260	0	3	11
Secondary nesters	0.00	0.000	0	0	0