Distribution and breeding ecology of boreal and northern saw-whet owls

in the Boreal forests of Alberta, Canada

by

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Abstract

The boreal forest is an ecologically dynamic region with a long history of natural disturbances. These dynamics now run at a different and more rapid pace in Alberta because of land-use change, forestry, and developments in the energy industry. Although boreal owls *Aegolius funereus* and northern saw-whet owls *Aegolius acadicus* are considered forest associated species, little is known about their distribution and breeding ecology in the boreal region of Alberta. In this thesis, I address this gap by evaluating what influences the spatial distribution of these owls during the breeding period across Boreal Alberta, while also assessing their habitat use and breeding performance in forests affected by variable green tree retention harvesting in northwest Alberta. For the first objective, I used acoustic recordings from 667 autonomous recording units (ARU) to document the presence of the targeted species and modelled these locations with climate, biotic, landscape, and forest disturbance variables using boosted regression trees to explain spatial patterns in owl occurrence across the region. Second, I investigated owl habitat use and breeding performance during 2016 by placing and monitoring 169 nest boxes in forest patches characterized by a combination of available cover types and harvest retention levels. Average minimum winter temperature contributed most to explaining the final distribution of boreal owls, while the most important predictor of northern saw-whet owl distribution was amount of cropland at the home range scale (i.e., 564-m buffer around each ARU). Human disturbances affected distribution of these owl species differently. Northern saw-whet owls were most often found near openings created by linear disturbances at the nest site scale (i.e., 150-m buffers), while boreal owls were associated with landscapes containing low levels of linear disturbances at the home range scale. The nest box experiment provides the first Canadian assessment of the habitat use and breeding performance of boreal and northern saw-whet owls in

partially harvested boreal forests. Boreal owls chose nest boxes placed in conifer-dominated stands with at least 50% green tree retention. In contrast, northern saw-whet owls were more tolerant of forest harvest, breeding in boxes placed in deciduous-dominated stands with at least 20% post-harvest tree retention. Results confirm that northern saw-whet owls bred in northwestern Alberta at >55 °N, a significant extension of known breeding range, but suggest that boreal owls have low productivity in these forests as shown in other areas that have been studied. This thesis highlights the advantages of combining passive audio surveys with distribution modelling, and the potential of local networks of nest boxes to obtain detailed information about two cryptic and under-studied species in the boreal forest.

Preface

This thesis is the original work of Zoltán Domahidi. No part of this thesis has been previously published. I contributed to the concept formation, study design, and collected field data at Ecosystem Management Emulating Natural Disturbances (EMEND) project site. I led the data analysis, and manuscript composition. John R. Spence, Scott E. Nielsen, and Erin M. Bayne contributed to the concept formation, data analysis, and thesis edits.

Chapter 2 of this thesis was developed in collaboration with Julia Shonfield. I was responsible for data analysis and manuscript composition. Julia Shonfield assisted with digital recognizers, provided part of owl occurrence data, and contributed to manuscript edits.

Acoustic recordings were provided by the Bioacoustic Unit (BU) and Alberta Biodiversity Monitoring Institute (ABMI). Access to Alberta Vegetation Inventory data was facilitated by Daishowa-Marubeni International (DMI) and Alberta Agriculture and Forestry, while ABMI provided human disturbance and land-cover data.

The nest box study, which is part of this thesis, was approved by the Alberta Environment and Parks – Fish and Wildlife Division, under the 17-098_U Peace license, and received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Nesting preference of owls in managed boreal landscapes", AUP00001335, 22/10/2014.

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Table of contents

List of tables

List of figures

List of appendices

Appendix 1: Field deployment of Autonomous Recording Units (ARU) using two different designs: a) grids of five units with one unit at the corners of a 1,600-m square and one central unit and b) four-unit grids with one ARU at each corner of a 600-m square.

Appendix 2: Predictor variables used to model spatial distribution of boreal and northern saw-whet owls in the Boreal Forest Natural Region of Alberta, Canada.

Appendix 3: BRT model characteristics and their predictive performance for boreal owls (BOOW) and northern saw-whet owls (NSWO). All models were developed with 10-fold cross-validation on data from 677 sites, tree complexity of 5 and learning rate of 0.005.

Appendix 4: Nest box dimensions used in my experiment at Clear Hills, Alberta, following Korpimaki (1985) with modification of the door to increase ease of access while maintaining security of eggs and nestlings. The boxes were made of rough - sawn spruce lumber with a layer of 100 mm of woodchips in the bottom of each assembled box to increase insulation and prevent egg breakage. The entrance hole of 79 mm is suitable for both boreal owls *Aegolius funereus* and northern saw-whet owls *Aegolius acadicus*, while restricting access of larger owls or other frequent cavity nesting birds like wood ducks *Aix sponsa.*

Appendix 5: List of candidate models predicting nest box occupancy based on landscape characteristics and scale of measurement at Clear Hills, Alberta in 2016. Nest site (NS) scale represents a 150-m buffer, while home range (HR) scale data are calculated within a 564-m buffer drawn around each nest box. The positive (+) and negative (-) signs for model components indicate the predicted effect of the variable.

Chapter One: General Introduction

1.1 Background

Knowing where species are or where we should expect them to be in an ever-changing landscape is an essential question for every conservationist or resource manager. Habitat—the place where an organism is found—refers not only to the physical characteristics of an area but it is the sum of all the resources that result in occupancy and ensure survival and reproduction (Hall et al. 1997). Species distributions are influenced by a multitude of physical and biological variables and to adequately predict habitat use we need complex models that capture the effects and possible interactions of these relationships (Aarts et al. 2013).

Different activities like foraging, roosting, nesting, migration, or wintering are generally associated with various habitat types. Studies of habitat use at local scales, focusing on the immediate surroundings of occupied territories, are often biased because they include mainly small, homogeneous areas. Habitat analysis that incorporates multiple spatial scales is desirable because elements influencing species occurrence at local level might differ from those acting over larger areas (Munoz and Real 2013).

We can't explain with a high degree of certainty how animals locate suitable areas, especially for particularly secretive and highly mobile species, but we know that the process of habitat selection involves characteristics present at different spatial scales like those of distribution range, home range and within the home range (Johnson 1980). Animals may locate suitable areas at the home range level based on genetic information inherited from ancestors (Hutto 1985), while finer scale selection (i.e., choosing a nest site within a territory) may be the result of early learning and experience (Wiens 1970; Nielsen et al. 2013). Given the general principle that habitats are selected because of their characteristics, presence of an animal in a territory means that the habitat there can potentially provide some, if not all, the resources necessary to meet the needs of the individual (Johnson 1980).

There are still many unanswered questions about habitat selection, including which features of the environment are chosen and how interspecific interactions influence territory occupancy (Janes 1985). All habitats that seem suitable in terms of physical characteristics might not always be available. For example, predators or competitors can prevent access to food or nesting

resources otherwise present in the territory. In birds for example, hole nesting specialists like secondary cavity nesters require facilitation by primary cavity excavators but competition from other tree hole users can limit availability of suitable nesting holes (Bonar 2000; Cooke and Hannon 2011; Korpimaki and Hakkarainen 2012; Ouellet-Lapointe et al. 2012). Species that exploit cyclic food resources might not occupy all available habitats every year (Korpimaki and Hakkarainen 2012) and it can be a difficult task to estimate the distribution range for such species, and to understand the pattern of population dynamics that shapes their somewhat dynamic distributions. Habitat quality also changes over time and it should not be assessed based solely on the presence or density of a species (Jansson and Andren 2003), but instead be linked with population demographics (Van Horne 1983; Hall et al. 1997). However, in the case of nomadic species that do not occupy available territories every breeding season, checking territory occupancy is easier than finding active nests and occupancy might provide reasonable assessment of habitat quality (Sergio and Newton 2003).

Changes in habitat quality on landscapes can result from natural disturbances, human activities, or a combination of both. Alteration, fragmentation, or habitat loss affects organisms differently. For birds of prey, species responses to habitat alteration can vary due to subtle differences in their ecology (Hockey and Curtis 2009). Sensitivity to habitat loss and fragmentation is generally higher for habitat specialists and for species with narrow dietary spectra (Hockey and Curtis 2009), although some such species might actually benefit from low levels of fragmentation (Hinam and Clair 2008).

1.2 The Boreal forest and my target species

The Boreal forest has a circumpolar distribution, occupying 11% of Earth's dry surface, and representing more than a quarter of the global forested land. In North America, it extends from Alaska to Newfoundland as a continuous green belt, while in Canada it represents the largest biome that is spread over 58% of the total land area (Schindler and Lee 2010). Globally, nearly two-thirds of boreal forests are managed, and in Canada 35 to 40% of the Boreal forest is included in industrial or forestry management plans (Gauthier et al. 2015). Birds provide a multitude of ecosystem services like nutrient and energy recycling, seed dispersion, insect predation and can have a major effect on boreal forest health and regeneration (Niemi et al. 1998).

The boreal forest is home to two small, cavity nesting owls, the boreal owl (Tengmalm's owl in Eurasia) *Aegolius funereus* and the northern saw-whet owl *Aegolius acadicus*. Boreal owls are associated with forests that are older than 70 - 120 years, the average rotation age of managed stands in the Boreal region (Burton et al. 1999), while northern saw-whet owls are more opportunistic and will breed in young forests if nest boxes are provided (Moser 2002; Marks et al. 2015). Both are obligate cavity nesters, mainly nocturnal and they are specialized for a diet of small rodents (Hayward et al. 1993; Johnsgard 2002; Korpimaki and Hakkarainen 2012). Although they are widely distributed throughout their range, there is little published information about the distribution and ecology boreal and northern saw-whet owls within the Boreal region of North America (Semenchuk 1992).

1.2.1 The boreal owl

The boreal owl is a circumpolar species inhabiting mainly the Eurasian and North American boreal forests with patchy distribution south of this biome in high elevation coniferous forests. There are four subspecies in Eurasia (*Aegolius funereus funereus, A.f. magnus, A.f. pallens and A.f. caucasicus*) and one in North America *Aegolius funereus richardsoni* (Korpimaki and Hakkarainen 2012). The global population trend is considered stable by the International Union for Conservation of Nature (IUCN), while the Status of Birds in Canada 2014 (https://wildlife-species.canada.ca/bird-status/index-eng.aspx?sY=2014&sL=e) report considers the Canadian population secure with an estimated population size of 50,000 to 500,000 adults.

In northern Europe, outside the Boreal biome these owls breed in high-elevation conifer forests in Germany, Switzerland, Austria, Czech Republic, Slovakia and Romania, while in the south their breeding range extends to northern Spain, Italy, Slovenia, Croatia, Serbia, Greece and Bulgaria (Castro et al. 2008; Lopez et al. 2010; Korpimaki and Hakkarainen 2012; Brambilla et al. 2013).

In Canada, the breeding range of the boreal owl extends from central Yukon, across northern Saskatchewan, northern Manitoba, northern Ontario, central Quebec and Labrador to southern British Columbia, including central Alberta, central Saskatchewan, southern Manitoba western and central Ontario, southern Quebec and New Brunswick (Johnsgard 2002). South of the Boreal forest these owls breed in a relatively narrow life zone in the high altitude subalpine fir *Abies*

lasiocarpa habitat types within the northern Rocky Mountains (Hayward et al. 1993) and locally in the higher mountains of Washington, Idaho, Montana, Wyoming, Colorado and northern New Mexico (Johnsgard 2002). Although a considerable part of the North American range falls within Canada (Figure 1.1), very little published information is available about the distribution and breeding biology of boreal owls. This species is elusive, nesting usually occurs in relatively inaccessible areas, and most Canadian records come from fall migration studies, Breeding Bird Censuses and Nocturnal Owl Surveys. The latest breeding bird survey, for example, shows that the relative abundance of this species has increased in the Boreal Forest Natural Region, although there is a debate whether this change might be attributed to the range expansion of pileated woodpeckers *Hylatomus pileatus* or due to increased survey efforts in the north (Naturalists 2007). Distribution and habitat associations of breeding boreal owls have been documented using call-playback surveys in only a handful of studies in the US (Palmer 1987; Hayward et al. 1993; Lane et al. 2001). In the Northern Rocky Mountains of Idaho, boreal owls were encountered predominantly in the mixed conifer and trembling aspen *Populus tremuloides* stands while the most important foraging sites were in spruce-fir forests (Hayward et al. 1993). In northeast Minnesota, there were more encounters of singing male boreal owls in older upland-mixed forest stands than in regenerating forests (Lane et al. 2001). Results emphasize the importance of high-elevation, old conifer forests and promote the use of forestry practices that preserve some of these forests (Hayward 1997) in order to maintain boreal owls south of the Boreal biome.

Boreal owls are obligate cavity nesters, occupying tree holes excavated mainly by black woodpeckers *Dryocopus martius* in Europe (Lopez et al. 2010; Korpimaki and Hakkarainen 2012), pileated woodpeckers and occasionally northern flickers *Colaptes auratus* in North America (Hayward et al. 1993). Documenting owls breeding in natural cavities is difficult as suitable nesting hole densities can be less than 2.2 cavities/km^2 (Bonar 2000). In Alberta, only five confirmed breeding records of boreal owls have been published (Semenchuk 1992), but detailed habitat associations or nest site descriptions are not available from the peer-reviewed literature. When the exact location of a nest is unknown, breeding is assumed from the presence of calling males or encounters of fledgling owls (Stahlecker 1997).

The best data on the matter has been collected using artificial next boxes as this species occupies them readily (Hayward et al. 1993; Lopez et al. 2010; Korpimaki and Hakkarainen 2012). In Finland, the most successful breeding attempts were in boxes placed in spruce forests and < 200 m from agricultural fields and, within forested habitats, old forests were the most preferred nesting place (Korpimaki and Hakkarainen 2012). In Norway, boreal owls chose more often nest boxes hung in open habitats with scattered trees rather than breeding in closed forests (Sonerud 1985), while in the Pyrenees Mountains of Spain, owls preferred boxes placed at altitudes over 2000 m above sea level (Lopez et al. 2010). In eastern Canada, the four documented nesting attempts from Nova Scotia come from a nest box experiment and the occupied boxes were in boreal forests dominated by balsam fir *Abies balsamea* and white birch *Betula papyrifera* (Lauff 2009). It seems that summer roost sites differ from nesting sites and that they are chosen based on temperature, rather than vegetation type (Hayward et al. 1993).

Boreal owls start breeding in their second year with most pair bonds lasting for only one breeding season (Korpimaki and Hakkarainen 2012). Males attract females through advertising calls that are often displayed within 100 m from a suitable cavity, although unmated males can hoot at many cavities before they pair up (Korpimaki and Hakkarainen 2012; Hayward et al. 1993). Mated females dedicate all their time to laying and incubating eggs, rearing the brood in the first weeks after hatching, while males are responsible for hunting and delivery of prey (Korpimaki and Hakkarainen 2012). There are no plumage differences between sexes, but females are considerably larger than males. Adult males weigh 93–139 g, females 132–215 g, while wing length of males varies between 163–179 mm and females measure between 171.5 and 198 mm (Hayward and Hayward 1991; Johnsgard 2002). The overlap of measurements between the sexes means that only about 90% of the adults can be reliably aged and sexed based on weight and body dimensions. Identification of nestlings and juveniles to sex is impossible without a blood sample (Korpimaki and Hakkarainen 2012). In North American studies, egg numbers were 2–4 (Hayward et al. 1993), while in Finland, females laid 2–8 eggs depending on small rodent abundance (Korpimaki and Hakkarainen 2012). Owlets hatch after 28 days of incubation, leaving the nest after 28–36 days (Johnsgard 2002).

Post-natal dispersal of boreal owls mostly reflects movement of juveniles and females, as they can disperse as far as 500–600 km from the previous breeding site (Korpimaki and Hakkarainen

2012). Males tend to be more sedentary, although changes in location of nest holes have been observed within the home range (Andersson 1980; Hayward et al. 1993; Korpimaki and Hakkarainen 2012). Changes in breeding location is mainly driven by food abundance, predation risk or poor breeding performance in the previous year, while autumn movements are predominantly influenced by the fluctuations of the prey species and the search for areas where small rodents are abundant (Cheveau et al. 2004; Cote et al. 2007; Korpimaki and Hakkarainen 2012). This species exhibits both nomadic behavior and site tenacity (Andersson 1980). Birds move over large distances in search of abundant prey and might breed in different areas between peaks of rodent cycles (Wallin and Andersson 1981; Hayward et al. 1993; Korpimaki and Hakkarainen 2012).

1.2.2 The northern saw-whet owl

Distribution of the northern saw-whet owl is limited to North America. It is one of the most abundant owl species on the continent (Marks et al. 2015) and inhabits a variety of forested areas with trees large enough to host cavities suitable for nesting or roosting. There is little geographical variation among populations. In addition to the nominate subspecies, only one subspecies, *Aegolius acadicus brooksi,* is recognized and it is restricted to the Haida Gwaii, British Columbia, Canada (Gill and Cannings 1997). IUCN assessed the global population of this species as decreasing while the Status of Birds in Canada 2014 (https://wildlife-species.canada.ca/bird-status/index-eng.aspx?sY=2014&sL=e) report considers the Canadian population secure. Data about population size are poor; estimated population size varies from 500,000–5 million adult birds (Environment Canada) to 50,000–150,000 pairs (De Ruyck et al. 2012).

The breeding range of northern saw-whet owls (Figure 1.2) extends from southern Alaska to the mountains of southern California, southern New Mexico and northern Mexico, across central Alberta, central Saskatchewan, central Manitoba, central Ontario to southern Quebec, northern New Brunswick, Prince Edward Island and Nova Scotia, and south to West Virginia and western Maryland (Johnsgard 2002). They also breed locally in the Mexican highlands and the mountains of eastern Tennessee and western North Carolina (Johnsgard 2002). Northern saw-whet owls are secretive and strictly nocturnal. Despite being widely distributed within Canada there is very little information published about key aspects of breeding biology and ecology in northern

populations of this species, with most of the published research coming from the United States (US). The northern limit of the distribution range is unclear; however, during the last survey of breeding birds in Alberta there were more owls recorded in the northwestern parts of the province, while a decrease in relative abundance was noted in the Parkland Natural Region relative to data from previous years (Naturalists 2007). The positive change the north probably reflects increased survey effort, while the decrease in the southern part of the province may be attributed to conversion of forested land to agriculture or human developments (Naturalists 2007).

Northern saw-whet owls are highly mobile and, although there is large inter-annual fluctuation in captured owl numbers at banding stations (Brittain et al. 2009; De Ruyck et al. 2012; Frye 2012; Kanda et al. 2016), population trends seem to be synchronized over large areas (De Ruyck et al. 2012). Fall movements are monitored extensively using mark-recapture methods in the eastern US and southeastern Canada, with more than 275,000 owls banded between 1960–2015 (Marks et al. 2015), but little has been published from western and northwestern Canada (Priestley et al. 2010).

In addition to use of next boxes, a popular technique for studying nocturnal owls and their habitat associations involves point counts of owls responding to conspecific calls broadcasted from an audio device (Johnson et al. 1981). In Idaho, occurrence of northern saw-whet owls was associated with forest patches of ponderosa pine *Pinus ponderosa*, Douglas-fir *Pseudotsuga menziesii,* and owls were found more frequently in landscapes with higher proportion of open terrain (grassland and shrubland) within 1 km of point counts (Scholer et al. 2014). In the east-central Sierra Nevada, US, owl occupancy rates were not influenced by snag density but increased with elevation and percentage of open canopy at the territory scale (Groce and Morrison 2010). In the forests of the Southern Appalachians, northern saw-whet owls were found only above elevations of 1360 m in spruce-fir and spruce-fir/northern hardwood ecotone zones (Milling et al. 1997), while in Central Mexico they occupied high elevation, contiguous pure pine stands, highly fragmented oak forests and oak-pine mixed forests (Ortiz-Pulido and Lara 2014). In east-central Alberta, northern saw-whet owls are among the most common nocturnal raptor species showing no clear association with particular habitat types, although they are absent from landscapes containing small and isolated forest patches (Grossman et al. 2008).

