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Habitat Use by Boreal Mammals in Response to Salvage Logging After an Insect Outbreak

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Habitat Use by Boreal Mammals in Response to Salvage Logging After an Insect Outbreak

by

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A THESIS

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Abstract

Post-disturbance logging (i.e., salvage logging) is controversial, as it may disrupt forest succession and alter wildlife habitat. I examined habitat use by moose (*Alces americanus*), snowshoe hares (*Lepus americanus*), lynx (*Lynx canadensis*), coyotes (*Canis latrans*), and little brown bats (*Myotis lucifugus*) in response to salvage logging after a bark beetle outbreak in Yukon, Canada. I monitored species occupancy in beetle-affected forests and salvage-logged stands of different tree retention levels and ages using wildlife cameras and bat detectors. Moose occupancy was highest in low-retention-logged stands with low cover and abundant shrubs. Snowshoe hares occupied stands with dense canopies and avoided logged stands (regardless of retention or age); lynx and coyote used similar habitat to hares. Logging had no significant effect on little brown bats, although bats avoided densely-treed stands. Diverse forest management strategies may benefit the most species, including salvage logging with variable retention and maintaining patches of beetle-affected forest.

Keywords: salvage logging, retention, spruce beetle, mammals, occupancy, habitat use

Preface

This thesis is original, unpublished, independent work by the author, Julie Thomas.

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Table of Contents

Abstract	ii
Preface.....	iii
Acknowledgements.....	iv
Table of Contents	vi
List of Tables	viii
List of Figures	ix
Chapter One: General Introduction.....	1
1.1 Natural Disturbances and Salvage Logging.....	1
1.2 Approaches to Applied Conservation Research	4
1.3 Occupancy Modelling.....	4
1.4 Thesis Overview	6
Chapter Two: Site Occupancy of Moose (<i>Alces americanus</i>), Snowshoe Hare (<i>Lepus americanus</i>), Lynx (<i>Lynx canadensis</i>), and Coyote (<i>Canis latrans</i>) in Response to Salvage Logging after an Insect Outbreak.....	8
2.1 Introduction.....	8
2.2 Methods	13
2.2.1 Study area	13
2.2.2 Study species	14
2.2.3 Study design	15
2.2.4 Occupancy surveys.....	16
2.2.5 Vegetation, forest, and landscape structure	16
2.2.6 Statistical analyses.....	18
2.3 Results.....	22
2.3.1 Moose	23
2.3.2 Snowshoe hare.....	26
2.3.3 Lynx and coyote	27
2.4 Discussion.....	28
2.4.1 Moose	28
2.4.2 Snowshoe hare.....	31
2.4.3 Lynx and coyote	34
2.4.4 Management implications	35
Chapter Three: Effects of Salvage Logging on Little Brown Bat (<i>Myotis lucifugus</i>) Occupancy Near its Northern Range Limit	54
3.1 Introduction.....	54
3.2 Methods	59
3.2.1 Study area	59
3.2.2 Study species	60
3.2.3 Study design	61
3.2.4 Bat surveys	62
3.2.5 Habitat and climate.....	63

3.2.6 Statistical analyses	64
3.3 Results	67
3.4 Discussion	69
3.4.1 Management implications and future work	72
Chapter Four: Summary and Conclusions	80
4.1 Study Limitations and Suggestions for Future Research	81
4.2 Management Recommendations	83
Literature Cited	86
Appendix A: Moran's I Spatial Correlograms	103

List of Tables

Table 2.1 Variable names, descriptions, and hypotheses for site- and landscape-level habitat variables used in occupancy models for moose and snowshoe hare in beetle-affected and salvage-logged forests in Yukon, Canada.....	37
Table 2.2 Variable names, descriptions, and hypotheses for site- and landscape-level habitat variables used in occupancy models for lynx and coyote in beetle-affected and salvage-logged forests in Yukon, Canada.	38
Table 2.3 Confidence set of occupancy (ψ) models for moose, snowshoe hare, lynx, and coyote in beetle-affected and salvaged forests in Yukon, Canada.....	39
Table 2.4 Model averaged parameter estimates, unconditional standard errors (SE), and 95% confidence intervals (CI) for moose, snowshoe hare, lynx, and coyote detection (ρ) and occupancy (ψ) in southwest Yukon, Canada.	40
Table 2.5 Confidence set of multi-state moose occupancy models in beetle-affected and salvage-logged forests in Yukon, Canada.....	41
Table 2.6 Model averaged parameter estimates, unconditional standard errors (SE), and 95% confidence intervals (CI) for moose multi-state models.....	42
Table 3.1 Variable names, descriptions, and hypotheses for site- and landscape-level habitat variables used in occupancy and detection models for the little brown bats (<i>Myotis lucifugus</i>) in salvage-logged and unsalvaged forests in Yukon, Canada.....	74
Table 3.2 Full set of detection (ρ) models for little brown bats (<i>Myotis lucifugus</i>) in beetle-affected and salvage-logged forests in southwest Yukon, Canada..	75
Table 3.3 Confidence set of occupancy (ψ) models for little brown bats (<i>Myotis lucifugus</i>) in beetle-affected and salvage-logged forests in southwest Yukon, Canada.	76
Table 3.4 Model averaged parameter estimates, unconditional standard errors (SE), and 95% confidence intervals (CI) for little brown bat (<i>Myotis luficugus</i>) detection (ρ) and occupancy (ψ) in southwest Yukon, Canada.	76