Northern saw-whet owls are secondary cavity nesters, relying on the availability of suitable cavities excavated mainly by northern flickers (Johnsgard 2002) and they readily occupy artificial nest boxes placed in a variety of forested habitats. Published reports of owls breeding in natural cavities is scant, most of the breeding information coming from nest box experiments, as with boreal owls. In Oregon, US, northern saw-whet owls successfully bred in boxes placed in young (2–5 years old) hybrid poplar plantations surrounded by shrub steppe desert and irrigated croplands (Moser 2002; Marks et al. 2015). In the shrub steppe deserts of southwestern Idaho dominated by big sagebrush *Artemisia tridentata,* northern saw-whet owls occupied nest boxes hung in willows *Salix* spp., Russian olives *Elaeagnus angustifolia* and black locusts *Robinia pseudoacacia* (Marks and Doremus 2000). A long-term experiment from northwestern South Dakota showed that owls occupied nest boxes placed in wooded ravines dominated by green ash *Fraxinus pennsylvanica* and stands of ponderosa pine surrounded by grasslands (Drilling 2013). Providing next boxes for these owls in the boreal forests of Quebec, Canada, documented the expansion of their known breeding range north of 50 °N (Buidin et al. 2006). In Alberta, Canada, northern saw-whet owls occupied nest boxes placed in mature mixed wood forests interspersed with agricultural fields and human developments in the boreal forest - aspen parkland transition zone (Hinam and Clair 2008).

Northern saw-whet owls start breeding in their second year and young couples breed as successfully as pairs formed by older birds (Marks et al. 2015). Male owls use advertising calls to attract females and sometimes form pair with more than one female (Johnsgard 2002; Marks et al. 2015). Given the migratory behavior of the species, pair bonds usually do not last beyond the breeding season and breeding birds do not show high degree of site fidelity (Drilling 2013). Plumage of northern saw-whet owls is similar between the sexes and sexual size dimorphism is less notable than in the boreal owl, making field identification of males and females almost impossible based on appearance. Adult males and females weigh 54–96 g and 65–124 g, respectively, while wing length of males varies between 133.5–139 mm and females measure 135–146 mm (Johnsgard 2002). Nonbreeding adults may be sexed in hand based on combination of weight and wing length, but it is unreliable in some cases due to large overlaps (Paxton and Watts 2008). Females lay 5–6 eggs and owlets hatch after 26–28 days of incubation, leaving the nest after 28–34 days (Johnsgard 2002).

Data about post-natal dispersal of northern saw-whet owls suggests very low site fidelity of both sexes of adults and nestlings. In Oregon, only one of 109 nestlings banded returned to breed in the same area while just three out of 52 marked adults occupied nest boxes in more than one year (Marks et al. 2015). A similar pattern was found in southwestern Idaho, where only one of 52 marked adults returned to breed in subsequent years (Marks and Doremus 2000). The fact that there are few re-nesting attempts of adult birds suggest that northern saw-whet owls are largely nomadic, at least in some parts of their range, and will breed in any area with abundant prey and adequate cavities (Marks and Doremus 2000).

1.3 Research questions

In my thesis work, I investigated the distribution and nesting ecology of boreal and northern saw-whet owls in the Boreal region of Alberta.

I was first interested to find out the relative importance of environmental conditions, vegetation characteristics, or biological components as factors of owl occurrence. Subsequently, I became interested in using the most influential components to model and predict spatial distribution of these species throughout the Boreal Forest Natural Region (BNR) of Alberta. Environmental conditions are factors that act over large areas and include elements of temperature and precipitation that are thought to limit species distribution. Pinpointing vegetation associations of these owls is crucial for owl conservation in the ever-changing boreal landscape. Most of data concerning my focal species come from forested regions that are substantially different from the boreal forests of Alberta, and so these descriptive aspects are new and useful for understanding the owls. Due to the different bioclimatic and vegetation conditions (Boonstra et al. 2016), natural disturbance regimes, patterns of resource extraction and the forest management approach (Burton et al. 1999; Gauthier et al. 2015), relationships observed in the high elevation conifer forests in the US and Europe, and the intensively managed forests of Fennoscandia and eastern US might differ for populations of northern forests in Alberta. Biological components I considered in this study were the presence/absence of facilitators (represented by the pileated woodpecker as main cavity producer for owls), competitors (simultaneous occurrence of boreal and northern saw-whet owls at a site) and predators (presence of great horned owl *Bubo*

virginianus). To confirm the presence/absence of the target species I used sound recordings from Autonomous Recording Units (ARU) placed at various locations in the BNR of Alberta during 2013–2016. All elements considered were examined at both nest site and home range scales.

To contribute to the understanding of breeding ecology of boreal and northern saw-whet owls in the boreal forests of Alberta, I initiated a nest box experiment in the Peace Region of northwestern Alberta, an area that is impacted by logging operations. Green tree retention forestry provides an alternative to traditional clearcutting that may have conservation benefits as it preserves some of the original forest structure (Woodley et al. 2006), is thought to maintain biodiversity (Work et al. 2004) and the cavity-nesting bird community (Schieck and Song 2006; Cooke and Hannon 2011). Nonetheless, it is important to understand what key features of the landscape should be included preferentially in retention prescriptions (Cooke and Hannon 2011). I used vegetation characteristics at both nest site and home range scales to investigate which habitat components are associated with and best predict owl occupancy. I measured reproductive success by repeated visits to occupied nest boxes. Understanding how cavity nesting owls respond to the disturbance created by forestry addresses the efficacy of forest management techniques to preserve old forest specialists, and in this thesis, I show that variable retention harvest has useful conservation potential.

Chapter Two: Spatial distribution of the boreal owl and northern saw-whet owl in the Boreal forest

2.1 Introduction

Understanding where and why species occur is essential to developing conservation or management plans, especially for rare (Rabinowitz 1981) or endangered taxa (Rushton et al. 2004; Munoz et al. 2005; Guisan et al. 2013; Harms et al. 2017). Spatial distribution of species is largely shaped in relation to environmental heterogeneity in climate, land cover, natural disturbance history, and biotic interactions in combination with constraints provided by species dispersal ability (MacArthur 1972; Block and Brennan 1993; Castro et al. 2008; Chen et al. 2011). While distribution patterns are often observed at national or continental scales, species distributions are scale dependent (Lehmkuhl and Raphael 1993; Scholer et al. 2014) with the main drivers changing with spatial resolution (Lopez-Lopez et al. 2006; Munoz and Real 2013; Di Vittori and Lopez-Lopez 2014). Nonetheless, species distribution is frequently explained in relation to land cover variables collected at a local scale, where the habitat is more homogeneous (Munoz and Real 2013).

One of the most common issues in studies of spatial distributions are where to sample the target species and what environmental data to collect (Rushton et al. 2004). Our knowledge of species distribution is limited to surveyed areas and in the case of a wide-ranging, unevenly distributed, rare, or cryptic species this becomes especially problematic. Records are often concentrated in small areas or dispersed with low sampling effort over large areas. Since it is impractical to allocate survey effort evenly across the entire landscape, researchers use models of spatial distribution to predict species occurrence for conservation planning and wildlife management (Buckland and Elston 1993). Indeed, more precise predictions of species' distributions are now occurring due to advances in survey techniques (Campos-Cerqueira and Aide 2016; Shonfield and Bayne 2017a), statistical modelling, and increased use of geographic information systems (Osborne et al. 2001; Elith et al. 2006; Young et al. 2012). Recently, the use of machine learning techniques, such as classification and regression trees, including boosted classification and regression trees, in ecology, has allowed identification of underlying processes and complex relationships between predictor and response variables in addition to providing accurate predictions (De'ath and Fabricius 2000; De'ath 2007; Elith et al. 2008). These techniques are

especially valuable for study of rare species found in remote areas, where obtaining large enough sample sizes for modelling and statistical analysis is problematic but for which knowledge of distribution is especially critical for conservation (Mi et al. 2014; Mi et al. 2017).

Owls are nocturnal birds of prey and despite having large estimated populations and wide ranges –which can span multiple states/provinces or even continents–data for many species are inadequate. Attempts to estimate population size and distribution rely mainly on national programs developed for monitoring multiple species like the Raptor Grid in Finland (Saurola 2009), and the Breeding Bird Survey (Sauer et al. 2013) and the Christmas Bird Count (Dunn et al. 2005) in North America. However, such surveys are not satisfactory for many owl species as they fail to cover species breeding in remote areas or are not conducted at the appropriate season to correctly estimate breeding population (Kirk and Hyslop 1998; Saurola 2009).

In North America, studies of owl habitat use are predominantly focused on species classified as at risk, such as the burrowing owl *Athene cunicularia* in the Canadian prairies (Haug and Oliphant 1990) and the northern spotted owl *Strix occidentalis* on the northwest coast of North America (Carey et al. 1990; Lehmkuhl and Raphael 1993; Folliard et al. 2000). Many other species remain understudied, although their conservation status is uncertain.

Boreal and northern saw-whet owls are two small, nocturnal species, with widespread and uneven distributions across North America (Johnsgard 2002). Here, habitat use of boreal owls has been studied in a few locations outside of Canada. In Colorado, USA, they inhabited high-elevation mature conifer forests (Palmer 1987), while in the Northern Rocky Mountains, USA, patch size was not important for breeding site selection, and owls used both conifer (82%) and aspen (18%) stands (Hayward et al. 1993; Hayward 1997). In Minnesota, USA, boreal owls were widely distributed at low abundance, and preferred upland mixed forests to low elevation conifer stands (Lane et al. 2001). For northern saw-whet owls, research about breeding habitat characteristics have been conducted in the Sierra Nevada, USA, where they preferred forested areas that included open canopy components at microhabitat (20 ha) scale (Groce and Morrison 2010). Similar results come from the Boise National Forest, Idaho, USA, where northern saw-whet owls were associated with forests that were found on flat terrain and contained higher proportion of non-forest land cover at 0.4-km scale (Scholer et al. 2014). In Canada, habitat use of breeding northern saw-whet owls was studied on Haida Gwaii, where they were often found in

landscapes containing a mixture of old and young forests (Gill and Cannings 1997). In central Alberta, they occupied landscapes that were more connected and contained between 16–100% forest cover (Grossman et al. 2008).

For breeding, these owls are associated with forests, where they occupy abandoned nesting cavities of pileated woodpeckers and northern flickers (Hayward et al. 1993; Johnsgard 2002). In North America, the effect of woodpeckers as nesting facilitators on the distribution of boreal and northern saw-whet owls is unknown. In Finland, however, including the presence of primary excavators improved climate-landcover distribution models of owls (Heikkinen et al. 2007), while modelling the overlap between the distribution of boreal owls and black woodpeckers in the Italian Alps, was used to inform management decisions for the conservation of boreal owls (Brambilla et al. 2013). We know from previous studies that predators of owls, can affect the distribution of boreal owls. For example, Sonerud (1985) found out that the presence of mammalian predators in Norway, determined boreal owls to choose more frequently nest boxes placed in clear cuts than closed, old spruce stands. In Finland, boreal owls preferred nest boxes that were outside Ural owl *Strix uralensis* territories (Korpimaki and Hakkarainen 2012). (Grossman et al. 2008) suggesting that the presence of great horned owls influences distribution and habitat use of breeding northern saw-whet owls in the agricultural landscape of central Alberta but did not test it directly.

Although the Boreal forest region of Alberta is experiencing major landscape changes due to developments in agriculture, forestry, and oil and gas industry that could pose conservation risks, factors associated with habitat use and distribution of these two small owls have not been studied in detail. In this study I used acoustic recordings from autonomous recording units (ARU) to document habitat associations of boreal and northern saw-whet owls in the Boreal Forest Natural Region of Alberta during the breeding season. I modelled the distribution of these owls using Boosted Regression Trees following Elith et al. (2008) to explore the capacity of climate, biotic, landscape, and forest disturbance variables to explain patterns in owl occurrence at two spatial scales. From this work, I predict the spatial distribution of boreal and northern saw-whet owls throughout Alberta's Boreal, generate distribution maps by selecting variables that allow highest predictive capacity, and discuss management implications.

2.2 Methods

2.2.1 Study area

The Boreal Forest Natural Region of Alberta is the largest natural region of the province, spanning over 58% (381,046 km^2) (Figure 2.1). Undulating forested plains and extensive wetlands dominate this region, with elevations ranging from 150 m at the Alberta-Northwest Territories border to 1100 m near the Alberta-British Columbia border (NaturalRegionsCommittee 2006). The climate is characterized by short, cool summers and long, cold winters, with a 5 °C temperature difference in mean annual temperature between the warmest and coldest parts of the region (NaturalRegionsCommittee 2006). Most of the precipitation falls during April–August, with the wettest regions experiencing 535 mm of annual average precipitation, and the driest areas receiving on average 377 mm (NaturalRegionsCommittee 2006).

Deciduous, mixed and conifer forest, interspersed with wetlands dominate the upland areas. However, cultivated areas are present where the length of the growing season and soils allow crop growth (NaturalRegionsCommittee 2006). Areas suited for cultivation grow barley and forage crops, and nearly 50% of the land has been converted to agriculture (NaturalRegionsCommittee 2006). In the remaining forested area trembling aspen and balsam poplar are the dominant broadleaf tree species, while conifer species include tamarack, white, and black spruce in moist areas, and lodgepole and jack pine in drier areas (NaturalRegionsCommittee 2006). Significant industrial forestry is conducted throughout the region, while natural gas and oil exploration and extraction is locally intensive.

2.2.2 Acoustic data

Recordings from SM2+ Song Meters (Wildlife Acoustics, Inc., Maynard, Massachusetts, USA), placed in grids (Appendix 1) throughout the region were analyzed for call of the species of interest (boreal and northern saw-whet owls, great horned owls and pileated woodpeckers). All units were deployed for at least two weeks between mid-March and mid-May. ARU placement, recording settings, and data storage protocols followed the methodology described by Shonfield and Bayne (2017b). Data from each unit was considered to represent an independent survey site and I assumed that the presence of a species within the detection radius of an ARU was evidence

that the site contains at least some elements necessary for breeding and survival (Block and Brennan 1993). Compared to the traditional point count protocol of hooting owls that typically uses call broadcasts to elicit responses of conspecifics, passive acoustic monitoring has numerous advantages (for a comprehensive review see Shonfield and Bayne 2017a), including collecting more information, creating permanent records that can be re-analyzed to answer additional questions (Campos-Cerqueira and Aide 2016), and reducing survey bias from drawing in owls in otherwise un-used areas as a reaction to call broadcasts (Kissling et al. 2010). Higher detection probabilities obtained from call broadcast surveys (Zuberogoitia et al. 2011) are compensated by the high number of survey opportunities provided by numerous scheduled recordings (Shonfield and Bayne 2017a).

I used Song Scope (Wildlife Acoustics, Inc., Maynard, Massachusetts, USA) to identify vocalizations of the target species, build automated species recognition programs (recognizers), and process recordings as described by Shonfield and Bayne (2017b). Recognizers were trained to detect the long-distance drumming, and both the '*cackle'* and '*wuk'* calls (Tremain et al. 2008) of pileated woodpeckers in the sound recordings. Presence of great horned owls was indicated by their territorial hoot (Kinstler 2009), while occurrence of boreal and northern saw-whet owls was identified from their staccato song (Bondrup-Nielsen 1984), and advertising call (Cannings 1993), respectively. For every station and each species, the list of detections generated by the recognizers were checked for Type I error, and validation stopped at the first confirmed detection. Although it is possible that multiple ARUs detected the same owl or the same unit detected different singing individuals during the study period, these possibilities do not affect the outcome of a presence or absence survey.

2.2.3   Predictor variables

To investigate the importance, and possible effects of climate, landscape characteristics, and biological factors on owl occurrence, I used an initial set of 38 predictor variables, including most of the factors thought to influence owl distributions (Appendix 2). Climatic variables were obtained for each surveyed location by using ClimateAB software package (Government of Alberta, Alberta Sustainable Resource Development, see http://www.srd.alberta.ca/MapsFormsPublications/Publications/AD.aspx), that calculates values

from climate grids based on monthly, annual, decadal, and 30-year normal climate data from 1901 to 2006 provided by standard weather stations across Alberta (Mbogga et al. 2010).

Landscape and human disturbance variables were obtained from the ABMI Wall-to-Wall Land Cover Map Version 2.1 (ABMIw2wLCV2010v1.0) and Human Footprint Inventory 2014 Version 3 from the Alberta Biodiversity Monitoring Institute (ABMI) (see: http://www.abmi.ca.). Area covered by each dominant forest cover type was calculated as percentage of total forested area. Each ARU was considered the center of a territory, and landscape variables were compiled at two scales, based on radius around the location of each unit: the nest site scale at 150-m radius, and the home range scale at 564-m radius. I did this by drawing concentric buffers around each ARU in ArcMap 10.4.1 (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute), and calculating percent area of the buffer covered by each cover type. Male boreal owls consistently vocalize within 100 m of potential nest sites (Hayward et al. 1993), and without knowing the exact location of a nest, I considered that the nest site scale (7 ha) was an adequate area to describe habitat associations in immediate vicinity of potential nest sites of owls while maintaining the spatial separation of observation sites. Hinam and Clair (2008) reported average home range size of northern saw-whet owls in Alberta at 89.4 ha (range: 11.7–137.0 ha), which is about half the area of boreal owl home ranges in Fennoscandia at 150 to 230 ha (Korpimaki and Hakkarainen 2012). My choice of the home range scale (analyzed as 100 ha) certainly includes the core area for most owls and provides information about breeding habitat across a wider area. At this scale, buffer overlap of certain ARUs was unavoidable however, it is consistent with field studies in the Northern Rocky Mountains, USA where 50% overlap of boreal owl territories was observed (Hayward et al. 1993).

The extent of human disturbance at my sites were quantified as percent area disturbed by the following three different human activities: industrial disturbances, hard linear and soft linear disturbances. Industrial disturbances included urban and rural industrial sites, mines, borrow pits, well sites and wind generation sites. Landscape alterations resulting from these disturbances were considered the most severe as they resulted in permanent loss of forested land and suitable hunting grounds for owls. As above, linear disturbances were divided in two categories: hard linear disturbances (impermeable surface layers like roads, railways, and runways), and soft

linear disturbances (vegetated linear disturbances that include transmission lines, pipelines, seismic lines, vegetated roads and trails, and vegetated verges of roads and trails). Hard linear surfaces are not suitable for owl foraging, fragment the landscape and negatively affect owls (Boves and Belthoff 2012; Silva et al. 2012). Soft linear disturbances can create hunting opportunities for owls, but at high densities can contribute to severe habitat fragmentation (Pattison et al. 2016). Fragmentation of forested habitats respectively, limits reproductive success of owls (Hinam and Clair 2008).

Incorporating biotic interactions into models improves predictions of owl distributions at certain scales (Heikkinen et al. 2007). In my study, I considered the presence/absence of nesting facilitators, competitors, or potential predators. I analyzed pileated woodpeckers as facilitators of owl nesting because both boreal and northern saw-whet owls breed almost exclusively in cavities created by primary cavity excavators (Hayward et al. 1993; Johnsgard 2002; Korpimaki and Hakkarainen 2012). Interspecific competition was modeled as the simultaneous presence of boreal and northern saw-whet owls at the same site, because these owls potentially compete for nest sites and prey, although there are few published accounts of competition between the two species (Lane 1991). Interactions within the nocturnal predator guild can alter spatial distribution of owls (Kajtoch et al. 2016; Morosinotto et al. 2017). Reports of direct predation are rare, however in Finland, the presence of Ural owls influenced habitat use by boreal owls (Korpimaki and Hakkarainen 2012), and in the agriculturally fragmented landscape of central Alberta, patch selection of northern saw-whet owls was influenced by the presence of great horned owls (Grossman et al. 2008). Thus, I used the presence/absence of great horned owl as an indicator of predation pressure.

2.2.4 Analysis

Models explaining and predicting owl distribution were developed in R (R Core Team 2015), using Boosted Regression Trees (BRT) implemented in the *gbm* (Version 2.1.3, Ridgeway 2007) and *dismo* (Version 1.1–4, Elith and Leathwick 2017) packages. A ten-fold cross validation method (Elith et al. 2008) was used to identify meta-parameter (De'ath 2007) settings, to build models, and make predictions across the region. Final model settings used a bagging fraction of 0.5, and a learning rate of 0.005 to build at least 1000 trees (Elith et al. 2008) and allowed complex interactions among predictors using a tree complexity of 5. To test the influence of

landscape features, climate, and biotic interactions on owl distribution, a global model containing all predictors was first built, and additional models then fit by successively eliminating the climatic, disturbance, and biotic parameters. Since the primary emphasis was on prediction, models were compared for their predictive capacity (Appendix 3) using the Area Under the Receiver Operating Characteristic Curve (AUC) and predictive deviance (Elith et al. 2008). Variables identified as unimportant to prediction by the model simplification function were dropped (Elith et al. 2008). The outputs generated by the final BRT model were used to examine the relative importance of predictor variables, and spatial distribution of predictions.

For spatial prediction, I used ArcMap to create a fishnet of 1 km x 1 km (100 ha) squares over the Boreal region of Alberta. This scale seemed reasonable to accommodate core areas for breeding owls and to allow identification at an operational level of areas of high probability for use by owls. Information about predictor variables retained in the final model were compiled as discussed above, using the centroids for each square, and used to create raster maps for each predictor. No predictions were made for squares with their centroids outside the Boreal boundary. Rasters then were combined into a raster brick, imported into R, and the overall model was used to predict values to each raster cell. These results were exported and visualized in ArcMap.

2.3 Results

Acoustic recordings were obtained from 677 Boreal sites in Alberta. Boreal owls were detected at 263 (39%) sites, northern saw-whet owls at 103 (15%) sites, and both species were present at 38 (5%) sites. Final models included only climatic, disturbance, and landscape variables for both species, as biotic components did not improve accuracy of model predictions. Predictive deviance of models was quite similar for both boreal owls (36.2%) and northern saw-whet owls (39.2%); with similar prediction accuracy for both northern saw-whet owls (AUC = 0.893) and boreal owls (AUC = 0.880). The top ten contributors for the models for both species contained seven climatic variables and three variables related to vegetation cover and human disturbance. Precipitation as snow, mean annual precipitation, average winter precipitation, and mean annual temperature were present in models for both species.

The strongest variable influencing predictions of boreal owl distribution was climate, expressed as the average minimum winter temperature. This variable contributed 24% to the model predictions and together with four additional climatic variables made a total contribution of 50% to the final model (Figure 2.2). Average winter minimum temperatures at sites where owls were detected was lower (-21.9 °C ± 0.11 °C; x̄ ± SE) than at unoccupied sites (-20.4 °C ± 0.04 °C). The most important landscape characteristic predicting boreal owl distribution during breeding was forest cover at the nest site scale, while linear disturbances at the home range scale affected the spatial distribution of boreal owls more than dominant landcover types at the home range scale (Figure 2.2). Used sites had less forest cover (44.9% ± 2.4) than unused sites (61.4% ± 1.8) and used sites were less affected (2.4% ± 0.2) by soft linear disturbances than unused sites (4.1% ± 0.1). Partial responses for some of the key variables indicated that boreal owls mostly occurred in cool environments with cold winters. Such responses also suggested that boreal owls chose areas including grassland in low amounts and avoided potential nest sites found in contiguous forests with soft linear disturbances (Figure 2.3). The predicted distribution of boreal owls (Figure 2.4) resulted from interactions among explanatory variables and reinforced the suitability of areas that offer a combination of nest sites with forest openings and home ranges with less than 20% grassland cover, found in landscapes characterized by cold winters (Figure 2.5).

The presence of cropland within the home range of potential breeders was most important in the final model for the distribution of northern saw-whet owl and made a 27% contribution to the final model (Figure 2.6). Cropland accounted for 0 to 88% (18.6% ± 2.9) of the area within the home range scale around used sample points (ARUs), while the average cultivated area represented only an average of 0.4% (range 0–91%) of the buffer around unused sites. Important climatic factors affecting northern saw-whet owl distribution included average temperatures both in the warmest and coldest period of the year, as well as precipitation as snow and average summer temperatures (Figure 2.6). Northern saw-whet owls occupied areas that were more likely to be cooler during summer (15.8 °C ± 0.05 °C vs. 16.1 °C ± 0.02 °C) and warmer during winter (- 17.0 °C ± 0.2 °C vs -18.0 °C ± 0.07 °C) than unused sites. Partial dependency plots indicated that northern saw-whet owls were most common during the breeding season on landscapes where cultivated land was interspersed with deciduous-dominated forests. Dependency plots also showed that northern saw-whet owls nested close to forest edges associated with soft linear disturbances as long they were cool during the summer with no substantial precipitation as snow

(Figure 2.7) The predicted distribution of northern saw-whet owls (Figure 2.8) highlighted the suitability of environments that offer combinations of cool summers and reduced snowfall, located in forested landscapes including agricultural fields as at least 20% of the home range (Figure 2.9).

2.4 Discussion

This study is among the few investigating factors affecting the spatial distribution of boreal and northern saw-whet owls in North America, and the first to rank importance of landscape features that predict owl presence during the breeding season using BRTs. Most of the predictor variables built into the models for both species were expressed as non-linear functions, and despite being 'noisy' in areas where data was scarce (sampling effort was much more intense in the eastern and southern part of the Boreal compared to the west and north), or relationships were influenced by multiple interactions (Leathwick et al. 2008), the models improve our understanding of factors that drive owl distributions, including those that are changing (e.g., climate and land use). Below I discuss the roles of climate, landcover type and human disturbance in shaping owl distributions.

2.4.1 Climate

My distribution models for boreal and northern saw-whet owls contained seven climatic variables among the top-ten predictors. Precipitation as snow, mean annual temperature, mean annual precipitation, and average winter precipitation were present in the final models for both species. This is consistent with previous studies highlighting the role of climatic elements in shaping distributions of birds of prey at regional or continental scales (Heikkinen et al. 2007; Castro et al. 2008; Brambilla et al. 2013).

Both winter and summer temperatures were important components of owl distribution models, although effects differed between the two species. Boreal owls seem to respond to seasonal extremes, while northern saw-whet owls are apparently influenced by temperatures during the warmest and coldest month of the year. Boreal owls were mostly present in cool areas of Alberta (Figure 2.3 a and Figure 2.3 b), supporting results for this species from the Pyrenees Mountains of Europe were breeding territories were confined to areas where mean January temperatures were between 1 °C and -3 °C maximum, and July temperatures did not exceed 17 °C (Lopez et al. 2010). Some boreal owls nesting in conifer forests of the Northern Rocky Mountains, USA,

experienced heat stress at roosting sites warmer that 18 °C (Hayward et al. 1993), although my work suggests that they prefer sites where average maximum summer temperatures are > 19 °C in Alberta. Although experimental data on heat tolerance of boreal owls is lacking, it is possible that their distribution is limited by the availability of sites with cool microclimate during the hottest part of the year. In spotted owls nesting in hot environments, for example, use of a habitat was strongly promoted by the availability of roost sites with cool microclimate created by dense, multi-layered canopies (Barrows 1981). My models showed that northern saw-whet owls also prefer cool environments, but they seem to be even more limited by heat, as the mean temperature of the warmest month was the second most influential predictor variable (Figure 2.7 b). Northern saw-whet owls were consistently found at sites <15 °C, and this seems to corroborate their inability to thermoregulate with rising humidity and ambient temperature (Ligon 1969).

Although rainfall was included among the top-ten variables in models for both species, its influence on owl distributions is unclear. Perhaps it is not the amount of precipitation but the timing and intensity of rainfall that is important. There is a direct link, for example, between rainfall patterns and breeding productivity of peregrine falcons *Falco peregrinus* nesting in cold climates (Anctil et al. 2014). The amount of precipitation as snow was important for both owl species. While conversion of precipitation as snow to actual snow depth is a complex procedure, using a snow/water ratio of 10:1 suggests that higher amounts of precipitation will result in deeper snow cover. Although snowfall amounts < 115–120 mm had a small negative effect, annual snowfall > 140–150 mm had a clear negative effect on boreal owl distribution (Figure 2.3 c). Nonetheless, boreal owls are often mentioned as a species that breeds in areas with deep snow cover (Hayward et al. 1993; Korpimaki and Hakkarainen 2012), although the specific relationship between their distribution and snow has not been tested in the Boreal Alberta. Male boreal owls start breeding early in the spring and often stay close to their former nest sites during the winter (Korpimaki and Hakkarainen 2012). Thin snow cover during winter increased their winter survival, but reduced nest productivity, apparently by depleting prey reserves by the time owlets hatch (Lehikoinen et al. 2011). It seems that the best areas for boreal owls are those that receive between 115–145 mm precipitation as snow (Figure 2.3 c). The smaller northern saw-whet owls showed strong affinity to areas where precipitation as snow does not exceed 100–105 mm and avoided breeding in areas where annual snowfall exceeds 125 mm (Figure 2.7 c). Boreal

owls are able locate prey moving both on top and underneath the snow and can plunge through moderately thick snow layers (Sonerud 1986). The northern saw-whet owl is much smaller and lighter, more like the northern pygmy owl *Glaucidium gnoma,* and likely would be able to catch prey moving only on top of or close to the snow surface (Sonerud 1986).

2.4.2 Landcover type

Boreal and northern saw-whet owls are forest associated species; thus, I expected their distribution to be strongly influenced by forest type and cover. My results underscore that, although landscape components are important, the key features explaining regional distribution differ between these species, and act at different scale.

For boreal owls, amount of forest cover at the nest site scale was the only landcover variable included among the top-ten explanatory variables. Previous nesting and roosting habitat suitability models developed for this owl in the in west-central Alberta used only components related to density of large trees, canopy closure, canopy height, and tree species composition. Similarly, distribution of potential boreal owl habitat in Idaho was inferred from occurrence of forested land in the subalpine-fir zone and Douglas-fir woodlands (Hayward et al. 1993), while their presence in northeast Minnesota was related to preferred habitat features within the forested landscape (Lane et al. 2001). However, in agreement with results from the Sierra Madre, northwestern USA, my model suggests that boreal owls across Alberta breed mainly in forests with openings close to the nest site and are not influenced consistently by the character of the surrounding forest (Herren et al. 1996).

Studies of boreal owls in northern Italy showed that probability of occurrence within a 1 km x 1 km square was positively associated with areas having at least 10% permanent grassland cover (Brambilla et al. 2013). In my study, grassland cover was more important at the home range scale, and the most often used areas by boreal owls included < 20% permanent grasslands (Figure 2.3 f). In Finland, nesting owls were most commonly found in areas less than 200 m from cultivated areas (Korpimaki and Hakkarainen 2012); however, amount of cropland was not retained in my final model for Alberta. These results may differ because I treated grasslands and croplands separately, while agricultural fields in Finland contained hayfields associated with high prey abundance (Korpimaki and Hakkarainen 2012).

In contrast, I found that presence of croplands within the forested landscape of northern Alberta were the main drivers of northern saw-whet owl occurrence at the home range scale, contributing nearly 27% to the final model. It seems that increasing cropland cover within the home range scale has a positive influence on the probability of owl occurrence (Figure 2.7 a), highlighting the importance of forests within agricultural landscapes. At the same time, northern saw-whet owls were most frequently encountered in areas where forests within their home range contained > 80% deciduous stands (Figure 2.7 d). The association of these owls with areas containing a mixture of cultivated lands and deciduous forests is not surprising since northern saw-whet owls were previously found to be the most common owl species in the agricultural landscape of central Alberta (Grossman et al. 2008). My results confirm that they frequently settle in forest patches near openings (Figure 2.7 f), reinforcing findings of Groce and Morrison (2010), who suggested that occupancy probability of northern saw-whet owls in the Sierra Nevada, USA, was positively correlated with percent of open canopy at local scale (20 ha). Although occurrence of northern saw-whet owls in southern Idaho was positively related to point counts with a higher proportion of open grassland and shrubland within 1-km radius (Scholer et al. 2014), the presence of grassland or shrubland had little explanatory power in my model.

2.4.3 Disturbances

Large-scale industrial activities are commonly viewed as the main cause of habitat destruction and fragmentation. Although industrial activity is present in most of the boreal region of Alberta, my results do not show strong effects on owl distribution. This was a surprise, given the fact that sampling effort was more intense in the eastern and southern part of the Boreal, where most industrial developments occur. Current research demonstrated that oil and gas exploration, and extraction in the western Canadian boreal region has important negative effects on migratory birds (Van Wilgenburg et al. 2013), and seismic lines are the major source of forest fragmentation in the boreal region (Pattison et al. 2016). Although the effects of these linear disturbances on owls are yet unknown, roads increased owl mortality through collision near high-traffic areas that cross forested habitats (Silva et al. 2012). Often considered less invasive than industrial developments, in my models, linear disturbances were included among the ten best contributing variables for both owl species, although it influenced them differently. For boreal owls, both soft and hard linear disturbances were among the top-ten contributors at the

home range scales. Soft linear disturbances represented 0–19% of boreal owl territories in Alberta, with the model demonstrating that amounts over 4–5% negatively affect the probability of boreal owl presence (Figure 2.3 e). In contrast, the distribution of northern saw-whet owls was influenced by the presence of soft linear disturbances within potential nest sites, with these owls preferring nesting close to forest edges created by soft linear disturbances (Figure 2.7 e). Although high levels of habitat fragmentation limited reproductive success of northern saw-whet owls in central Alberta (Hinam and Clair 2008), my study suggests that they do not avoid breeding near areas impacted by soft linear disturbances if the landscape is not highly fragmented at the scale of the home range. Presence of northern saw-whet owls near vegetated linear features confirm findings that—within forested habitats—open areas created by edges might provide improved hunting opportunities (Hayward and Garton 1988).

2.5 Conclusions and management implications

BRTs are becoming more popular for modelling habitat selection, and have been successfully used to model the distribution of New Zealand's diadromous and non-diadromous fish species (Leathwick et al. 2008), identify habitat associations of wintering great bustards *Otis tarda dybowskii* in China (Mi et al. 2014), and predict rare species distribution in under sampled areas (Mi et al. 2017). The ability to handle considerable number of predictors, identify and rank important variables, model interactions, while maintaining strong predictive performance, make BRTs an effective technique that combines elements of statistical and machine learning methods (De'ath 2007; Elith et al. 2008). The predictive models developed here for owls have multiple potential uses, including development of maps predicting owl occurrence in remote locations, assisting land managers in planning exploration and resource extraction, and identifying priority areas for future research and conservation. These models however, have their limitations and can be improved by adding more sample points from the western part of the Boreal, and considering different variables and using different scales. Because the Boreal forest is undergoing continuous change, landcover and disturbance variables used here are likely to change. As new information becomes available—including factors affecting owl distribution—distribution maps can be easily updated to reflect these changes.

Although presence of these forest-associated owls is most often related to landscape characteristics, my study demonstrates that climate has a strong influence on predicting their

potential distribution at regional scale. For example, various temperature data and precipitation as snow were major predictive components—at least at the scales considered by this study—of the final models. This is particularly important in the Boreal parts of Alberta because climate stations in the Boreal regions of western Canada have reported temperature increases of 2–4 °C in the past 40 years with forecasts predicting winter temperature increases of 4–6 °C (Schindler and Lee 2010). According to these projections, the temperature increase will not be matched by increases in precipitation, favoring the shift of forests to the drier climate space currently occupied by the woodland/shrubland biome (Gauthier et al. 2015).

Such a shift would likely be problematic for the boreal owl because it is associated with old coniferous forests. The distribution predicted in Figure 2.4 shows that already large areas of the southern parts of the boreal region are unsuitable for this species. It is possible that these owls can occupy different forest types, as studies in Idaho suggest strong selection for some component of aspen stands (Hayward et al. 1993); however, more research needed to investigate the effect of climate on the boreal owl. My results indicate that research about forest management and timber harvesting techniques should consider climate and landscape changes in addressing conservation concerns for boreal owls. According to the model developed here, even if all other predictor values remain at their mean, temperature increases alone could limit the distribution of this species.

Climate however, is not the only thing changing in the western Boreal region. Warming and drying could facilitate increases in frequency and severity of natural disturbances, pathogen outbreaks and species invasions (Dale et al. 2001), and thereby reduce forest cover. Forestry will remain a strong industry in the region and continue to alter the amount and configuration of forest cover. Although timber extraction practices emulating natural disturbances might become industry standard in Alberta, logging can still reduce densities of primary excavators (Bonar 2001) and thereby indirectly influence owl distribution. To minimize this potential effect, it is essential that placement of unharvested retention patches is considered in future industrial development in relation to habitat requirements needed for both cavity producers and owls.

Increased industrial activity is projected, including activities that create linear disturbances such as exploration and development of in-situ oil sands across more than 4 million hectares in northern Alberta (Schindler and Lee 2010). Because such linear disturbances seem to influence

boreal owls, spatial distribution of this species could be affected by future developments in the energy sector.

Agriculture is another important landscape component in boreal Alberta. Although presence of croplands did not have a strong influence on the distribution of boreal owls, in Finland, they avoided large, open areas, and agricultural fields (Korpimaki and Hakkarainen 2012). In contrast, cultivated areas were positively associated with the presence of northern saw-whet owls, and were the principal factor shaping their distribution. The predicted distribution of northern saw-whet owls in this region is patchy, with most of the suitable areas found in the southern and western parts of Alberta where climate and topography are most suited for agriculture. However, conversion of forested land to agriculture is still happening in the north, and this together with the warming climate could contribute to northward range shift of this species which presently reaches its northern limit in the Boreal zone of Alberta. Range expansion may be facilitated if contiguous forests will open up by increases in open canopy landscape —including croplands— as northern saw-whet owls persisted in the highly fragmented agricultural region of central Alberta if forest patches were connected, and large enough to accommodate an owl territory (Grossman et al. 2008).