List of Figures

Figure 2.1 Map of study sites in southwest Yukon, including high-retention logged (n=38), low-retention logged (n=22), and un-salvaged spruce beetle sites (n=30).	43
Figure 2.2 Photos of an aerial view of spruce bark beetle infestation (A); spruce beetle affected stand (B); low-retention logged stand (C); and high-retention logged stand (D). ..	44
Figure 2.3 Photos of salvage-logged stands of two different age categories: 0 – 10 years post-harvest (A), and 11-25 years post-harvest (B).	45
Figure 2.4 Transect layout for vegetation and forest structure surveys.....	46
Figure 2.5 Examples of wildlife photographs captured with Reconyx Hyperfire cameras from May-October 2016 near Haines Junction, Yukon.....	47
Figure 2.6 Comparison of mean vegetation and forest structure measurements between low-retention salvage-logged (LR), high-retention salvage-logged (HR), and unsalvaged beetle-affected stands (US) in southern Yukon, Canada.	48
Figure 2.7 Comparison of mean vegetation and forest structure measurements between young salvage-logged stands (0-10 years post-harvest) and old salvage-logged stands (11-25 years post-harvest) in southern Yukon, Canada.	49
Figure 2.8 Model-averaged estimates of moose occupancy as a function of canopy cover (A), distance to water (B), woody debris (C), and stand type (D) in southwest Yukon, Canada.....	50
Figure 2.9 Model-averaged estimates of snowshoe occupancy as a function of overstory tree density (A), canopy cover (B), lateral cover (C), and shrub + herb+ grass cover (D) in southwest Yukon, Canada.....	51
Figure 2.10 Mean estimates of snowshoe hare, lynx, and coyote occupancy in salvage logged stands of different retention levels (low/high) and ages (0-10 years and 11-25 years post-harvest), and in un-salvaged forest stands in southwest Yukon, Canada.	52
Figure 2.11 Model-averaged estimates of lynx (A) an coyote (B) occupancy versus predicted snowshoe hare occupancy in beetle-affected salvage logged and un-salvaged stands in southwest Yukon, Canada.....	53
Figure 3.1 Model-averaged predictions of little brown bat (<i>Myotis lucifugus</i>) detection and occupancy in bark-beetle affected and salvage-logged forests in southwest Yukon, Canada, including the probability of detection in early and late sampling periods (A), and the probability of occupancy as a function of tree basal area (B), canopy cover (C), distance to water (D), distance to forest edge (E), and total edge (F).....	77

- Figure 3.2 Model-averaged predictions of little brown bat (*Myotis lucifugus*) occupancy as a function of tree basal area (A) and distance to town (B) in beetle-affected and salvage-logged stands in southwest Yukon, Canada, during the early (1 June – 15 July) and late (16 July – 31 August) sampling periods 78
- Figure 3.3 Predicted estimates of little brown bat (*Myotis lucifugus*) occupancy in salvage-logged stands of different retention levels (low/high) and in unsalvaged forest stands in southwest Yukon, Canada..... 79

Chapter One: General Introduction

1.1 Natural Disturbances and Salvage Logging

Natural disturbances shape the structure and function of forests around the world (Attiwill 1994). Boreal forests are dynamic ecosystems that cycle continuously through phases of regeneration, often driven by fire and insect outbreaks (McCullough et al. 1998). Fires may raise productivity and accelerate nutrient cycling (Bonan and Shugart 1989), whereas bark beetles — another major agent of tree mortality (Veblen et al. 1991) — create forest gaps that increase plant and invertebrate diversity (Müller et al. 2008). Bark beetles may alter conditions in favour of sub-dominant tree species (Veblen et al. 1991), promoting a mosaic of forest types at the landscape scale (McCullough et al. 1998). A broad range of forest types and successional stages are required to meet the diverse needs of animals in the boreal forest (Fisher and Wilkinson 2005).