2.6 Figures
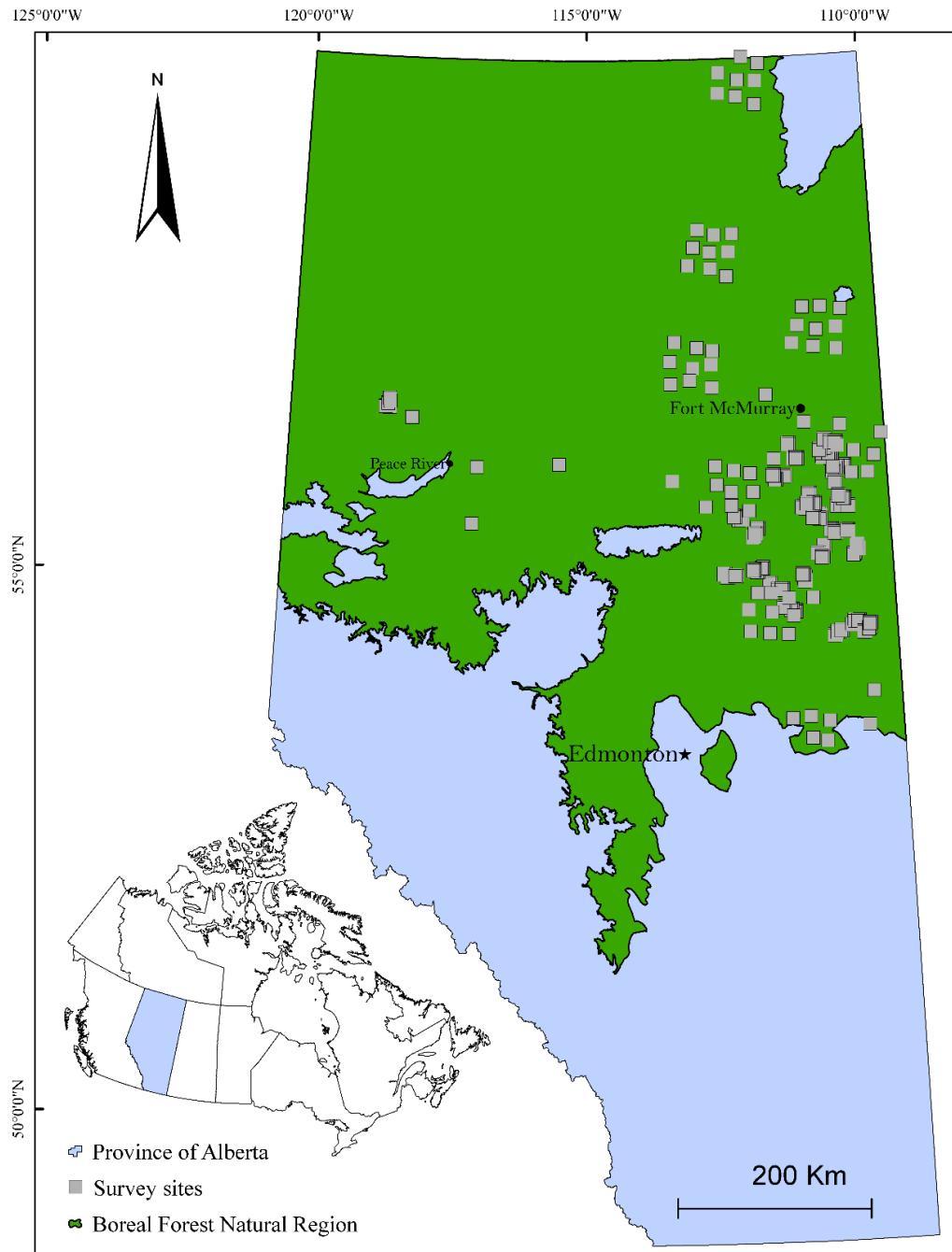
Figure 2.1: Map showing the extent of the Boreal Forest Natural Region and location of survey sites (n = 677) within the Province of Alberta, Canada.
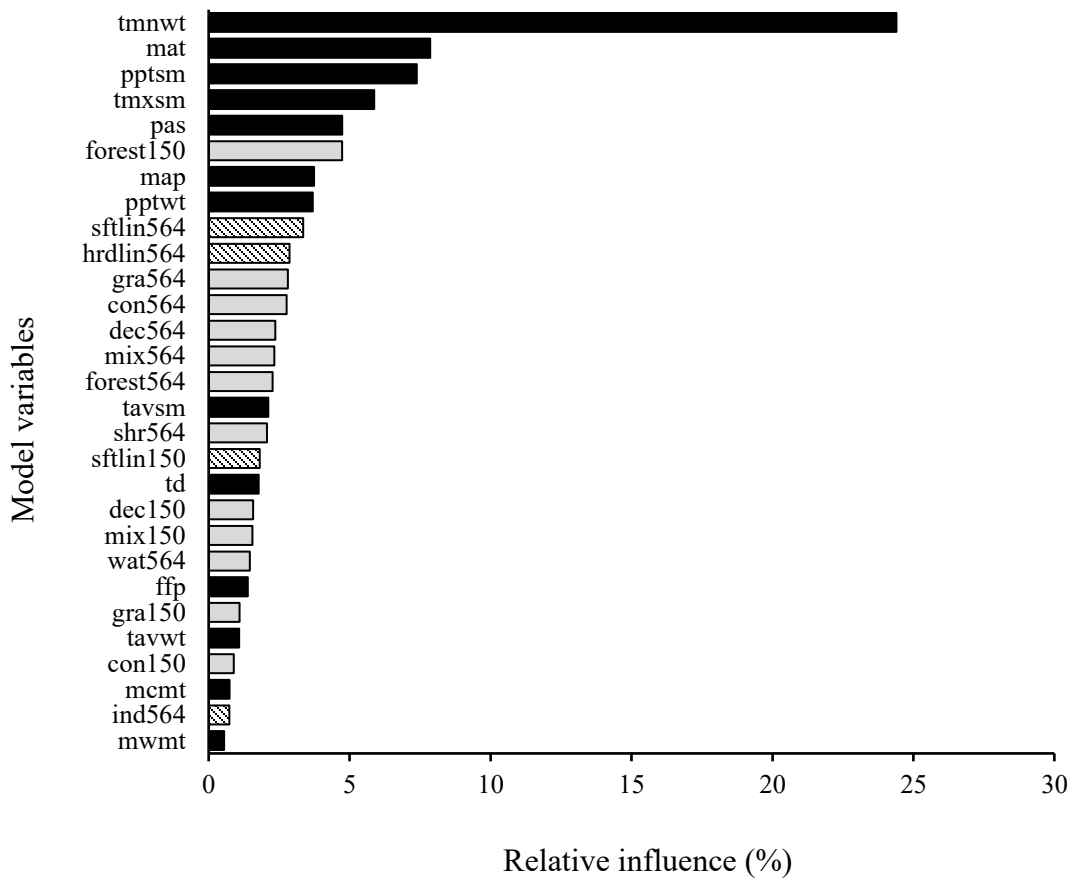
Figure 2.2: Relative influence (%) of predictor variables (n = 29) in the final BRT model explaining distribution of boreal owl in the Boreal Forest Natural Region of Alberta, Canada. The model was developed using 10-fold cross-validation on data from 677 sites, with a learning rate of 0.005 and tree complexity of 5. Dark bars represent climatic variables, gray bars show landcover types, while bars with diagonal stripes correspond to variables related to human disturbance. For variable explanation see Appendix
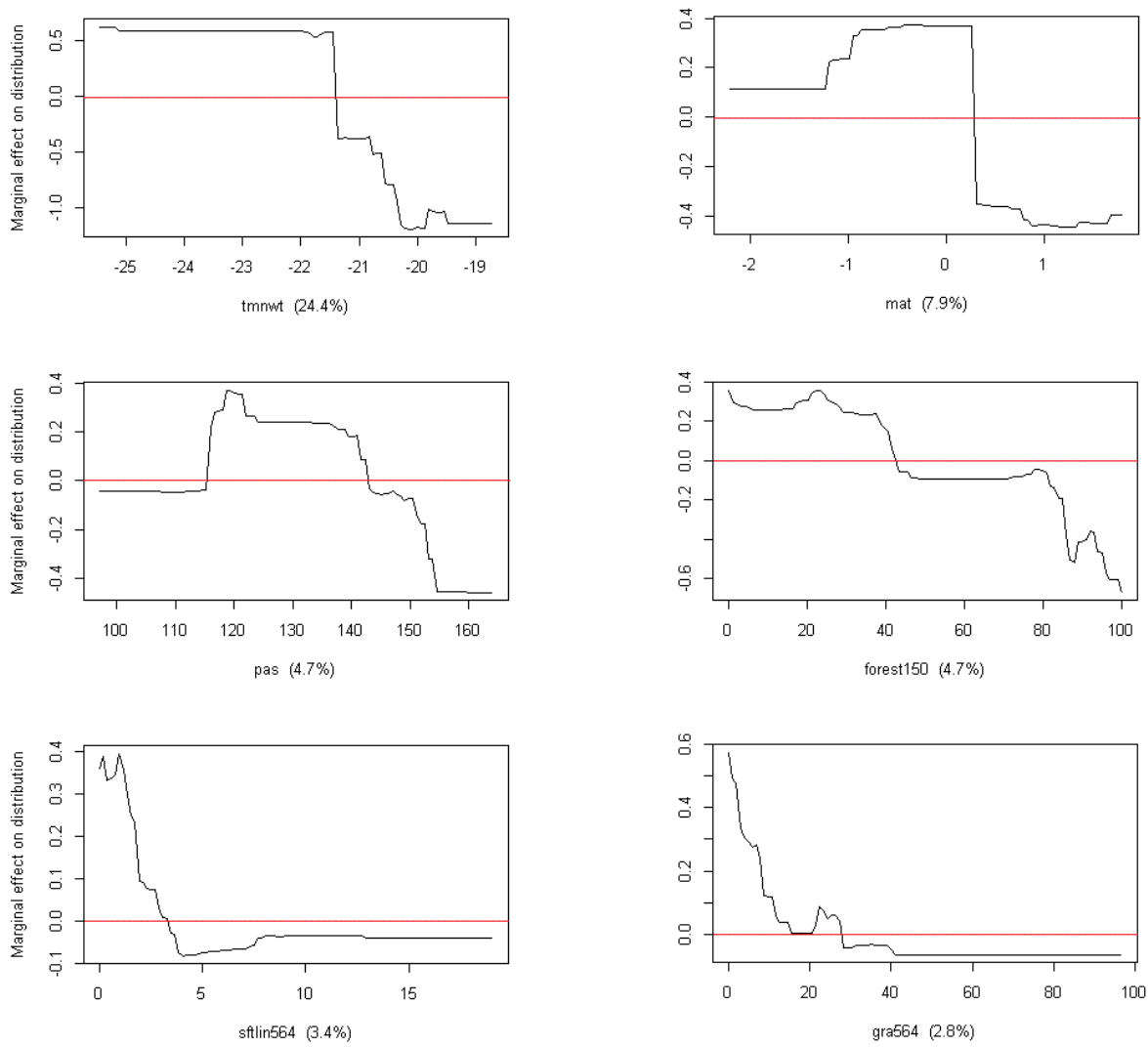
Figure 2.3: Partial dependency plots showing the effect of: **a)** average minimum winter temperature (°C); **b)** mean annual temperature (°C); **c)** precipitation as snow (mm); **d)** percent forest cover at nest site scale (%); **e)** percent area covered by soft linear disturbances at home range scale (%), and **f)** percent grassland cover at home range scale (%), on the distribution of boreal owl after accounting for the average effects of all other variables in the model. Numbers in parenthesis show relative contribution of each variable to the model. Values above the horizontal red line are associated with preference while values below represent avoidance for each variable. For explanation of variables see Appendix 2.
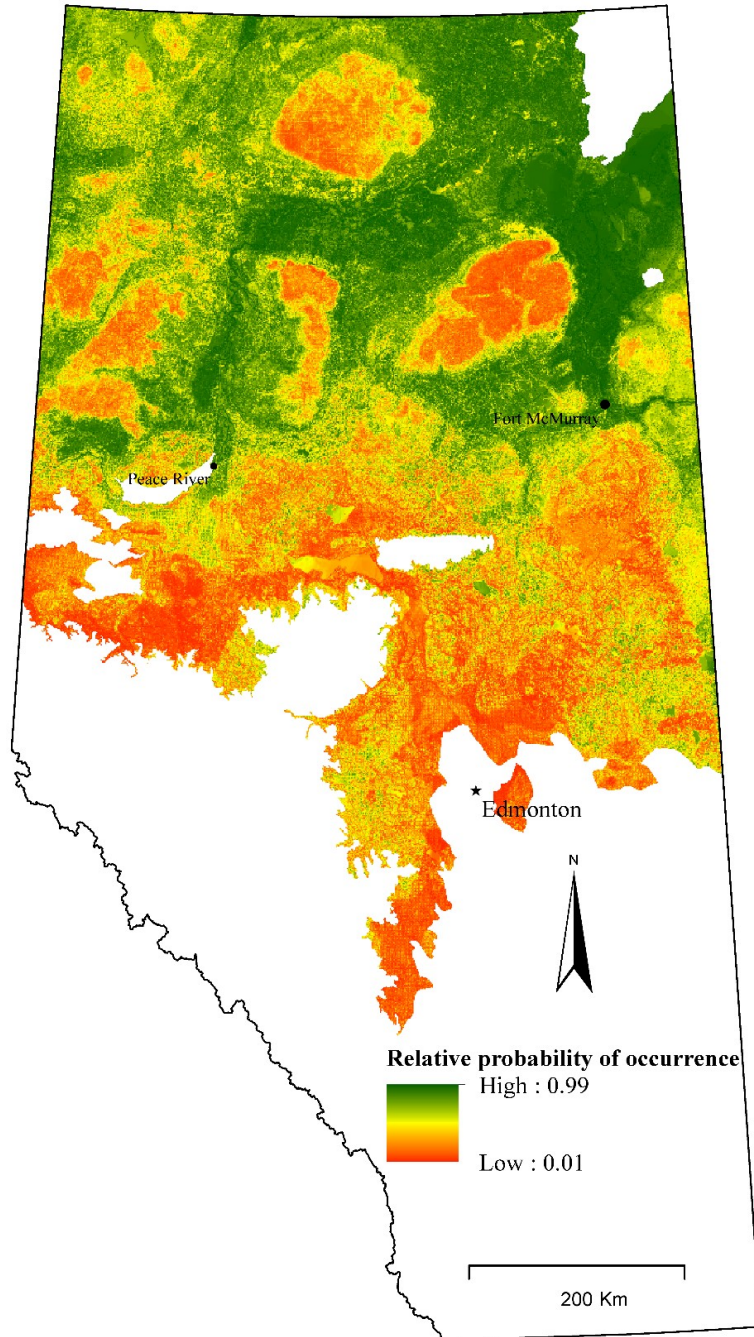
Figure 2.4: Predictive breeding distribution of boreal owl *Aegolius funereus* in the Boreal Natural Region of Alberta, Canada. The map resulted from the final BRT model developed with 29 explanatory variables, including elements of climate, land cover and human disturbance.
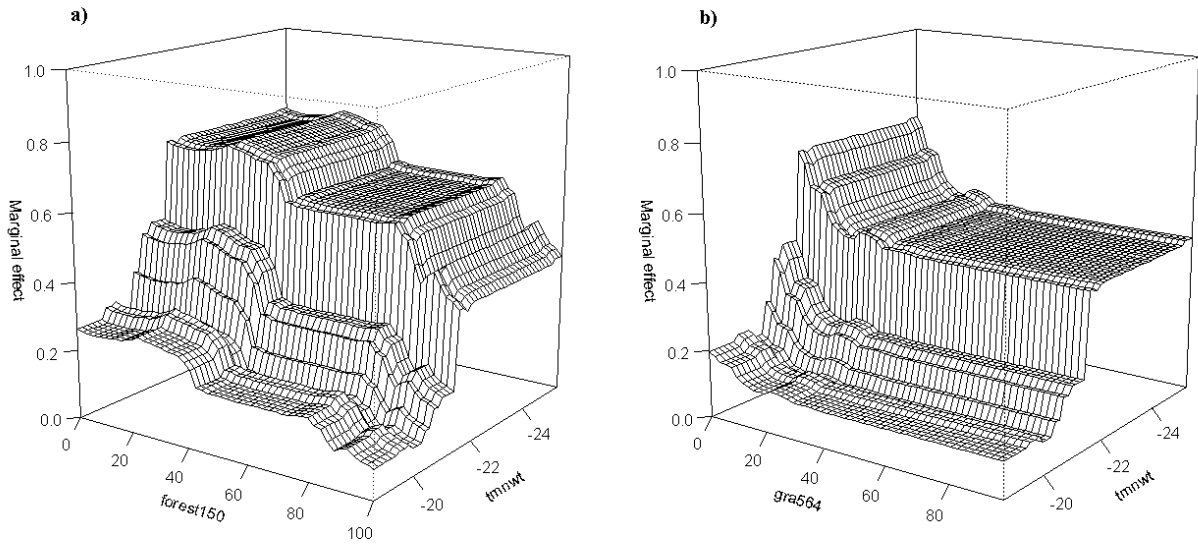
Figure 2.5: Three-dimensional partial dependency plots showing how interactions between **a)** forest cover at nest site scale (forest150) and minimum winter temperature (tmnwt), and **b)** percent grassland cover at home range scale (gra564) and minimum winter temperature (tmnwt) influence the breeding distribution of boreal owl. The final BRT model allowed for fourth-order interactions, suggesting complex relationships between variables. All variables, except those shown, are held at their mean. For explanation of variables and measurement units see Appendix 2.
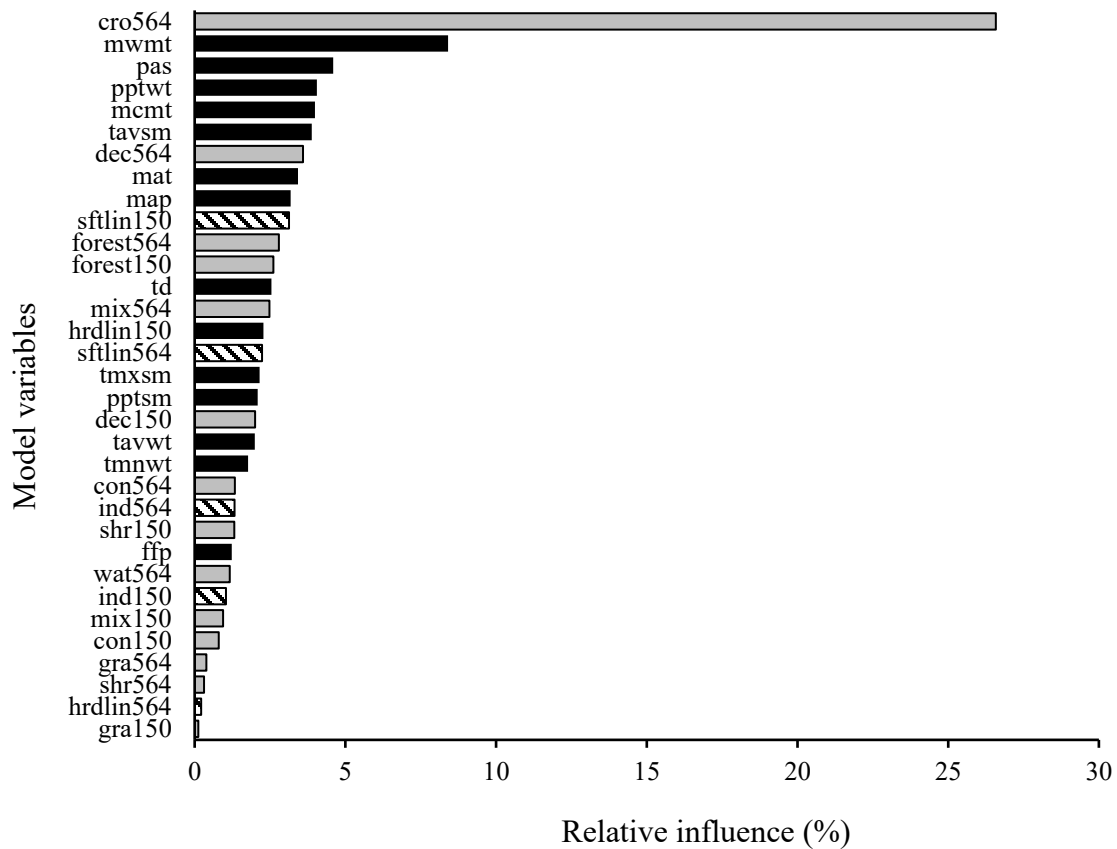
Figure 2.6: Relative influence (%) of predictor variables (n = 33) in the final BRT model explaining distribution of northern saw-whet owl in the Boreal Forest Natural Region of Alberta, Canada. The model was developed using 10-fold cross-validation on data from 677 sites, with a learning rate of 0.005 and tree complexity of 5. Gray bars show landcover types, dark bars represent climatic variables, while bars with diagonal stripes correspond to variables related to human disturbance. For variable explanation see Appendix 2.
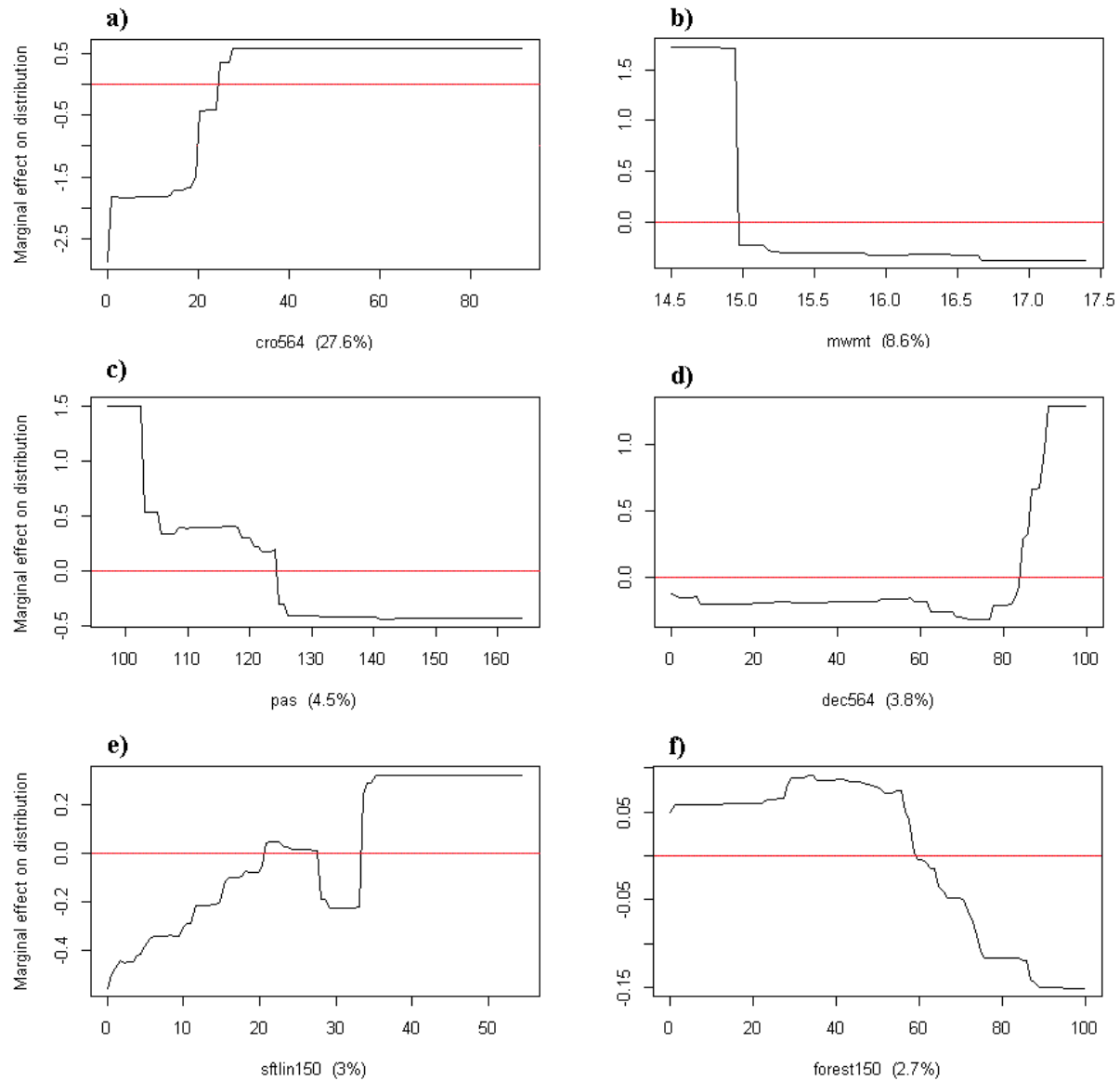
Figure 2.7: Partial dependency plots showing the effect of: **a)** percent cropland cover at home range scale (%); **b)** mean warmest month temperature (°C); **c)** precipitation as snow (mm); **d)** percent deciduous forest cover at home range scale (%); **e)** percent area covered by soft linear disturbances at nest site scale (%), and **f)** percent forest cover at nest site scale (%), on the breeding distribution of northern saw-whet owl after accounting for the average effects of all other variables in the model. Numbers in parenthesis show relative contribution of each variable to the model. Values above the horizontal red line are associated with preference while values below represent avoidance for each variable. For explanation of variables see Appendix 2.
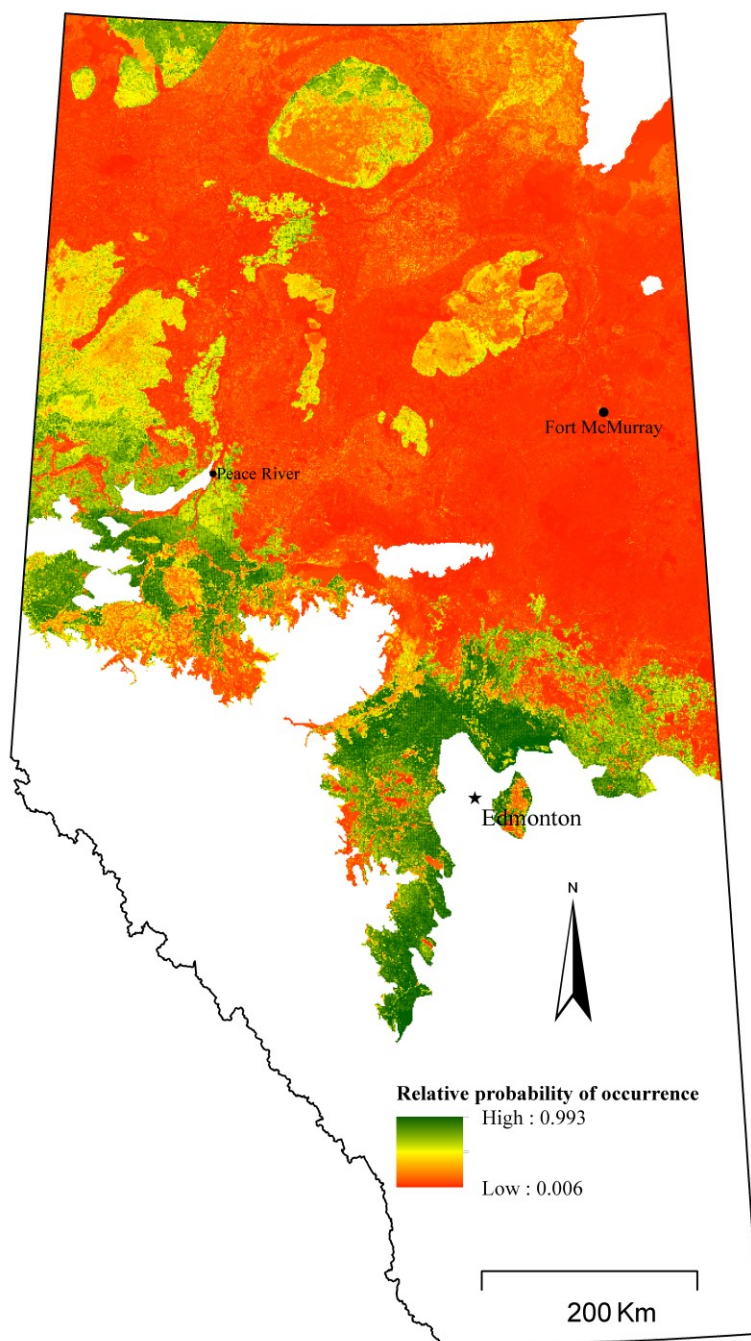
Figure 2.8: Predictive breeding distribution of northern saw-whet owl *Aegolius acadicus* in the Boreal Natural Region of Alberta, Canada. The map resulted from the final BRT model developed with 33 explanatory variables, including elements of land cover, climate and human disturbance.
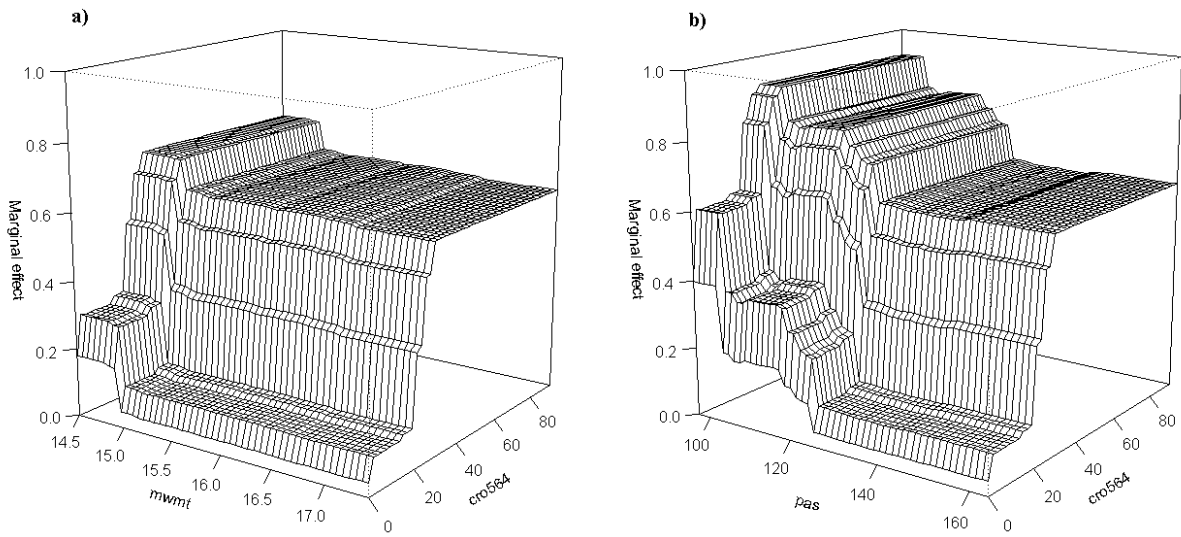
Figure 2.9: Three-dimensional partial dependency plots showing how interactions between **a)** average warmest month temperature (mwmt) and percent cropland cover at home range scale (cro564), and **b)** precipitation as snow (pas) and percent cropland cover at home range scale (cro564) influence the breeding distribution of northern saw-whet owl. The final BRT model allowed for fourth-order interactions, suggesting complex relationships between variables. All variables, except those shown, are held at their mean. For explanation of variables and measurement units see Appendix 2.

Chapter Three: Breeding ecology and reproductive success of owls on managed Boreal landscapes

3.1 Introduction

Once thought to be ideal habitat for cavity nesting owls (Hayward et al. 1993; Korpimaki and Hakkarainen 2012), the Canadian Boreal forest is changing under the cumulative effects of natural disturbances, resource extraction and global change (Schindler and Lee 2010; Gauthier et al. 2015). More than 35% of the Canadian Boreal forest is managed (Gauthier et al. 2015) however, there has been a growing tendency to replace traditional clear-cutting with management and harvesting techniques that promote conservation of old growth and forest biodiversity (Burton et al. 1999; Etheridge and Kayahara 2013; Lindenmayer et al. 2006; Thorpe and Thomas 2007; Fedrowitz et al. 2014). Sustainable forest management, as approached through variable retention harvests is introducing additional change thought to enhance conservation goals (Work et al. 2003). However, the impact of such changes on cavity-nesting owls is not well understood.

Boreal owls are associated with old forests where the density of natural cavities seems to be higher (Hayward et al. 1993), and it is important to know combinations of cover type and retention levels required to produce occupancy in stands affected by partial logging. Northern saw-whet owls seem to tolerate a wider range of habitat conditions (Grossman et al. 2008; Hinam and Clair 2008; Drilling 2013), and some even nest in commercial tree plantations if nest boxes are provided (Moser 2002; Marks et al. 2015), but their response to variable retention forestry is unknown. Detailed information about nesting habitat requirements of cavity nesting owls is required to develop best practices for retention design and to ensure conservation of these owls in partially harvested stands.

In natural conditions, breeding of these two small owl species is tied to forests containing large trees with cavities resulting from fungal decay or excavations of large woodpeckers like the pileated woodpecker and northern flicker (Hayward et al. 1993; Bonar 2000; Cooke and Hannon 2011; Korpimaki and Hakkarainen 2012). Locating nest sites for study in such areas is difficult as owls of these species often breed in remote locations where lack of roads and deep snow conditions restrict access (Hayward et al. 1993; Castro et al. 2008; Korpimaki and Hakkarainen

2012). As a result, most breeding data comes from nest box experiments (Hayward et al. 1993; Lauff 2009; Lopez et al. 2010; Korpimaki and Hakkarainen 2012) because boxes provide an efficient (Korpimaki and Hakkarainen 2012) and cost effective (Hayward et al. 1992) method to document breeding, examine habitat associations of nesting owls and provide important demographic data to assess population trends and changes in habitat quality.

As secondary cavity users, both boreal and northern saw-whet owls are part of the cavity nesting web (Cooke and Hannon 2011) and are thus threatened by clear-cutting (Hayward 1997; Korpimaki and Hakkarainen 2012) that eliminates the largest trees from forest stands (Lopez et al. 2010). Green tree retention forestry leaves trees as potential resource for cavities after harvest that may preserve cavity nesting communities, (Woodley et al. 2006; Cooke and Hannon 2011); however, it is not clear the retention level (Lance and Phinney 2001) needed or what structures to retain (Thorpe and Thomas 2007; Cooke and Hannon 2011; Straus et al. 2011) to maintain cavity nesting owls in the boreal forest. Moreover, it is unknown how breeding density of owls is affected as the density of primary cavity excavators is reduced in partially harvested stands (Straus et al. 2011), resulting in lower cavity density and inherently higher competition among secondary cavity nesters (Bonar 2000).

Associations between these small owl species and forest cover are still evolving and there is little information about the scale at which these owls respond to habitat change. For boreal owls, detailed habitat descriptions of known breeding sites are available at nest site (0.4 ha; (Hayward et al. 1993; Lauff 2009) or at home range (225–314 ha) scale (Laaksonen et al. 2004; Hakkarainen et al. 2008; Korpimaki and Hakkarainen 2012), and habitat comparison at both scales is scarce. In contrast, none of the published nest box experiments (Moser 2002; Buidin et al. 2006; Drilling 2013; Marks et al. 2015) have associated nest box occupancy and breeding success of northern saw-whet owls with habitat characteristics.

I used next boxes to evaluate the responses of boreal and northern saw-whet owls to variable retention forestry in the western Boreal region of Alberta. My specific objectives were to document owl breeding across three different forest types and a range of retention levels, to describe breeding habitat, to identify the most important variables associated with owl occupancy and to report reproductive success. I compared habitat variables between used and available habitat at both the nest site and home range scale. To assess the importance of

landscape features and scale I built and tested a priori models predicting nest box occupancy at each of these scales. Finally, I compared productivity of owls breeding in partially logged stands with data from other forest types.

3.2 Methods

3.2.1 Study area

This work was conducted in the Clear Hills region of Alberta, Canada, including the land base of the Ecosystem Management Emulating Natural Disturbance (EMEND) Project, located 90 km northwest of Peace River, Alberta (56°46'13"N, 118°22'28"W) (Figure 3.1). Elevation of the site ranges from 470 to 920 m. The mean annual temperature of the region, based on normal climate data from 1901 to 2006 (Mbogga et al. 2010), is -0.2 °C with cold winters (avg.= -15.7 °C), cool summers (avg. = 3.6 °C) and 146 frost free days. Part of the 476 mm of moisture the region receives annually, 141 mm falls as snow although there is high inter-annual variation in both measures. The upland mixed wood landscape includes a mixture of poplar species and conifer patches that are predominantly white spruce *Picea glauca*. Forests on the wetter areas contain open and closed canopies of black spruce *Picea mariana* and tamarack *Larix laricina* with sparse understory vegetation dominated by mosses and Labrador tea *Rhododendron groenlandicum*.

This predominantly forested region was historically shaped by fire (Work et al. 2004; Bergeron 2012)—the main natural disturbance agent in the area—and more recently by the intensification of logging and oil and gas exploration. North American beavers, *Castor canadensis*, also influence the landscape by damming streams and selectively removing deciduous trees, creating conifer dominated forest pockets around beaver ponds (Z. Domahidi, pers. obs. 2015). There are few roads but old and more recent cut lines, in-stand access roads and exploration lines provide access to remote areas.

The EMEND experiment was not designed to test owl responses to variable retention tree harvesting but offers a suitable land base for studies of cavity nesting owls in a landscape affected by forestry operations. The experimental template (description of the complete experimental design is available from Spence et al. 1999; Work et al. 2010) is a patchwork of conifer-dominated (CD, conifers > 70% of the canopy), deciduous-dominated (DD, conifers < 30% of the canopy), deciduous-dominated with conifer understory (DU) and mixed (MX,

relative equal composition of conifer and deciduous trees) compartments subjected to clearcuts, five green tree retention levels: 10%, 20%, 50%, 75% and unharvested controls. Trees were retained by operators, independent of size, status and species. Each compartment is 10 ha, tree harvesting was executed in winter of 1998–99, and all cover types and treatments are replicated three times. In this thesis, I used compartments with 20%, 50%, 75% retention and unharvested controls in three cover types (CD, DD and MX), for a total of 36 experimental units.

3.2.2 Nest boxes

I studied boreal and northern saw-whet owls at EMEND and on the surrounding landscape using nest boxes to document breeding, examine habitat associations of nesting owls and provide demographic data to assess population trends and changes in habitat quality. Nest box experiments typically have small sample sizes but are better suited to collect high-quality breeding data than call-playback surveys or passive recordings provided by ARUs. Long-term studies in Finland revealed that only 47% of male owls detected during point counts managed to attract a female and breed (Korpimaki and Hakkarainen 2012). Therefore, including numerous owl detections in modelling breeding habitat requirements without confirming that nesting has occurred could inflate models with data that is not reflecting characteristics of actual nest sites.

During 2015–2016 I placed and monitored 169 nest boxes suitable for boreal and northern saw-whet owls at EMEND (72 boxes) and in the surrounding landscape (97 boxes). Nest boxes were built of rough cut spruce boards of 2 cm thickness, following a box design that offers adequate insulation and space for a brooding female and cached prey items provided by the male owl (Korpimaki 1985). However, my box design (Appendix 4) was modified slightly to allow quick, safe access during inspections and easy cleaning after the breeding season. Since these owls do not bring any nest material in the occupied cavities, the bottom 10 cm of the box was filled with aspen chips and shavings to mimic woodpecker excavations by providing insulation and preventing egg breakage.

In the field, boxes were hung on live or dead trees at an average height of 5.2 m (range: 2.7–6.2 m), using sections of a Swedish tree climbing ladder. I did not follow any patterns of box orientation but made sure that there was a small opening in front of the box to allow a direct flight path to the entrance hole. Two boxes were placed in the three different cover types in each

of the selected 36 EMEND harvest and control compartments, spaced at a minimum distance of 200 m (range: 204–647 m) from each other. Additional boxes were placed in unharvested CD, DD and MX stands outside EMEND that were at least 10 ha in size, and in residual trees found in recent (1–5 years) clear-cuts. Candidate forest patches were initially selected based on Google Earth images. Feasibility of access and dominant overstory species were confirmed using a 3-D photo visualization and interpretation station at Daishowa Marubeni International (DMI) Peace River Pulp Division Woodlands office. Boxes were not evenly distributed on the landscape but rather along existing roads and trails to facilitate relatively quick access. The average distance between these landscape nest boxes was 1,274 m (568–2,968 m). Not all cover types were equally available for box placement as many DD stands had been previously harvested and the regenerating trees (10–15 years old) were too dense and too small to support boxes.

3.2.3 Habitat characterization at nest site and home range scale

At each nest box, I noted the main surrounding cover type, box height, orientation of the entrance hole, tree diameter at breast height (DBH) and tree status (dead or living). Landscape characteristics were tabulated using ArcMap 10.2.2 (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) at two scales: 1) nest site (NS, 3.14 hectares or 100 m radius circle centered on the nest box) and 2) home range (HR, ~100 hectares 564 m radius circle centered on the nest box), using georeferenced vegetation layers from the Alberta Vegetation Inventory (AVI) polygons and the Alberta Biodiversity Monitoring Institute (ABMI) Wall-To-Wall Vegetation Layer. I calculated average forest age and canopy height, percent composition of the three dominant cover types (CD, DD, MX), percent shrub land, grassland and agricultural land for each nest box. To obtain the amount of old forest coverage, I compiled amount of forest that was 100+ years old, calculated from the stand initiation or stand replacing disturbance. To investigate if occupancy was associated with the intensity of human activity, I calculated proportion of disturbed land at both NS and HR scale. Disturbances included all the industrial footprint present on the landscape (mine sites, well pads, borrow pits, pipelines, roads and trails) and were compiled from the ABMI's Human Footprint GIS layer.

3.2.4 Nest box use

The initial set of 39 boxes were set out during October–December 2014, while the rest of the 130 boxes were deployed during August–October 2015. Based on published nest initiation dates,

every box was checked at least twice during April–June to confirm occupancy and to cover the timing of both early breeders and possible replacement clutches. Initial visits consisted of a quick glance into the box, using a home-made observation device assembled from an extendable pole, wireless inspection camera and a cell phone. Occupant species, eggs, cached prey or any other signs of occupancy (e.g., feathers, additional nest material) were noted and future check dates were scheduled based on the initial findings. Boxes that were filled with squirrel nest material were re-checked and cleaned promptly early in the season. Any sign of damage (e.g. entrance hole enlarged by woodpeckers) or potential predation (e.g. bear claw marks on the tree) was noted at every visit. All boxes were cleaned after the breeding season ended.

3.2.5 Reproductive success

Boxes occupied by owls were re-visited during the 2016 breeding season to assess fecundity and hatchling survival using a ladder until the clutch failed or nestlings were at fledgling age (28–30 days old). Reproductive success was measured as: (1) nesting effort (number of eggs laid), (2) hatching success (% of eggs hatched) and (3) fledging success (% fledglings reaching 28–30 days). The number of eggs per nest box was determined either through direct observation or inferred from the number of nestlings and unhatched eggs present in the box. The time of nest initiation was calculated based on a 2-day egg laying interval (Korpimäki 1981) for incomplete clutches or as the combination of nestling age, incubation time and laying interval for clutches discovered at nestling stage. Hatch time for incomplete clutches was determined based on a 29-day incubation period (Korpimäki 1981), counted from the date of the second egg. Owlets that were in the nest box at 28–30 days after hatching were considered fledged.

3.2.6 Analysis

To infer habitat preference of cavity nesting owls in different cover types and retention levels I determined if usage was selective (Johnson 1980) by comparing used habitat components to their availability at the stand (10 ha) scale.

To investigate what habitat features play important role in nest box occupancy I defined eight a priori models (Appendix 5) for both nest site and home range scale. The hypotheses represented in the models are based on literature research and contain habitat features thought to be relevant for owl occupancy as follows:

(H0) null model of equal occupancy among boxes (.);

(H1) old forest cover hypothesis expressed as average forest age (forage)

(H2) forested land hypothesis measured as percent forest cover (% forest)

(H3) dominant cover hypothesis expressed as % mixed wood cover in the area (% mix);

(H4) old forest landscape hypothesis included % of old forest cover (% old forest);

(H5) disturbance hypothesis used % of disturbed landscape (% disturbed);

(H6) open habitat hypothesis included % grassland cover (% grass); and

(H7) forest intactness hypothesis measured as percent green trees retained (% ret).