Fires and insect outbreaks are often viewed as ecological disasters and threats to economic livelihood and biodiversity (McFarlane et al. 2006, Steelman and McCaffrey 2011). Public opinion often favours controlling natural disturbances and removing dead trees from the landscape (McGrady et al. 2016). “Salvage logging” is the term used for harvesting trees that have been killed by natural disturbance (although dead and remnant live trees are often taken; Schmiegelow et al. 2006). A key motivation for salvage logging is to recover the economic value of the dead wood and return the forest to a commercially productive state (Peter and Bogdanski 2010, Mansuy et al. 2015). In the case of bark beetle outbreaks, the impetus may be to reduce fuel loads and prevent catastrophic fires (Shore et al. 2003), although the link between bark beetle damage and fire risk is tenuous (Bebi et al. 2003, Hood et al. 2017). Salvage logging also has proposed ecological benefits. For example, it may accelerate the return to mature forest, thus

benefitting obligate old-growth species (Sessions et al. 2004). Logging burned or beetle-killed forest is preferable to logging intact forest for disturbance-averse species (e.g. woodland caribou [*Rangifer tarandus caribou*]); it creates overlapping rather than adjacent disturbances, minimizing the overall footprint (Beguin et al. 2015). However, salvage logging can interrupt forest regeneration and reduce habitat value for the multitude of species that benefit from natural disturbance, depleting overall biodiversity (e.g. Hutto 2006, Lindenmayer and Noss 2006, Schmiegelow et al. 2006, Thorn et al. 2018).

Most research on the ecology of salvage logging has focused on vascular plants, invertebrates, and birds (Thorn et al. 2018). Bark beetles cause partial or patchy tree mortality, with negligible effects on understory plants (Fischer et al. 2015). In contrast, salvage logging may alter early-successional plant communities in favour of deciduous species, resulting in a shift from coniferous to deciduous stands (Timoney et al. 1997, Goodman and Hungate 2006). Salvage logging reduces the quantity of standing and downed wood (Lewis 2009), causing a decline in saproxylic invertebrates (Thorn et al. 2018). Snag-dependent bird species that nest in cavities (e.g., woodpeckers) may be abundant in burned (Hutto 2008) or beetle-affected stands (Edworthy et al. 2011), but are largely absent from salvage-logged stands (Morissette et al. 2002) where they have lower nesting success (Saab et al. 2007).

Few published studies have examined the consequences of salvage logging for mammals (reviewed in Saab et al. 2014). Southern red-backed voles (*Myodes gapperi*), which are associated with mature forest, were less abundant in salvage logged stands (Sullivan et al. 2010). Abundance of northern red-backed voles (*Myodes rutilus*) declined following a bark beetle outbreak, but did not respond to subsequent salvage logging (Lance et al. 2006). Insectivorous bats were generally unaffected by post-beetle salvage logging, with the exception of open-habitat

specialists that preferred salvage-logged stands (Mehr et al. 2012). Elk (*Cervus elaphus*) experienced higher predation in salvage-logged stands due to loss of cover and improved predator access via logging roads (Hebblewhite et al. 2009). For other mammals, knowledge is largely informed by predictive modelling (Proulx 2009) or speculation based on species' natural history and response to other disturbances (Bunnell et al. 2004). Logging retention (i.e., the number of trees retained) and stand age may influence habitat value for mammals (Fisher and Wilkinson 2005, Sullivan et al. 2010), further complicating the issue.

Most research on the ecology of salvage logging has focused on previously burned forests (Thorn et al. 2018). However, bark beetles are increasingly influential agents of tree mortality in boreal forests as a consequence of climate warming (Bentz et al. 2010, Fettig et al. 2013). Beetle-affected forests have different successional trajectories than burned forests (Stevens-Rumann et al. 2015), and the impacts of post-infestation salvage may therefore differ from those of post-fire salvage for the same species (e.g. passerines, Kroll et al. 2012).

Anthropogenic climate warming is expected to increase the severity and frequency of bark beetle infestations, particularly at high latitudes (Bentz et al. 2010). Warming has been implicated as the cause of recent, severe spruce beetle (*Dendroctonus rufipennis*) outbreaks in Yukon and Alaska (Berg et al. 2006). Post-infestation salvage logging (and logging in general) is a relatively new practice in the northern boreal forest, and few studies have examined salvage logging at such high latitudes — particularly the effects on mammals (but see Lance et al. 2006, Randall 2009). The impacts of salvage logging may vary with climate and latitude, both of which influence nutrient cycling rates and productivity (Hart and Chen 2006). Logged stands decline in productivity along a latitudinal gradient, which reduces the value of these stands to wildlife (Gagné et al. 2016).

1.2 Approaches to Applied Conservation Research

Conservation research often focuses on anthropogenic impacts to a single “indicator species” that is associated with high biodiversity, is sensitive to environmental stressors, or is closely affiliated with specific environmental conditions (Simberloff 1998). For example, the black-backed woodpecker (*Picoides arcticus*) is associated with severe burns and is used to monitor the impacts of post-fire salvage logging (Saab et al. 2007, Hutto 2008). However, management strategies that focus on the needs of one species may occur to the detriment of others, and they will fail to address the needs of the entire community (Simberloff 1998).

An alternative to the detailed single-species approach is to conduct ecosystem-oriented research, with an emphasis on broad patterns of biodiversity at the landscape-scale (Lindenmayer et al. 2007). However, such high-level approaches are unlikely to address the causal processes governing species responses to anthropogenic disturbance. To strike a balance between these opposing methods, one solution is to focus on a suite of species with different functions, niches, trophic levels, or spatial requirements to represent a larger taxonomic group (Lambeck 1997); this is the approach I have adopted for mammals. Such studies have become feasible owing to recent development of compact remote monitoring devices (e.g. wildlife cameras; Steenweg et al. 2017).