I predicted that forest age, forest, and percent of old forest cover at nest site scale would have a positive effect on occupancy probability as they are related to published work about owl nesting success (Hayward et al. 1993; Laaksonen et al. 2004; Lopez et al. 2010; Korpimaki and Hakkarainen 2012). Nest box occupancy was expected to increase with increasing green tree retention as high retention maintains structural complexity and resemblance to old growth stands, and thus should be preferred by old forest specialists. I expected that disturbances on the landscape would negatively influence owl occupancy at both nest site and home range scale. I predicted that increasing amount of open habitat at the nest site scale would have negative effects on owl due to high predation risk, especially for the young fledged owls (Korpimaki and Hakkarainen 2012). However, presence of grassland at the home range scale might have a positive effect on nest box use as habitat heterogeneity that includes openings and edges increase prey abundance and offers more hunting opportunities (Hinam and Clair 2008; Korpimaki and Hakkarainen 2012; Brambilla et al. 2013; Liebana et al. 2013).

I modelled occupancy probability using logistic regression (Hosmer and Lemeshow 2000) analysis with binomial response: (0) box not used and (1) box used by owls, performed in R (R Core Team 2015). There was no collinearity (Pearson correlation > | 0.7 |) among variables used in the proposed models. Box placement height, entrance orientation and host tree DBH did not significantly predict occupancy and they were eliminated from all subsequent models. Candidate models were ranked for support using Akaike's Information Criterion corrected for small sample

size (AICc), where smaller AICc values indicate more support for the model (Burnham and Anderson 2004).

3.3 Results

3.3.1 Nest box use

During the 2016 breeding season, 64 (39%) of 164 nest boxes available for study were used (of the 169 boxes placed one was destroyed because of forest harvesting, and four boxes could not be accessed after beavers flooded the access trail). Ten of these (6%) were occupied by owls (Table 3.1). Four were used by boreal owls, four by northern saw-whet owls and species identity could not be confirmed for two boxes. In these latter two cases, the nest boxes contained cached prey, but no owls were detected and there was no sign of laid eggs or hatched young. At both the nest site and home range scale, boxes occupied by boreal and northern saw-whet owls had higher coverage of coniferous forest and contained less mixed wood than unused boxes (Figure 3.2). Used boxes had more deciduous coverage than empty boxes at the nest site scale but average deciduous cover at home range scale was higher for the unoccupied nest boxes (Figure 3.2). At the nest site scale, owls occupied boxes in less disturbed areas but contained more disturbed land at home range scale than unused nest boxes (Figure 3.2). At the home range scale, owl boxes had lower shrub but higher grassland coverage than unoccupied boxes (Figure 3.2).

Occupied territories were 60.8–100% (90.2 ± 5.1; $\bar{x} \pm$ SE) forested at the nest site scale and 62.7–100% (85.4 ± 3.5) at the home range scale. Shrubland and grasslands were completely absent at the nest site scale but present in proportions of 0–37.2% (5.3 ± 3.6) and 0–12.4% (2.7 ± 1.4), respectively, at the home range scale (Table 3.2). Owls used nest boxes located in all three cover types studied and, interestingly, in all retention levels, except clear-cuts. Owls used more nest boxes placed in deciduous forests than it was available, and boxes placed in the conifer dominated or mixed wood cover type were used less than they were available (Figure 3.3). Although 50% of the occupied boxes were in unharvested stands, owls used boxes hung in low retention (20%, 50%) compartments more than available while nest boxes placed in clear-cuts, 75% retention and unharvested stands were used less than they were available (Figure 3.4). At nest site scale, boreal owls used conifer dominated patches and northern saw-whet owls occupied boxes in deciduous forests while at landscape scale, boreal owl territories were still conifer-dominated but norther saw-whet owls nested in more diverse landscapes (Table 3.2).

3.3.2 Nest box occupancy in relation to habitat characteristics

Logistic regression models were fit using data from 161 nest boxes (three boxes had to be excluded as forest inventory data was unavailable), categorized as used and unused. The most supported candidate model explaining nest box occupancy by all owls was the dominant cover hypothesis (+ % mix100) at the nest site scale (Akaike weight, wi = 0.413) followed by the null (.) model (wi = 0.082) of equal occupancy (Table 3.3) that was 5.06 times less supported (evidence ratio (ER) of Akaike weights wi) than the top AICc model (Δi = 1.71). The forested landscape model applied at the home range scale (+ forest564) was the least supported among candidate models (Δi = 5.29). The open habitat hypothesis (+ % grass564) applied at the home range scale was the second least supported model and was 13.6 times less likely to explain nest box use by owls. Three other candidate models had less support (Δi = 3.25–4.50) than the two top-ranked models but are still plausible, with Akaike weights within 10% of the most supported model. These include the habitat disturbance hypothesis (- % disturbed564) for the home range scale, the open habitat model at nest site scale (- % grass100) and the dominant cover hypothesis (+ % mix564) for the home range scale.

None of the tested parameters were statistically significant; however, including percent mixed wood cover at the nest site scale improved model fit when compared to the null model of equal occupancy. Retention of the dominant cover model as plausible at both scales suggests that, while cover type is an important habitat feature, measurements at the nest site scale are a better indicators of nest box occupancy. A positive effect of disturbance alone on occupancy at the home range scale, while is still plausible, is less likely (ER = 5.08) than is an effect of dominant cover. Forest age at both scales and across retention levels had less support than the plausible models above but was still a better predictor of occupancy than was simple forest cover and percent old forest at both nest site and home range scales (Table 3.3).

3.3.3 Reproductive success

Among the total of ten boxes used by owls I documented eight nesting attempts during the 2016 breeding season. These nest boxes accounted for a total of 30 eggs: one with six, two with five, one with four, two with three and two boxes with two eggs each (mean = 3.75 ± 0.52) (Table 3.4). Two nests initiated by boreal owls failed before clutch completion. Although one of them contained two eggs and three cached prey items on May 17, the eggs did not hatch. The second

nest was started on May 31 and the female laid two eggs but on July 2 the nest box was empty. The six boxes in which eggs successfully hatched produced 2–5 owlets (mean = 3.6 ± 1.03) but two nests failed before fledging, one probably from predation while the other appeared to be due to parental abandonment. Thus, four of the six nests that produced owlets collectively produced 11 fledglings (range 2–4, mean = 2.7 ± 0.4) and all these fledglings successfully left the box.

Observed timing of nest initiation differed between the two species. For boreal owls, earliest nest initiation occurred on April 10 while the latest clutch was started on May 31. For northern saw-whet owls the earliest clutch was started on May 10 and the latest clutch was initiated on June 15. Boreal owl young fledged in late June, while all northern saw-whet owlets were close to fledging on August 10. During 22 nest box checks I counted a total of 35 stored prey items (range = 1–7, mean = 3.5) with more prey items stored during the egg laying and incubation period that the nestling stage.

3.4 Discussion

3.4.1 Nest box use and habitat preference

Owls used nest boxes in all three cover types in both uncut forest and stands that had been harvested to retention prescriptions 17 years earlier, but they apparently avoided clear-cuts. Boreal owls nested exclusively in conifer dominated patches, occupying four nest boxes (2.4% overall) representing 4.8% of boxes placed in conifer dominated stands. Nest site choice and occupancy rate is comparable to that observed in uncut forests of the Northern Rocky Mountains, USA, where only 3 nesting attempts were observed over four years in 45 nest boxes placed in conifer forests (Hayward et al. 1993). Occupancy rate for nest boxes at EMEND was higher than occupancy rates in the Yukon (1%; Korpimaki and Hakkarainen 2012), but lower than in Finland between 1966–82 (15%, Korpimaki and Hakkarainen 2012) or China, where occupancy varied between 6–10% over five years for boxes placed in selectively logged forests lacking large trees (Fang et al. 2009).

Northern saw-whet owls also nested in four boxes (2.4%) at EMEND, all in deciduous and mixed wood stands, as is consistent with the low occupancy reported (2.5%, range: 0–4.5%, n = 6 years) at their northern breeding limit in the Boreal region of Quebec, Canada (Buidin et al. 2006). In contrast, box occupancy was much higher percentage in the southern part of their

breeding range: 3–36% at the hybrid poplar plantation at Broadman Tree Farm in north-central Oregon, USA (Moser 2002; Marks et al. 2015) and a yearly average of 15% at the Custer National Forest in South Dakota, USA (Drilling 2013). It is not clear whether the difference in occupancy rates is due to lower owl densities at the northern edge of their range or the relative availability of cavities in these different forest types.

3.4.2   Nest box use and retention forestry

At my research site, northern saw-whet owls used different habitats than did boreal owls, occupying more intensely harvested forest patches and apparently avoiding unharvested stands. In general, northern saw-whet owls used nest boxes placed in more varied landscapes containing both deciduous dominated and mixed wood patches. Their nest sites were in predominantly deciduous cover (range: 74.1–100, 93.4 ± 6.4) although the MX component cover increased (range: 0–48.5, 25.3 ± 10.9) at the home range scale (Table 3.2). They did not nest in uncut forests but used boxes placed in stands where previous logging had removed at least one quarter of the trees (two boxes in 20%, one in each 50% and 75% retention). In contrast, boreal owls occupied residual conifer dominated patches that resembled uncut forests where at least 50% of the trees are retained. Three out of four nests were in uncut stands while one was in a cut block with 50% tree retention. Conifer cover, as expected, was high at both nest site and home range scales (NS = 90.2 ± 9.7, HR = 80.1 ± 9.1) and only low levels of the mixed wood component appeared at the home range scale (range: 2–8, 5.7 ± 1.5).

Variable retention forestry that creates a mosaic of stands of different cover types, including uncut patches that resemble old forests, may maintain cavity nesting owls on Boreal landscapes. My findings complement those of other studies showing that on logged landscapes at least 30% retention, in patches of minimum 10 ha are needed to maintain most cavity users associated with old boreal forests (Cooke and Hannon 2011). However, my nest box data reveals that boreal and northern saw-whet owls react differently to disturbance caused by partial logging. Although my data are admittedly limited, nest site choices observed for boreal owls corroborates their dependence on old conifer forests (Hayward et al. 1993; Korpimaki and Hakkarainen 2012). Nest box use by northern saw-whet owls at my research site underscores their willingness to breed in a broader range of forest types and under various disturbance levels, if cavities are available (Moser 2002; Drilling 2013; Marks et al. 2015).

Low retention compartments lack the structural complexity of old forests. Stands with 20% green tree retention were at the time of my research 17 years post-harvest, and covered by dense aspen regeneration, with only few trees large enough to potentially host a natural cavity created by primary cavity excavators. The absence of boreal owls from low retention patches, even when nest boxes are provided, is consistent with suggestions that they key on forests with structural complexity (Hayward et al. 1993). The apparent preference of northern saw-whet owls for younger stands could be explained by their higher maneuverability and lighter wing loading than boreal owls, allowing them to hunt in dense vegetation (Hayward and Garton 1988). The different response of the two species confirms findings suggesting that raptors having apparently similar nesting requirements, prey and hunting habits, respond differently to habitat alteration due to subtle differences in their ecology (Hockey and Curtis 2009). Although both cavity nesting owl species were present, low forest retention levels and habitat alteration seems more likely to impact an old-forest specialist like the boreal owl than a habitat generalist like the northern saw-whet owl.

3.4.3 Occupancy modelling

Maintaining secondary cavity nesters in landscapes affected by logging is possible either by providing artificial nest boxes or maintaining forest structures that ensure both persistence of old cavities and presence of primary excavators for continuous production of new ones while the forest regenerates (Bonar 2000; Cooke and Hannon 2011; Ouellet-Lapointe et al. 2012). Behavior of primary excavators did not change in partially harvested forests with either aggregated or dispersed retention (Ouellet-Lapointe et al. 2012); however, cavity densities might be considerably reduced over time unless large trees are included in retention (Bonar 2001; Cooke and Hannon 2011). This is particularly important for secondary cavity nesters like the boreal and northern saw-whet owl that cannot enter smaller cavities created by yellow-bellied sapsuckers *Sphyrapicus varius* or hairy woodpeckers *Picoides villosus*.

The dominant cover model was among the five plausible models retained at both scales, suggesting that the amount of mixed wood in retained patches on post-harvest landscapes is an important consideration when designing harvest and retention patterns to support owl conservation. The top model was 41% likely to be the best explanation for nest box occupancy. However, the effect of mixed wood cover on occupancy probability is small and the current

occupancy data used to develop the model is limited to one breeding year. The power to detect treatment effects (at $\alpha = 0.05$) is only 0.093 for a small effect, 0.33 for a medium effect and 0.68 for a large effect. Power analysis also revealed that to detect a medium effect with 80% certainty, I would need at least 46 occupied boxes. To meet this target in a single year (under the assumption of the analysis) requires an occupancy rate of 46% for the number of nest boxes I had available or, under optimistic occupancy rates of 10%/year I would need to monitor more than 450 boxes. None of these options is feasible for a two-person crew in a single breeding season. Model results show that mixed wood cover at both scales negatively influenced owl occupancy. As I previously indicated, mixed wood stands were the least used compared to their availability (Figure 3.3). This suggests that conservation of these owls in the boreal mixed wood landscapes affected by variable green tree retention harvesting is more likely if a combination of CD and DD patches are retained instead of MX stands.

Surprisingly the amount of forest cover identified as a most generally important component of owl territory quality (Hayward 1997; Laaksonen et al. 2004; Hakkarainen et al. 2008; Hinam and Clair 2008; Korpimaki and Hakkarainen 2012) was not among the most supported models. As expected for forest associated species, grassland cover at the nest site scale had a strong negative effect on occupancy probability for both species. Disturbance at the home range scale, on the other hand, had a small positive effect on owl occupancy probability. This seems to support other findings that these species avoid breeding in contiguous, even aged forest tracts (Hayward et al. 1993; Korpimaki and Hakkarainen 2012). Moderate disturbance can open up the landscape and increase foraging opportunities, especially when prey densities in mature forests are low (Hayward et al. 1993; Hinam and Clair 2008; Korpimaki and Hakkarainen 2012).

3.4.4   Reproductive success

Both of my focal species successfully raised nestlings in this study. Northern saw-whet owls started breeding one month later than boreal owls, laid twice as many eggs as boreal owls, and were more successful in raising nestlings. Three of four northern saw-whet owls fledged at least two owls while only one of four boreal owls produced fledglings (Table 3.4). Although my results are limited, below I compare information about breeding between my results from forests of north-western Alberta affected by variable green tree retention harvesting with published information from the eastern Boreal region of Canada impacted by defoliators, high elevation,

largely uncut forests from the USA and the northern forests of Fennoscandia affected by commercial logging.

3.4.4.1   Timing of breeding

Nest initiation period for boreal owls at my study site is comparable to laying dates at Chamberlain Basin, Idaho, USA (April 12–May 24, Hayward et al. 1993). However, these owls started breeding earlier in both Nova Scotia, Canada (March 20–June 1, Lauff 2009) and Finland (March 13 to May 2, Korpimaki and Hakkarainen 2012). The latest clutch laid at EMEND was probably a replacement or a second clutch initiated by a polyandrous female (see Korpimaki and Hakkarainen (2012) for criteria). Laying dates are strongly influenced by food abundance but also by weather conditions, and breeding can start earlier in years with thin snow cover during the winter that improves body condition of adult owls (Lehikoinen et al. 2011; Korpimaki and Hakkarainen 2012). In the winter of 2015/16 snow cover was very low at EMEND, with some areas in unharvested conifer stands completely snow free in January 2016 (Z. Domahidi pers. obs.). However, boreal owls did not start breeding in the Clear Hills as early as Finnish owls do in similar conditions.

Timing of nest initiation for northern saw-whet owls breeding at EMEND is comparable to birds breeding in the Mignan Region, Quebec, Canada where reported nest initiation dates range from early-April to mid-June (Buidin et al. 2006). Nest initiation dates are seldom reported from northern saw-whet owl nest box experiments conducted in their southern breeding range; however, in one study they started nesting in early-March (Marks et al. 2015). It appears that variable weather conditions (colder weather and relatively deep snow that could be still present in March and early-April) and prey availability determines northern saw-whet owls breeding at higher latitudes to start nesting later than conspecifics in the southern part of their range (Marks et al. 2015).

3.4.4.2   Nesting effort

Northern saw-whet owls in partially harvested stands from Alberta laid more eggs (mean = 5, range: 4–6) than conspecifics in the boreal forests of Quebec (mean = 3.5, range: 1–6; Buidin et al. 2006). Conspecifics breeding in young poplar plantations in Oregon laid slightly more eggs (mean =5.8, range: 5–7; Marks et al. 2015) but my results are more comparable to data form

Custer National Forest, South Dakota, USA where average clutch size was 4.9 eggs/nest (range: 3.8–6; Drilling 2013). Boreal owl egg production (Table 3.4) at my study site was less than reported from Nova Scotia, Canada (mean = 3.5, range: 3–4; Lauff 2009) or central Idaho (mean = 2.95, range: 2–4; Hayward et al. 1993); however, if considering only data from complete clutches, the results are comparable, with an average of 3 eggs/nest produced at EMEND. Owls nesting in Alberta produced 47% fewer eggs than did Finnish owls in the poorest vole years (mean = 4.75, range: 4 – 5.4; Korpimaki and Hakkarainen 2012), although year to year variation of clutch size in Fennoscandia was high (mean = 5.71, range: 1 – 10; Korpimaki 1987). The positive correlation between nest box dimensions and average clutch size is well documented for boreal owls, nest boxes with a square shaped bottom of 20 cm X 20 cm producing the largest clutches (Korpimaki 1985). Differences in egg production at EMEND can't be attributed to the variability of nest box size as I used nest boxes with measurements similar to experiments in Nova Scotia, Canada and Finland (Korpimaki 1985; Lauff 2009).

3.4.4.3   Hatching success

Boreal owls at my study site were 42% less successful at hatching eggs than birds breeding in spruce-fir forests affected by spruce budworm in Nova Scotia, Canada (Lauff 2009) or Finnish owls breeding in highly managed boreal forests that hatched 86.7% of the total eggs laid (Korpimaki and Hakkarainen 2012). Nestling production from 2006 in Alberta (average of 1.25/nest) was worse than in Finland, where average number of hatchlings varied from 2.5 to 5.8 per nest (Korpimaki and Hakkarainen 2012). My results likely reflect the fact that two of four nests in my experiment were deserted or depredated before incubation started. Considering only the data from nest boxes where at least one egg hatched, the hatching success in Alberta was 83.3%, a value comparable to both eastern Canada and Finland.

In contrast, northern saw-whet owls hatched 85% of their eggs and produced 17 nestlings with an average of 4.25 young per nest. This hatching success is comparable to averages found in poplar plantations in Oregon, USA (83% and 4.33 young/nest; Moser 2002); however, owls at EMEND were slightly less successful than those in nest boxes in Custer National Forest (96% and 4.8 owlets/nest; Drilling 2013).

3.4.4.4 Fledging success

Boreal owls at EMEND fledged 0.5 young per nest, less than birds in Idaho, USA (mean = 2.3; Hayward et al. 1993) or the mean number in Finland (1–4.3) where fledging success varied, with abundance of the main prey (Korpimaki and Hakkarainen 2012). Their fledging success was 35%, lower than documented in both Nova Scotia, Canada (62%; Lauff 2009) and Finland (59%; Korpimaki and Hakkarainen 2012). Low fledging success for this species at EMEND in 2016 most likely resulted from nest abandonment in the late stages of the breeding period, when three well developed nestlings (estimated 18–20 days old) were found dead in one nest box. Female boreal owls often desert their first-laid clutch in the late nestling period to re-mate and lay a second clutch (Eldegard and Sonerud 2009; Korpimaki and Hakkarainen 2012). In these situations, male owls are left to provision for the young alone and fledglings have a 30% lower chance to survive to independence. In addition, the timing of a severe snow storm in my research area coincided with the estimated time of death of the nestlings. It is possible that the male provisioning this nest either perished or was unable to feed the young.

Fledging success for northern saw-whet owls was 52.9%, with 2.25 fledglings per nest, comparable to data from the northern limit of their breeding range in the Mignan Region, Quebec (mean = 2.8, range = 1–6; Buidin et al. 2006). Breeding owls at EMEND fledged fewer young in 2016 than the long-term average (3.4 fledgling/nest), but well within the range (0.4 to 4.1 young/nest) recorded for saw-whet owls breeding in boxes in wooded ravines surrounded by grasslands in the more southern part of the species range (Drilling 2013; Marks et al. 2015).

Fledging success is generally a reliable index of avian fitness (Weatherhead and Dufour 2000), although its usefulness has not been empirically tested on either boreal or northern saw-whet owls. Presently available data, including that from EMEND, suggests that fledging success in populations of northern saw-whet owls does not vary much across North America; nonetheless more data are needed to identify high quality habitat features related to owl fitness and to evaluate breeding performance under fluctuating environmental conditions. Fledging data for boreal owls suggests that they are less productive than northern saw-whet owls and is consistent with the generalization that North American boreal owls lay fewer eggs and raise fewer young than do conspecifics in Fennoscandia (Hayward et al. 1993). Northern saw-whet owls seem to accommodate landscape changes resulting from variable retention harvesting, but population

fitness for a habitat specialist like the boreal owl could be reduced and have important consequences for owl conservation.

3.5 Conclusions

The network of nest boxes established at EMEND provides a good start for the long-term monitoring of these forest dwelling species and my early findings suggest that uncut forest patches of sufficient size will be required to conserve populations of the boreal owl on harvested landscapes. We know that habitat alteration and low fledging success contributed to negative growth rates (-2.1 to -2.3% per year) of local boreal owl populations in Finland, where the species is now being considered near threatened (Korpimaki and Hakkarainen 2012). We also know that reduction of old growth forest cover is a main factor affecting male survival and reproductive success for boreal owls (Laaksonen et al. 2004; Korpimaki and Hakkarainen 2012), and that reduction of forest patch size and increasing fragmentation decreases reproductive output for northern saw-whet owls (Hinam and Clair 2008). Considering the large-scale habitat alteration underway in the Canadian Boreal region, longer-term studies for both boreal and northern saw-whet owls could usefully focus on landscape characteristics that promote preservation of breeding populations of these species during post-harvest recovery of stands impacted by variable retention logging.

3.6 Tables

Table 3.1: Nest box occupancy during the 2016 breeding season at Clear Hills, Alberta. A nest box was marked used if presence of species, or any sign of usage (e.g., cached prey, eggs, feathers) was detected inside the box. Identity of users remained unknown when animal presence was never detected at the box, but signs indicated clear use by either group (owls or squirrels).

Occupancy		Number of Boxes	Percent
American kestrel	*Falco sparverius*	2	1.2
Boreal owl	*Aegolius funereus*	4	2.4
Northern flicker	*Colaptes auratus*	5	3
Northern flying squirrel	*Glaucomys sabrinus*	3	1.8
Northern Saw-whet owl	*Aegolius acadicus*	4	2.4
Red squirrel	*Tamiasciurus hudsonicus*	36	22
Unknown owl	*Aegolius* sp.	2	1.2
Unknown squirrel		8	4.9
Empty boxes		100	61
Total		164	100

Table 3.2: Landscape composition (proportion) of 10 owl territories at nest site (100-m radius buffer around each box) and home range (564-m radius buffer around each box) scale at Clear Hills, Alberta, 2016. Data was compiled in ArcMap 10.2.2, using georeferenced vegetation layers from the Alberta Biodiversity Monitoring Institute (ABMI) Wall-To-Wall Vegetation Layer.

	Species									
	BOOW	BOOW	BOOW	BOOW	NSWO	NSWO	NSWO	NSWO	OWSP	OWSP
Habitat component	**Proportion of habitat at nest site scale**									
Conifer	100	100	100	61	0	0	0	0	76	0
Deciduous	0	0	0	0	100	100	100	74	0	65
Developed	0	0	0	19	0	0	0	0	0	35
Grassland	0	0	0	0	0	0	0	0	0	0
Mixed	0	0	0	0	0	0	0	26	0	0
Shrubland	0	0	0	0	0	0	0	0	0	0
Habitat component	**Proportion of habitat at nest home range scale**									
Conifer	95	92	55	79	4	0	1	10	63	0
Deciduous	0	0	0	0	87	68	28	35	13	82
Developed	0	0	0	8	10	7	8	12	0	10
Grassland	0	0	0	0	0	8	12	0	0	7
Mixed	5	8	8	2	0	15	49	38	19	0
Shrubland	0	0	37	5	0	2	3	6	0	0

BOOW = Boreal owl *Aegolius funereus*; NSWO = Northern Saw-whet owl *Aegolius acadicus*;
OWSP = Unidentified owl *Aegolius* sp.

Table 3.3: Akaike's Information Criterion adjusted for small sample size (AIC$_c$) of the regression models of nest box occupancy at Clear Hills, Alberta. Models are ranked according to AIC$_c$, where smaller numbers represent more evidence that the given model is the best approximation among the set of candidate models. The line within the table separates the plausible models from those with very little evidence supporting nest box occupancy. Plausible models are within 10% of the highest Akaike's weight (w_i).

Model	Model Variables	K	AIC$_c$	Δ_i	w_i
H3$_a$	+ % mix$_{100}$	2	73.59581	0	0.413
H0	.	1	76.83865	3.243	0.082
H5$_b$	- % disturbed$_{564}$	2	76.84659	3.251	0.081
H6$_a$	- % grass$_{100}$	2	76.85333	3.258	0.081
H3$_b$	+ % mix$_{564}$	2	78.09898	4.503	0.043
H1$_b$	+ forage$_{564}$	2	78.31022	4.714	0.039
H1$_a$	+ forage$_{100}$	2	78.54162	4.946	0.035
H7	+ % retention$_{100}$	2	78.54354	4.948	0.035
H4$_b$	+ % oldforest$_{564}$	2	78.62841	5.033	0.033
H4$_a$	+ %oldforest$_{100}$	2	78.65945	5.064	0.033
H5$_a$	- % disturbed$_{100}$	2	78.67729	5.081	0.033
H2$_a$	+ % forest$_{100}$	2	78.72876	5.133	0.032
H6$_b$	+ % grass$_{564}$	2	78.81656	5.221	0.030
H2$_b$	+ % forest$_{564}$	2	78.88802	5.292	0.029

Table 3.4: Breeding parameters at eight nest boxes where at least one egg has been laid for boreal owl (BOOW) and northern saw-whet owl (NSWO) at Clear Hills, Alberta, 2016.

Box	Species	Nest initiation date	Fledging date	Eggs laid	Hatched young	Fledglings
3	BOOW	31-May	NA	2	0	0
25	NSWO	12-Jun	10-Aug	5	4	3
43	NSWO	08-Jun	10-Aug	6	5	2
53	NSWO	15-Jun	10-Aug	4	4	4
61	BOOW	02-May	28-Jun	3	2	2
77	BOOW	10-Apr	NA	3	3	0
82	NSWO	10-May	NA	5	4	0
114	BOOW	NA	NA	2	0	0

3.7 Figures
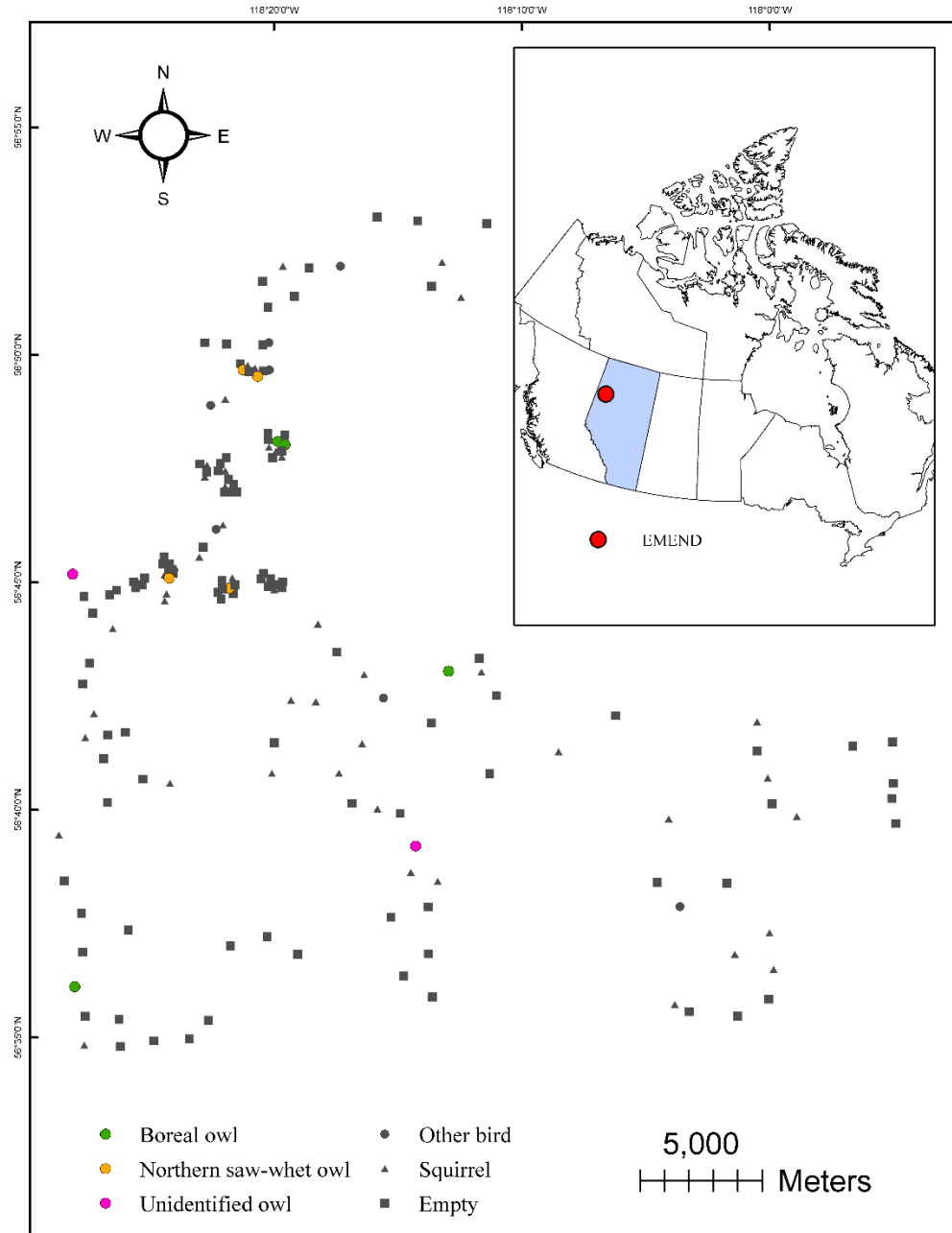
Figure 3.1: The nest box experiment in the Clear Hills region of northwestern Alberta, Canada. The inset map shows the location of the Ecosystem Management Emulating Natural Disturbance (EMEND) project site (56°46'13"N, 118°22'28"W), which represented the core of the experiment. The larger map presents the spatial arrangement of nest boxes (n = 164), and the symbols reflect box use in 2016.

Figure 3.2: Landscape composition of unused boxes and nest boxes occupied by owls at **(a)** nest site (100-m buffer around each box) and **(b)** home range (564-m buffer around each box) scale at Clear Hills, Alberta in 2016. Error bars represent Standard Error of means.

a)
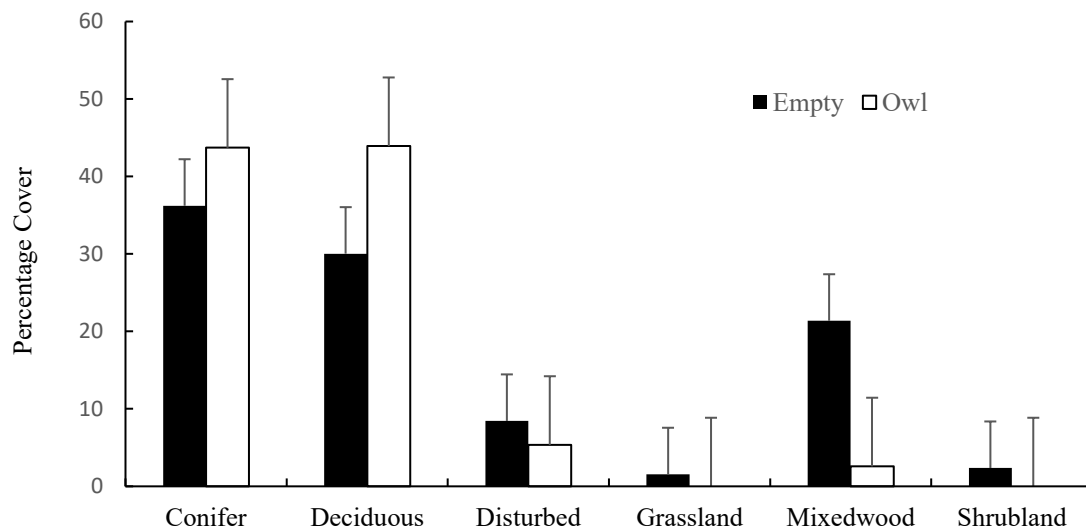
b)
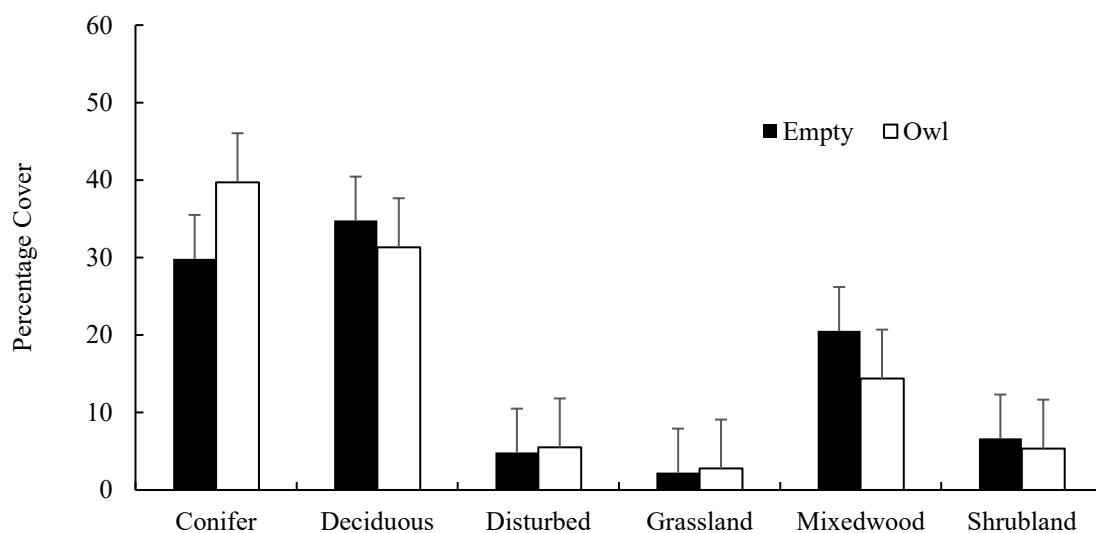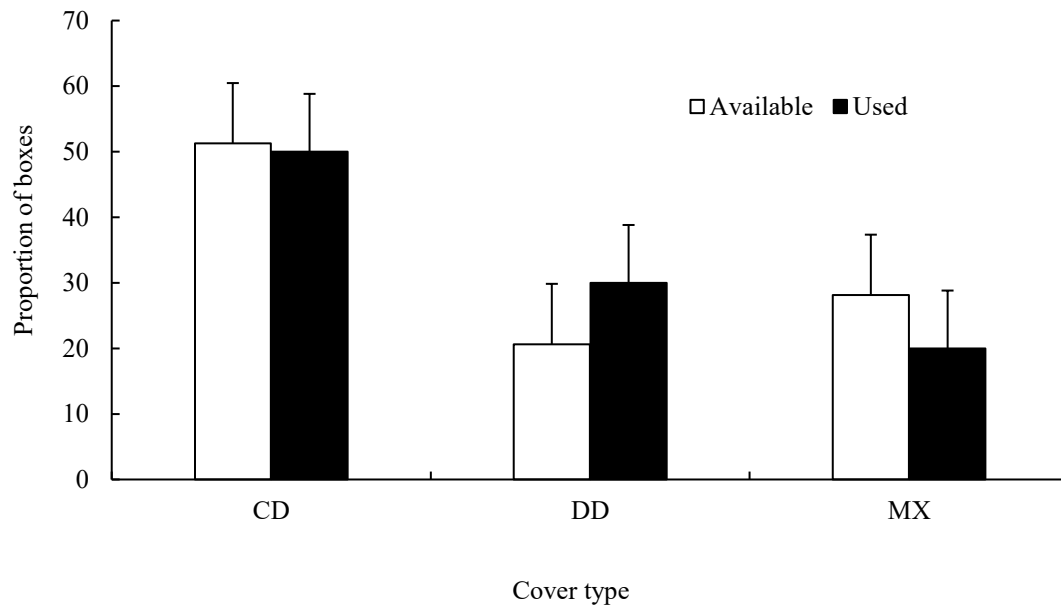
Figure 3.3: Mean proportion of nest boxes in conifer dominated (CD), mixed wood (MX) and deciduous dominated (DD) forest patches, available and used by 10 cavity nesting owls at Clear Hills, Alberta in 2016. Error bars represent Standard Error of mean.
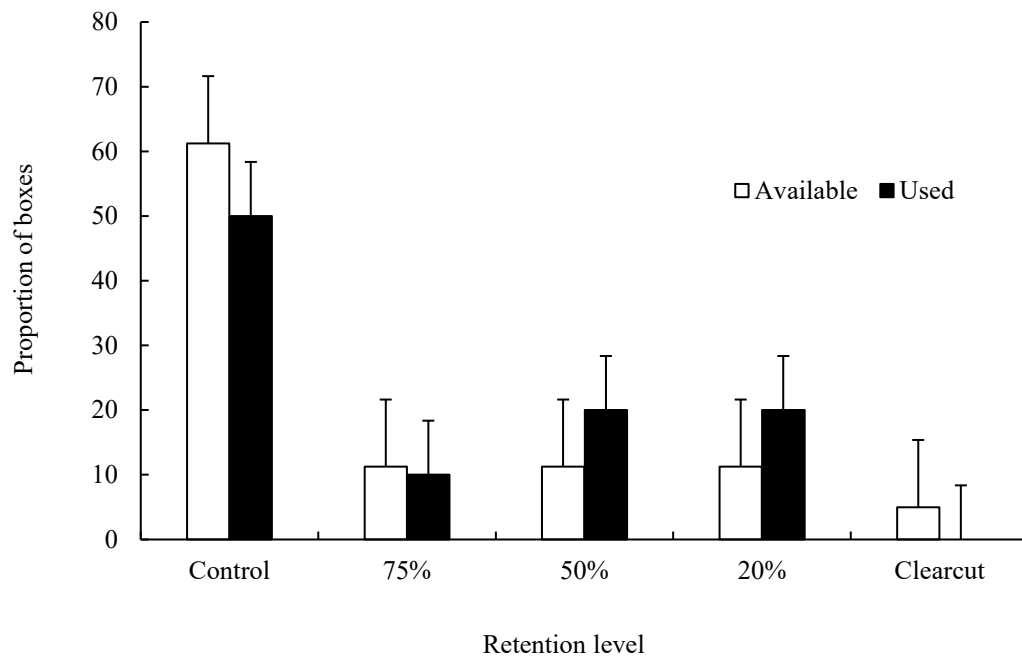
Figure 3.4: Proportion of available (n = 169) and used (n = 10) nest boxes in stands affected by five harvest levels at Clear Hills, Alberta in 2016. Used data represents pooled occupancies for boreal owl *Aegolius funereus*, northern saw-whet owl *Aegolius acadicus*, and unidentified owl *Aegolius* sp. Error bars represent Standard Error of mean.

Chapter Four: General discussion and conclusion

4.1 Summary and implications

The life of boreal and northern saw-whet owls is tied to forests. They breed in abandoned woodpecker cavities excavated in large trees, and during the day they roost in thick vegetation to hide from predators. The boreal forest is undergoing rapid change in Alberta, and both natural and human disturbances shape the spatial patterns of old forest cover, potentially influencing these owls. The idea of pursuing the work in this thesis came after reading conservation oriented results from Finland, showing that even though the boreal owl was a common forest predator there during the 1950s and 1960s, it is now considered near threatened due to landscape changes, and severe alteration of forest age and structure (Korpimaki and Hakkarainen 2012).

Both boreal and northern saw-whet owls are included in the Canadian Landbird Monitoring Strategy (http://www.cws-scf.ec.gc.ca/canbird/pif/p_intro.htm). Boreal owls are ranked high with respect to national responsibility, and medium with respect to population concern; while northern saw-whet owls are assigned a medium national responsibility, and medium population concern (Downes et al. 2000). The status of both species is currently considered secure, although existing census techniques might be inadequate to monitor owl populations, and improved monitoring activity for both species is recommended (Downes et al. 2000). Most species are rare with rarity defined in several different ways (Rabinowitz 1981; Espeland and Emam 2011). Although the overall population these owls is considered to be large and their distribution (range) widespread, local abundance is low. As such, I believe that without detailed information concerning their actual distribution and vital rates, we should not consider the status of these owls to be secure.