1.3 Occupancy Modelling

Occupancy modelling is a likelihood-based method for estimating the probability of species occupancy at a given site or patch while accounting for imperfect species detection (i.e., the probability of false absences; Mackenzie et al. 2002). This approach is commonly used to obtain information on general habitat use and species distribution at a landscape scale (e.g. Long

et al. 2011, Kaiser and O’Keefe 2015), or to monitor long-term population trends (Mackenzie et al. 2006). More recently, occupancy models have been used to answer targeted questions about anthropogenic impacts on wildlife; for example, the effects of clear-cut logging on common nighthawks (*Chordeiles minor*; Farrell et al. 2017), the influence of forest loss and climate change on snowshoe hares (*Lepus americanus*; Saultaire et al. 2016), and the effects of post-fire salvage logging on nesting owls (Clark et al. 2013).

Occupancy modelling has similarities with logistic regression — both approaches use binary (presence/absence) data — but logistic regression assumes species are always detected when present. Modelling approaches that do not include a detection component can result in biased occupancy estimates, to the extent that occupancy and detection are confounded (Guillera-Arroita et al. 2014). With hierarchical occupancy models, the probability of detection is explicitly modelled with data collected during repeat sampling, and models can account for variable detection rates across habitat types (e.g. vegetation densities) and survey conditions (e.g. weather, different observers) (Mackenzie et al. 2002).

Occupancy models are based on a set of assumptions. First, they assume that species are never falsely detected when absent. Detection at a given site is assumed to be independent of other sites (i.e., no spatial autocorrelation; Mackenzie et al. 2002); however, there are modelling approaches to deal with spatial dependence (MacKenzie and Bailey 2004). Sites are assumed to be closed to changes in occupancy through the duration of the sampling period. This assumption is frequently violated in wildlife studies, as wide-ranging animals can readily move between sites, particularly when sites are defined by point sampling devices in continuous habitat (Efford and Dawson 2012). When the closure assumption is violated, occupancy should be interpreted as

“use”: the probability that a portion of the continuous landscape is used by *any* individual during the survey period (Mackenzie et al. 2006).

Occupancy models have advantages and limitations. They are useful for monitoring rare or elusive species for which abundance estimates are not feasible (Mackenzie et al. 2006). Presence/absence surveys are also conducive to non-invasive research methods (e.g. camera traps, snow-tracking, acoustic recordings). However, a large number of sites — and many repeat samples per site — are required to obtain precise occupancy estimates, particularly if detection probabilities are low (Mackenzie and Royle 2005). Generally, occupancy cannot be used as a substitute for abundance, as the relationship between occupancy and abundance is unlikely to be proportional (Stanley and Royle 2005). When used to quantify habitat use, occupancy models implicitly assume a direct link between species presence, habitat use, and habitat quality. Measures of species performance (e.g. survival, growth, or reproduction) in different habitats may be necessary to gain a true sense of habitat value.

1.4 Thesis Overview

In this thesis, I examine patterns of habitat use by five mammal species in response to salvage logging after a spruce beetle (*Dendroctonus rufipennis*) outbreak in Yukon, Canada, using an occupancy modelling approach. I compare species occupancy in salvage-logged stands of various tree retention levels and successional stages, and discuss the management implications of my findings. My objective was to monitor representative mammal species of different ecological niches and trophic levels. However, several taxonomic groups are absent due to timing constraints or data deficiency (arboreal sciurids, mustelids, and ursids). Small mammal (Rodentia and Insectivora) responses to salvage logging have been comparatively well-studied in

the boreal forest (e.g. Lance et al. 2006, Sullivan et al. 2010, Kronland and Restani 2011), so I excluded this group.

In Chapter Two I compare the effects of post-infestation salvage logging on habitat use by terrestrial mammals, including two ecologically important herbivores (moose [*Alces americanus*] and snowshoe hare) and two prominent boreal forest predators (lynx [*Lynx canadensis*] and coyote [*Canis latrans*]). In Chapter Three, I present an analysis of salvage logging impacts on the insectivorous little brown bat (*Myotis lucifugus*), where it occurs near the northern limit of its geographic range. Chapter Four includes a summary of my findings and a discussion on study limitations, management implications, and suggestions for future work.

Chapter Two: Site Occupancy of Moose (*Alces americanus*), Snowshoe Hare (*Lepus americanus*), Lynx (*Lynx canadensis*), and Coyote (*Canis latrans*) in Response to Salvage Logging after an Insect Outbreak

2.1 Introduction

Natural disturbances such as forest fires and insect outbreaks shape the composition, structure, and function of boreal forests (Attiwill 1994). Although these disturbances are part of natural ecosystem function, they typically invoke a management response, including attempts to control the extent and severity of the disturbance or manage the aftermath (Noss et al. 2006, Fettig et al. 2007). One such response is post-disturbance logging (i.e. “salvage logging”), the practice of harvesting fire- or insect-killed trees to minimize economic losses (Peter and Bogdanski 2010, Mansuy et al. 2015) and reduce wildfire risk (Shore et al. 2003). The ecological consequences of salvage logging are poorly understood, although it is claimed to aid forest recovery (Sessions et al. 2004) and improve wildlife habitat (Beguín et al. 2015), and is occasionally used as a management tool in parks and protected areas (Shore et al. 2003, Mehr et al. 2012, Thorn et al. 2018). Alternatively, evidence suggests that salvage logging may disrupt post-disturbance succession, reduce ecosystem services, remove biological legacies (e.g. snags), and alter wildlife habitat (reviewed in Hutto 2006, Lindenmayer and Noss 2006, Noss et al. 2006, Schmiegelow et al. 2006). Salvage logging has become contentious in recent years (Lindenmayer and Noss 2006). This debate may become increasingly relevant, as climate warming is predicted to increase the frequency and severity of natural disturbances (Dale et al. 2001, Berg et al. 2006, Bentz et al. 2010, Fettig et al. 2013), generating more opportunities to salvage log.

Fire has historically been the predominant disturbance agent in the North American boreal forest (Stocks et al. 2002); however, insect outbreaks are increasingly influential agents of

tree mortality (Berg et al. 2006, Werner et al. 2006, Raffa et al. 2008). Forests affected by bark beetles have different successional trajectories than burned forests (Stevens-Rumann et al. 2015), and the impacts of post-infestation salvage may differ from those of post-fire salvage for the same species (Kroll et al. 2012). With respect to wildlife, the impacts of post-infestation salvage logging have been documented for many bird species (Drever and Martin 2010, Edworthy et al. 2011, Kroll et al. 2012), but few published studies have examined consequences for mammals (reviewed in Saab et al. 2014).

Mammalian responses to post-infestation salvage logging are expected to vary, with potential benefits for early-seral species and negative consequences for species that require mature forests (Saab et al. 2014). For herbivores associated with early- or mid-successional forests (e.g. some ungulates, lagomorphs, and rodents [Fisher and Wilkinson 2005]), canopy gaps created by beetle disturbance may stimulate growth of understory vegetation and improve food availability (Stone 1995, Klenner and Arsenault 2009). This effect could be enhanced by removal of additional trees during post-disturbance salvage logging, particularly in northern boreal forests where ground disturbance from harvest machinery may be necessary to stimulate an understory response (Allen et al. 2006, Jonášová and Prach 2008). Selective salvage logging may have relatively minor impacts on understory vegetation, but clear-cut logging completely alters early-successional communities and can cause a shift from coniferous to deciduous stands (Timoney et al. 1997, Goodman and Hungate 2006). Clear-cutting may result in the greatest food enhancements for herbivores, particularly during mid- successional stages when deciduous shrubs are abundant.

For some mammals, salvage logging removes concealment and escape cover provided by beetle-killed trees, which can otherwise remain standing for 30 years after an infestation (Garbutt

et al. 2006). This loss of structure can increase predation risk for ungulates such as moose (*Alces americanus*), elk (*Cervus canadensis*), and deer (*Odocoileus* spp.) (Mysterud and Ostbye 1999, Kunkel and Pletscher 2000, Hebblewhite et al. 2009). In a system where moose populations are limited by predators, moose may prefer habitat that provides tree cover over habitat with high food availability across all seasons (Dussault et al. 2005b). These preferences are most pronounced for females with calves, because calves are more susceptible to predation (Miquelle et al. 1992, Dussault et al. 2005b, Oehlers et al. 2011). In addition, road building associated with salvage logging improves access for wolves (*Canis lupus*) (Whittington et al. 2005, 2011) and human hunters (Rempel et al. 1997), which may increase ungulate mortality. For snowshoe hares (*Lepus americanus*), the loss of canopy cover and lateral cover may significantly increase risk of predation by aerial and terrestrial predators (Hodges 2000, Feierabend and Kielland 2015), particularly in early-successional stands where understory shrub cover has not yet recovered (Hodges 2000). Logging practices that retain many residual trees could mitigate these negative impacts (Hodson et al. 2010b, Ruel et al. 2013), provided that residual trees are not reduced to windthrow in subsequent years. Woody debris from windthrow or felled unmerchantable timber (i.e., slash) provides cover for snowshoe hares and other small mammals (Thompson et al. 2003, Strong and Jung 2012), but may increase the energetic costs of movement for large ungulates with few offsetting benefits (Parker et al. 1984).