As I could find no previously published studies about the distribution and breeding ecology of these species in the Boreal region of Alberta, in this thesis I emphasized pattern description and hypothesis exploration rather than formal hypothesis testing. Specifically, I used recordings from passive audio surveys to better understand where boreal and northern saw-whet owls occur in Boreal Alberta and modelled their distribution using boosted regression trees. Analysis of these data illuminates the most influential (correlated) factors affecting the spatial distribution of these owls, and supports development of maps predicting the distribution (occurrence) of these species

throughout Boreal Alberta. Finally, I set up a nest box study in the northwest part of Alberta to examine local habitat preferences and breeding ecology of the boreal and northern saw-whet owls in an area affected by forest harvests, including those with different levels of green tree retention within harvest blocks. This study highlights the effectiveness of combining passive audio surveys with distribution modelling (Campos-Cerqueira and Aide 2016), and the value of nest box experiments (Hayward et al. 1992) in obtaining detailed information on two cryptic species.

Results were mostly in line with previous knowledge regarding ecology of boreal and northern saw-whet owls, but also revealed several new aspects that should be considered for future research in support of forest management and owl conservation. For instance, my study showed that climatic factors are important predictors of the distribution of both species, highlighting the role of snow as an important factor shaping owl distribution. It also suggested that projected climate change will affect future owl distribution. However, the temperature and precipitation limits identified by these models should not be regarded as thresholds related to the physiology of owls, because climate data comes from weather stations most often placed in open areas, and as such, microclimatic conditions created by local topography and vegetation cover are not correctly represented (Mbogga et al. 2010). At the same time, climate could be a proxy for other biota (e.g., small rodents), that influences owl distribution but was not considered in this study.

My results confirmed that the northern saw-whet owl is a generalist species, found in a variety of forested landscapes if suitable nesting cavities exist, while boreal owls are old conifer specialists. In a predominantly forested landscape, presence of croplands influenced the distribution of northern saw-whet owls. This does not mean that they are dependent on the presence of croplands alone, as models showed that they also need deciduous-dominated forests, found in climatically favorable areas. The nest box experiment confirmed the importance of deciduous stands highlighted by the distribution model, as northern saw-whet owls exclusively used boxes in stands that were deciduous-dominated at the nest site scale and deciduous-dominated or a mixture of deciduous and conifer composition at the scale of the home range. My study also revealed that northern saw-whet owls were present north of their previously known distribution, and that they successfully bred in partially harvested forests in northwestern Alberta at >55 °N. Distribution of boreal owls was influenced more by climate and disturbances than forest cover

type. Nest box use however, confirmed their association with old conifer stands as they selected nest boxes that were in conifer-dominated stands at both the nest site and home range scales.

Being secondary cavity nesters, both boreal and northern saw-whet owls are dependent on primary cavity excavators (Hayward et al. 1993; Korpimaki and Hakkarainen 2012). In areas of overlap where many raptor species coexist, predation and interspecific competition might also contribute to spatial distribution, and nest site selection (Cody 1985; Rosenzweig 1985; Hayward and Garton 1988). Both distribution modelling and the nest box experiment confirmed that the breeding ranges of these two species overlap in the boreal forest. Biotic interactions should therefore be considered when studying breeding ecology or modeling the distribution of these species. However, the predictive capacity of my distribution models did not improve when the presence/absence of potential competitors, predators, or nest site facilitators were included. This may reflect the scale at which analyses were conducted, as incorporating biotic interactions at 10-km scale did improve climate-land cover distribution models of Finnish owls (Heikkinen et al. 2007).

The effect of biotic interactions on nest box occupancy and breeding success was not directly tested, but intra- and interspecific competition did not seem to affect nesting owls. Northern saw-whet owls nested in relative proximity of conspecifics, the minimum distance between two occupied nest boxes was 659 m. Similar results were obtained in the commercial poplar plantations in Oregon, where owls nested within 0.5–1.2 km of nest boxes occupied by conspecifics (Marks et al. 2015). The early nesting boreal owls in my study occupied nest boxes 11.4 km apart; however, a second cutch was initiated only 330 m from a nest box that contained four boreal owl nestlings. These nest box results showed that the breeding range of boreal and northern saw-whet owls overlaps in the Boreal region of Alberta. It is probable that some home ranges overlapped within species, although significant local overlap between these two species seems unlikely as the minimum distance between occupied boreal and a northern saw-whet owl nest boxes was 2,770 m.

4.2 Resource management and owls

Disturbances in the boreal forest caused by activities of forestry and the oil and gas industry influenced the two species differently. These differences should be considered when planning

harvest patterns or future exploration work, or when considering mitigation plans for forest loss. Research in the Clear Hills of Alberta, suggests that stands of different age and structure created by partial retention harvesting with implementation of variable harvest levels might be a good option to maintain both species on the landscape. However, the nest box data suggest that these two species respond differently to harvest intensity. Nest boxes placed in recent (1–5 years) clear cuts were simply not used by owls. Boreal owls needed uncut stands or patches with at least 50% green tree retention after harvest, while northern saw-whet owls used forests that were more intensely harvested, at least after 17 years of stand recovery. Patches harvested at EMEND with 20% tree retention resembled young forests, unsuitable for owls. However, these stands are embedded in a landscape containing traditional clear cuts and uncut forest patches, creating a mosaic of forested landscape with uneven age and structure. The choice of northern saw-whet owls to occupy nest boxes placed in low retention stands, given that suitable boxes in higher retention or uncut patches were available at close range was surprising however, it is in line with other studies that found them breeding in landscapes containing a mixture of young and old forests (Gill and Cannings 1997). One year of nest box work did not provide enough data to make comparisons of owl use among retention levels. However, breeding parameters of boreal owls observed during 2016 were similar to conspecifics breeding in the high elevation, uncut forests of the Northern Rocky Mountains, US, while breeding success of northern saw-whet owls in the partially cut forests of Boreal Alberta did not differ from that observed in the more southern part of their range.

My work suggests that owl distribution is affected by different types of human disturbances and that these differ between these two species. Industrial developments included in this study are different from timber harvest as they usually result in removal of trees altering the landscape for a long period of time. Although linear clearings might seem less invasive than large-scale surface mining, they are present throughout the Boreal region, and likely influence owl distribution more than the industrial developments. My data suggest that presence of linear disturbances affected the distribution of boreal and northern saw-whet owls in different ways. Boreal owls were negatively affected by the presence of linear clearings represented by pipelines, vegetated transmission lines, seismic lines, and roads, as they were associated with areas containing low levels of soft linear disturbances at the home range scale. In contrast, northern saw whet owls did not avoid breeding close to edges created by linear disturbances. Perhaps they are accustomed to

breeding in fragmented landscapes, although (Hinam and Clair 2008) concluded that high levels of fragmentation negatively affects their breeding output.

The potential benefit of using species distribution models to guide research and conservation actions, including placement of nest boxes for boreal owls, has been highlighted before (Brambilla et al. 2013). As both boreal and northern saw-whet owls nest in old woodpecker cavities, use of predictive models developed here can assist harvest planners to identify areas suitable for both woodpeckers and owls. In this way, conservation-significant forest loss could be mitigated by ensuring that unharvested patches are of high quality for both primary cavity producers and secondary cavity nesters like boreal and northern saw-whet owls. In areas where habitat requirements of woodpeckers and owls differ, placement of nest boxes could be used to maintain boreal and northern saw-whet owls. In this case, predictive distribution models, rather than expert opinion, can be used to inform management decisions to place suitable nest boxes in high-quality areas (Brambilla et al. 2013).

4.3 Future research

As linear disturbances influenced both owl species, albeit quite differently, study of the effect of such disturbances on nesting success and productivity of these owls should be considered a priority. Although presence of competitors, predators, and nesting facilitators were of minor predictive value in this study, investigation at different scales might reveal important interactions that could not be detected in the analyses examined in this thesis. To improve knowledge about the breeding distribution of these owls throughout the boreal forest, more research is needed in the western and northern parts of the boreal, where current land-use is very different compared to the eastern and southern regions. Repeated site occupancy has been linked with high quality habitat for certain species (Sergio and Newton 2003), including boreal owls (Korpimaki and Hakkarainen 2012); however, occupancy should not be used alone as an indicator of habitat quality (Van Horne 1983). The large-scale distribution model developed here can be linked with finer scale nest box occupancy and breeding performance data collected over several years to determine if there are significant correlations between high quality areas and breeding success. In addition, long-term monitoring of owl breeding success in nest boxes could reveal the effects of important factors that alter habitat quality.

4.4 Final conclusion

This thesis improves our understanding of distribution of the most common small owls in the Boreal region of Alberta and provides information about their habitat use and breeding performance in landscapes affected by forestry. The study has some limitations that must be acknowledged. While it identifies important components affecting the distribution and nest box use of owls, it is possible that there are other environmental and biotic variables capable of better explaining owl distribution. It is also possible that certain disturbances, like soft linear disturbances, are associated with habitat types (e.g., peat bogs) that are avoided by owls but were not considered as a separate land cover variable in this study. Distribution maps were developed based on land cover and disturbance variables referenced to year 2014 and as such they are unable to account for recent, large scale natural disturbances like forest fires. Breeding data collected during a single season, should be just the start of a long-term study that examines owl response to variable retention timber harvesting. My study gives us some insight into what drives owl distribution at regional scales and what is important to owls when choosing an actual nest site. Despite its limitations, results of this work could save important resources necessary to identify areas of high probable occupancy, especially with more data about habitat characteristics associated with the presence and breeding performance of boreal and northern saw-whet owls.

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Appendices
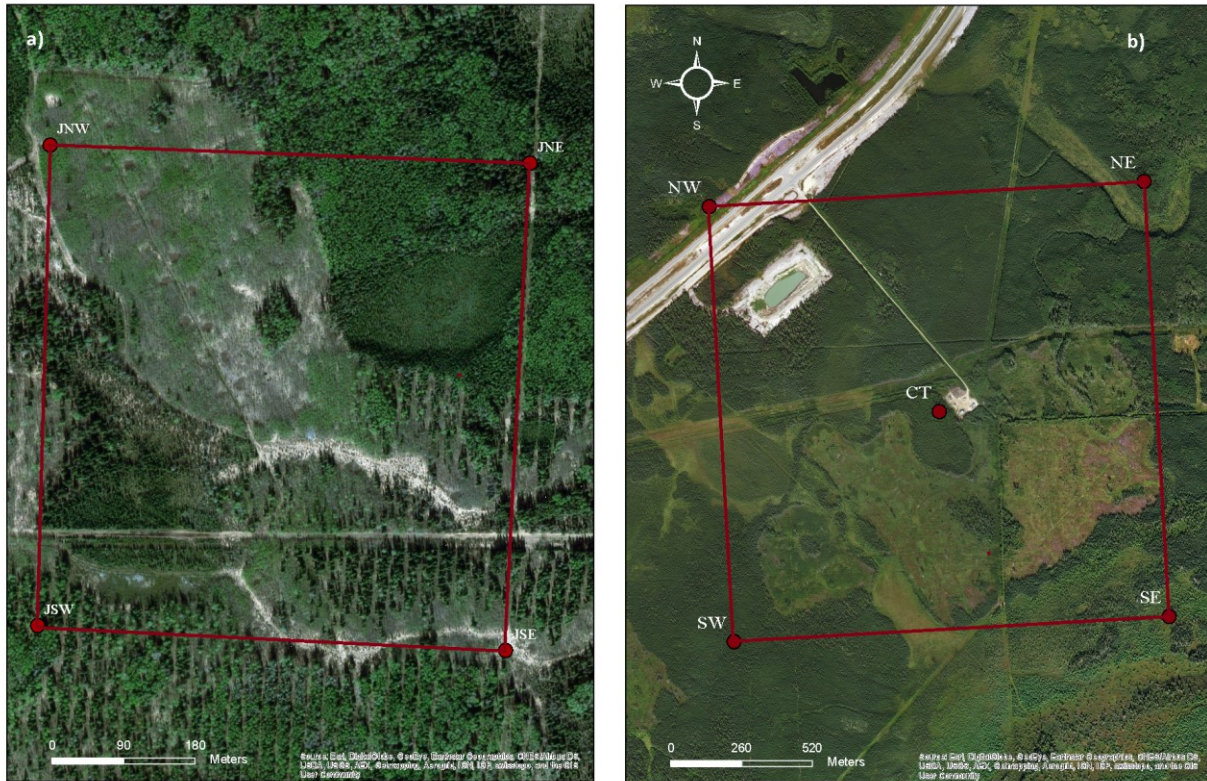
Appendix 1: Field deployment of Autonomous Recording Units (ARU) using two different designs: a) grids of five units with one unit at the corners of a 1,600-m square and one central unit and b) four-unit grids with one ARU at each corner of a 600-m square.

Appendix 2: Predictor variables used to model spatial distribution of boreal and northern saw-whet owls in the Boreal Forest Natural Region of Alberta, Canada.

Code	Variable
[a]boow	Presence / absence of boreal owl
[a]ghow	Presence / absence of great-horned owl
[a]nswo	Presence / absence of northern saw-whet owl
[a]piwo	Presence / absence of pileated woodpecker
[b]con150; con564	Percent conifer forest at nest site* (NS); home range** (HR)
[b]cro150; cro564	Percent cropland within NS; and HR
[b]dec150; dec564	Percent deciduous forest within NS; and HR
[b]for150; for564	Percent forest cover within NS; and HR
[b]gra150; gra564	Percent grassland cover within NS; and HR
[b]mix150; mix564	Percent mixed wood forest within NS; and HR
[b]shr150; shr564	Percent shrubland cover within NS; and HR
[b]wat150; wat564	Percent area covered by water within NS; and HR
[c]hrdlin150; hrdlin564	Percent hard linear disturbances[+] within NS; and HR
[c]ind150; ind564	Percent industrial disturbances[++] within NS; and HR
[c]sftlin150; sftlin564	Percent soft linear disturbances[+++] within NS; and HR
[d]ffp	Frost-free period
[d]map	Mean annual precipitation (mm),
[d]mat	Mean annual temperature (°C)
[d]mcmt	Mean coldest month temperature (°C)
[d]mwmt	Mean warmest month temperature (°C)
[d]pas	Precipitation as snow (mm)
[d]pptsm	Summer precipitation (mm)
[d]pptwt	Winter precipitation (mm)
[d]tavsm	Summer mean temperature (°C)
[d]tavwt	Winter mean temperature (°C)
[d]td	Temperature difference between mwmt and mcmt, (°C)
[d]tmnwt	Winter mean minimum temperature (°C)
[d]tmxsm	Summer mean maximum temperature (°C)

* Nest site (NS) represents a 150-m buffer around each Autonomous Recording Unit (ARU)

** Home range (HR) represents a 564-m buffer around each ARU

+ Hard linear disturbances include permanent roads and railways

++ Industrial disturbances include mining sites, borrow pits, well sites, wind generation sites, urban and rural industrial developments

+++ Soft linear disturbances include vegetated transmission lines, pipelines, seismic lines, vegetated road/trails, vegetated road verge

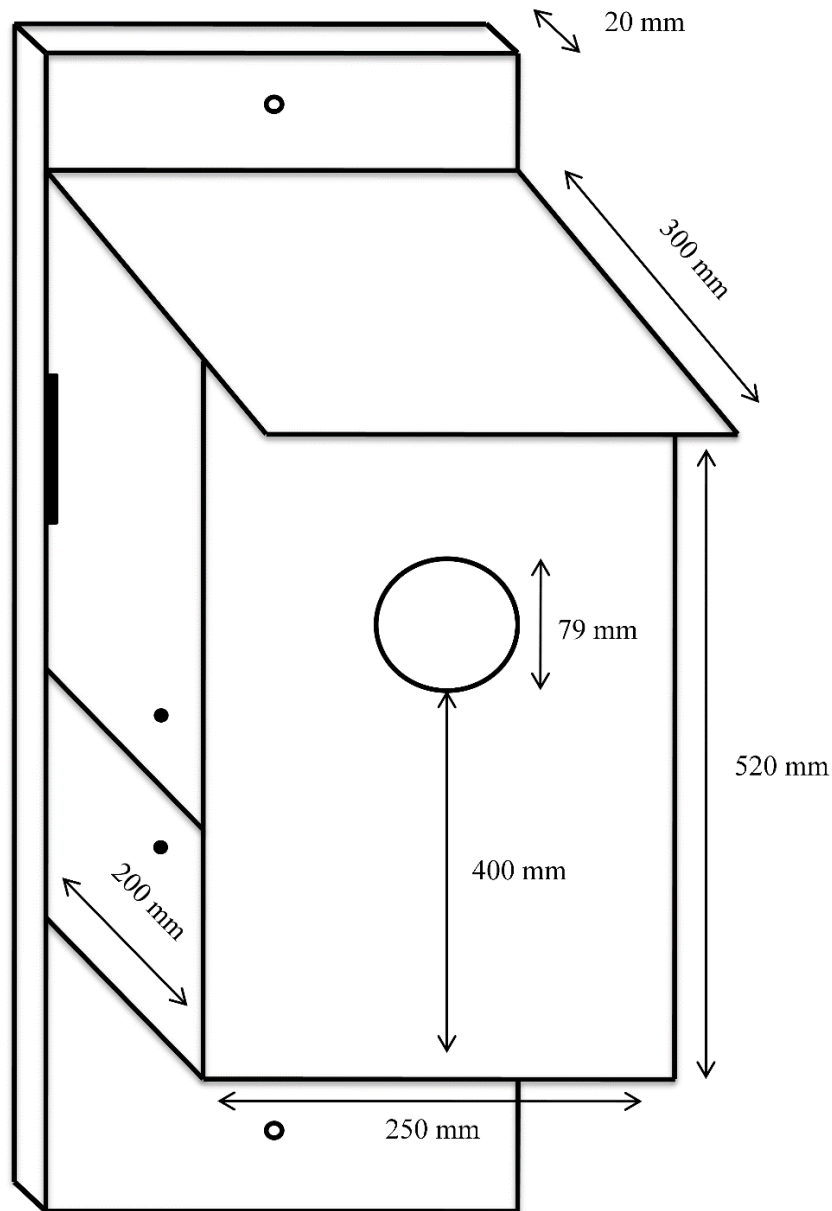[a] Biotic variables related to nesting facilitators, competitors, and predators

[b] Landscape variables related to major land cover types

[c] Human disturbance related variables

[d] Climatic variables

Appendix 3: BRT model characteristics and their predictive performance for boreal owls (BOOW) and northern saw-whet owls (NSWO). All models were developed with 10-fold cross-validation on data from 677 sites, tree complexity of 5 and learning rate of 0.005.

	BOOW		NSWO	
	Base model	Best model	Base model	Best model
No. of trees	2050	1900	1250	1400
No. of predictors	38	29	38	33
Deviance explained (%)	36.1	36.2	38.2	39.2
AUC	0.878	0.880	0.887	0.893

Appendix 4: Nest box dimensions used in my experiment at Clear Hills, Alberta, following Korpimaki (1985) with modification of the door to increase ease of access while maintaining security of eggs and nestlings. The boxes were made of rough - sawn spruce lumber with a layer of 100 mm of woodchips in the bottom of each assembled box to increase insulation and prevent egg breakage. The entrance hole of 79 mm is suitable for both boreal owls *Aegolius funereus* and northern saw-whet owls *Aegolius acadicus*, while restricting access of larger owls or other frequent cavity nesting birds like wood ducks *Aix sponsa.*

Appendix 5: List of candidate models predicting nest box occupancy based on landscape characteristics and scale of measurement at Clear Hills, Alberta in 2016. Nest site (NS) scale represents a 150-m buffer, while home range (HR) scale data are calculated within a 564-m buffer drawn around each nest box. The positive (+) and negative (-) signs for model components indicate the predicted effect of the variable.

Model ID	Hypothesis	Scale	Model components
H0	Null	N.A.	.
H1$_a$	Old forest	NS	+ forage$_{100}$
H1$_b$	Old forest	HR	+ forage$_{564}$
H2$_a$	Forest cover	NS	+ % forest$_{100}$
H2$_b$	Forest cover	HR	+ % forest$_{564}$
H3$_a$	Dominant cover	NS	+ % mix$_{100}$
H3$_b$	Dominant cover	HR	+ % mix$_{564}$
H4$_a$	Forested land covered by old forest	NS	+ % oldforest$_{100}$
H4$_b$	Forested land covered by old forest	HR	+ % oldforest$_{564}$
H5$_a$	Disturbance	NS	- % disturbed$_{100}$
H5$_b$	Disturbance	HR	- % disturbed$_{564}$
H6$_a$	Open habitat	NS	- % grass$_{100}$
H6$_b$	Open habitat	HR	+ % grass$_{564}$
H7	Forest intactness	NS	+ % ret$_{100}$