For predators in the boreal forest, such as lynx (*Lynx canadensis*), coyotes (*Canis latrans*), and wolves, stand selection is closely linked to prey availability (Murray et al. 1994, O'Donoghue et al. 1998, 2001, Mowat and Slough 2003, Long et al. 2011, Kittle et al. 2017). Habitat selection may also depend on the ability to detect and access prey (Boisjoly et al. 2010, Kittle et al. 2017); for example, lynx may avoid stands with dense saplings despite the

abundance of snowshoe hares (Fuller et al. 2007). Predator responses to post-infestation salvage logging are likely contingent on prey responses. However, logging may enhance detectability and accessibility, and predators may use open habitats (e.g. logged stands) more than their prey (O'Donoghue et al. 2001, Boisjoly et al. 2010). This advantage may decline as understory cover increases with stand age (Fisher and Wilkinson 2005).

Habitat choices for prey species are often influenced by trade-offs between food availability and predation risk (Myserud and Ostbye 1999, Verdolin 2006). During post-harvest succession in the boreal forest, forage availability may peak at a different successional stage than vertical or lateral cover does, thus imposing these trade-offs on herbivores (Hodson et al. 2011). Similarly, predators experience trade-offs between prey density and accessibility (Fuller et al. 2007), and the balance between these competing factors will likely shift through successional time (Fisher and Wilkinson 2005). These mechanisms are likely to influence habitat selection by wildlife in forests affected by bark beetle outbreaks and salvage logging.

The objective of my study was to quantify the impacts of post-infestation salvage logging on habitat use by terrestrial mammals in southwestern Yukon, with a focus on moose, snowshoe hare, lynx, and coyote. Moose and snowshoe hare are ecologically important species in the boreal forest, owing to their strong influence on plant and predator assemblages (Molvar et al. 1993, Hayes and Harestad 2000, O'Donoghue et al. 2001, Krebs et al. 2001), and they have local economic and cultural significance. Both species are considered early-seral specialists with shrub-dominated diets (Hodges 2000, Jung et al. 2015). Lynx and coyote were included in this study to examine the trophic consequences of salvage logging via impacts to their primary prey, snowshoe hares.

Specifically, my objective was to compare the effects of different salvage logging practices on these mammals by assessing three stand types: a) logged stands with low structural retention (< 250 stems/ha); b) logged stands with high structural retention (≥ 250 stems/ha); and c) unsalvaged stands affected by spruce beetles (*Dendroctonus rufipennis*). I sought to infer the mechanisms behind mammal response to salvage logging by assessing stand and landscape characteristics that influence habitat suitability (food availability and predation risk for herbivores, prey availability and accessibility for predators). If moose and snowshoe hare selected habitat based on food availability, they should preferentially use low-retention salvage-logged stands. If they selected habitat for cover, then unsalvaged stands should be preferred. If food and cover were both important, then high-retention salvage-logged stands should be optimal in terms of balancing these conflicting requirements. Given the importance of predation as a limiting factor for moose and snowshoe hare in the northern boreal forest (Larsen et al. 1989, Hodges 2000), I predicted that both species should favour unsalvaged stands as cover from predators. I anticipated that lynx and coyote generally select the same stands as snowshoe hares, but they should show higher relative use of logged stands (particularly young stands) where prey are easiest to detect.

Another objective was to measure changes in mammal habitat use through successional time, by comparing salvage-logged stands of two age categories: a) 0–10 years post-harvest, and b) 11–25 years post-harvest. If food availability and concealment cover (from shrub growth) increase over time in salvage-logged stands, snowshoe hare and moose should prefer 11–25-year-old stands over 0–10-year-old stands. Habitat preferences of lynx and coyote should parallel those of their prey, snowshoe hare. However, these predators may use 11–25-year-old stands relatively less than hares, if high shrub and sapling densities impede prey detection and capture.

2.2 Methods

2.2.1 Study area

I conducted research near the town of Haines Junction (60.7522°, -137.5108°, elevation 599 m) in southwestern Yukon, in the Boreal Cordillera ecozone of Canada (Smith et al. 2004). Forests are characterized by homogenous white spruce (*Picea glauca*) overstories with willow (*Salix* spp.) understories and a groundcover of moss and ground shrubs (Smith et al. 2004, Garbutt et al. 2006). Trembling aspen (*Populus tremuloides*) stands are rare but present in previously logged or burned areas. The average age of overstory spruce in the study area is 170 years (Hawkes et al. 2014). The climate is dry and cool; average annual precipitation is 250–300 mm/year, and mean July temperatures vary from 7–12°C (Smith et al. 2004).

From 1990 to 2005, a severe infestation of spruce bark beetles affected over 360,000 ha of forest in this region (Garbutt et al. 2006, Hawkes et al. 2014). On average, forest stands had $32\% \pm 21.1$ SD tree mortality caused by spruce bark beetles (Randall et al. 2011), and almost no forests in the region were unaffected by beetles (Garbutt et al. 2006). Salvage logging began in the 1990's and is ongoing. Stands with the highest beetle mortality were generally selected for logging, although existing road access, community fire risk, recreational value, and fish and wildlife habitat were also considered during stand selection (Alsek Renewable Resource Council 2004, Resource Assessment Technical Working Group 2006). At the time of my study, salvage logging affected less than 5% of the forest landscape in the area, and many high mortality stands had not been logged. An average of 25% stand retention was required in designated High Wildlife Value Areas, which comprised over 86% of the region (Resource Assessment Technical Working Group 2006). Nevertheless, stand retention varied extensively across the study area. Clear-cut logging (i.e. near complete removal of live and beetle-killed trees) was practiced in

areas where reducing fire risk was a high priority, or where windthrow was an issue. Retention levels exceeded 25% in some stands where trees were selectively removed on an individual basis. Most logging occurred on a relatively small scale (cuts were < 30 ha). Aside from post-infestation logging and associated roads, there were few anthropogenic disturbances on the landscape. This provided a unique opportunity to study salvage logging in relative isolation, without the confounding influence of other human impacts.

2.2.2 Study species

Snowshoe hare are abundant in this region (Hodges 2000) and were near the peak of their population cycle during the study in 2016 (Boonstra et al. 2018). Their primary predators in southwest Yukon are lynx and coyote, but aerial predators may also influence hare abundance and behaviour (Hodges 2000, O'Donoghue et al. 2001). Portions of the study area are key moose habitat (Government of Yukon 2016). Moose abundance declined significantly from 1998 to 2008 (Westover et al. 2009) and remains low in this region (Government of Yukon, unpublished data). Wolves are the most important predators of moose in Yukon (Hayes and Harestad 2000), although grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) also prey on calves (Larsen et al. 1989). Both moose and snowshoe hare predominantly eat shrubs and deciduous saplings (Hodges 2000, Jung et al. 2015), although hares will also eat herbaceous plants and graminoids (Seccombe-Hett and Turkington 2008). Predation, rather than food limitation, is likely the primary cause of mortality for both species in this area (Larsen et al. 1989, Hodges 2000).

2.2.3 Study design

I conducted field work from 18 May to 2 October 2016. The study included 90 sites, with 60 salvage logged stands and 30 unsalvaged stands (Fig. 2.1, Fig. 2.2). I categorized salvaged stands as high retention if post-harvest overstory tree densities were 250 – 820 trees/ha ($n = 38$), and low retention if densities were 20 – 250 trees/ha ($n = 22$). While I use “retention” as a descriptive term, tree densities prior to salvage-logging were unknown, so these categories more accurately reflected tree densities at the time of my study rather than true retention (i.e., what remained after logging). These categories generally aligned with silvicultural prescriptions; low-retention stands were prescribed for fuel abatement, whereas high-retention stands were logged for timber value (with preservation of wildlife habitat as a priority). Within each retention class, approximately half of the stands were at an early stage of post-disturbance succession (0–10 years old), and half were at a mid-successional stage (11–25 years old) (Figure 2.3). These age classes reflect meaningful vegetation changes for moose and snowshoe hare in the boreal forest, in terms of food and cover (Fisher and Wilkinson 2005). I obtained stand ages from logging records or historical Landsat satellite imagery when necessary.

All study sites were located within a 25 km radius of the town of Haines Junction (Figure 2.1). This area was relatively flat with minimal variation in elevation (ranging from 600 m to 900 m). Unsalvaged sites were randomly selected (with some concessions for accessibility), but salvage logged sites were selected intentionally to achieve an adequate sample for each retention and age category. Sites were separated by at least 300 m, with an average of $741 \text{ m} \pm 484 \text{ SD}$ between neighbouring sites.

2.2.4 Occupancy surveys

I recorded mammal activity using 50 wildlife cameras (Hyperfire PC800, Reconyx, Holmen, Wisconsin, USA). Cameras are non-invasive and effective monitoring tools for large mammals (McShea et al. 2009, O’Connell et al. 2011, Shannon et al. 2014, Burton et al. 2015), and for smaller mammals such as snowshoe hare (Villette et al. 2017). Cameras were rotated through 90 sites during two phases; half of the sites were surveyed from 22 May to 27 July, and the remainder were surveyed from 28 July to 2 October. To maintain consistency among sites, I did not place cameras along trail features. I selected camera locations randomly within each salvage-logged or unsalvaged stand and directed cameras towards forest openings to improve detection. I positioned cameras on trees 50 cm above ground level to record both small and large species. Camera images were processed using Timelapse 2 software (Greenberg Consulting Inc., Calgary, Alberta, Canada). I defined individual wildlife capture events as either a) consecutive photos of different species, b) consecutive photos of different individuals of the same species (if individual recognition was possible), c) consecutive photos of unknown individuals of the same species separated by > 30 minutes (if individual recognition was not possible), or d) non-consecutive photos of the same species. A 30-minute lag between capture events is typical for large mammals (e.g. Kinnaird et al. 2003), and is also a suitable “hit rate” for snowshoe hares in the study area (Villette et al. 2017). Information was recorded about sex and age class (young-of-the-year, juvenile, adult) when possible.

2.2.5 Vegetation, forest, and landscape structure

I measured understory vegetation and forest structure at each site to characterize habitat value in terms of food and cover (Table 2.1, Table 2.2). I used habitat characteristics as a proxy for predation risk, as prey often have a stronger response to habitat features than to actual

predator abundance (Verdolin 2006). I collected vegetation data along three 40-m transects that originated at the camera location; one transect was in the centre of the camera detection zone, and the other two were perpendicular to the first (Figure 2.4). I determined tree species composition, tree density (trees/ha), and basal area (m^2/ha) using the point-centred quarter method (Cottam and Curtis 1956), taking measurements at the central camera location and at the 20-m and 40-m locations on each transect (seven locations total). Trees were classified as overstory trees if the diameter at 1.3 m (DBH) was ≥ 5 cm, and understory trees if DBH was < 5 cm. At each of the seven locations described above, I used a convex spherical densitometer to record canopy cover (%), and I measured lateral cover (%) with a 2-m tall cover pole at 5-m distances from the sampling point in each cardinal direction (Griffith and Youtie 1988). I classified percent ground-vegetation cover (herbaceous plants, grasses, shrubs, moss, and lichen) in seven 0.5 m^2 circular plots at each sampling location. I counted the number of deciduous stems at the 20-m location on each transect, within $1 \times 10 \text{ m}$ rectangular plots ($\text{stems}/10\text{m}^2$) (Dussault et al. 2005b). Deciduous stems included shrubs and deciduous trees $\leq 2 \text{ m}$ tall; however, only stems with at least one twig $\leq 0.5 \text{ m}$ above the ground were included in snowshoe hare analyses (this height reflects summer availability for hares). I measured the abundance of coarse woody debris by counting the number of downed trees ($\geq 4 \text{ cm}$ diameter) intersecting each 40-m transect (Forester et al. 2007).

Wide-ranging animals, including ungulates and large predators, may respond to habitat characteristics at the landscape-scale (Fisher et al. 2011, Long et al. 2011). Land cover data with adequate resolution were not available for the study area, so I developed a land cover product through classification of Sentinel-2 satellite images at 20-m resolution (European Space Agency

Copernicus Program). I used supervised maximum-likelihood classification techniques in ArcGIS version 10.4.1 (ESRI, Redlands, California, USA) to distinguish three classes: forest, open, and water. Classification accuracy was 90% as verified with a combination of ground surveys and aerial imagery at 100 random locations throughout the study area. I then calculated forest cover (%) and total forest edge (m) within a 500-m radius of each site using Fragstats version 4.2.1 (University of Massachusetts, Amherst, Massachusetts, USA). I also calculated the density of linear disturbances within 500 m (km/km^2) (roads, transmission lines, pipelines, and cutlines) using the Line Density tool in ArcGIS. Lastly, I measured the distance to the nearest permanent water body (lakes, wetlands, and streams) and the distance to the nearest forest edge (i.e. edge of logged stand, road, or pipeline) with the Point Distance tool. Vector data were provided by the Yukon Department of Environment. Hypotheses regarding the influence of landscape-scale variables on moose, snowshoe hare, lynx, and coyote are outlined in Table 2.1 and 2.2.

2.2.6 Statistical analyses

I compared vegetation and forest structure among stand-types (low retention, high retention, and unsalvaged) with ANOVAs and post-hoc Tukey's HSD tests in R version 3.4.3 (www.r-project.org). I used independent samples t-tests to compare understory tree density, lateral cover, deciduous stem density, and shrub + herb + grass cover between stand age categories (0–10-year-old logged stands, 11–25-year-old logged stands). I \log_{10} transformed basal area, overstory tree density, and understory tree density to meet assumptions of normality and homoscedasticity.

I analyzed camera data using single-season occupancy models with the R package *RPresence* (version 2.12.6, Mackenzie and Hines 2017). Occupancy models allow the use of

presence/absence data to assess landscape-level patterns in habitat use while accounting for imperfect species detection, which is a common problem in wildlife studies (Mackenzie et al. 2002, 2006). Models incorporated the effects of site-specific covariates on occupancy (ψ), as well as site- and survey-specific covariates that could influence detection rates (ρ). Although data were analyzed using an occupancy modelling framework, the results should be interpreted as relative habitat use rather than patch occupancy because animal home ranges were larger than the spacing between camera units (Mackenzie et al. 2006, Efford and Dawson 2012) for all species other than snowshoe hare.

In addition to examining general moose occupancy, I investigated whether females with calves had different habitat preferences using multi-state occupancy models (Nichols et al. 2007, Mackenzie et al. 2009). Models used the parameterization outlined in Nichols et al. (2007), with three possible occupancy states: unoccupied (state 0); occupied by moose of any age or reproductive status (state 1); and occupied by females with calves (state 2). Only young-of-the-year calves were included in state 2. Two occupancy parameters were modelled: ψ^1 is the probability of occupancy by any moose, and ψ^2 is the probability of occupancy by females with calves given that a site is occupied by moose. These models facilitated a comparison of habitat preferences between reproductive females and non-reproductive adults.

Wildlife camera data are continuous and must be divided into discrete sampling periods for occupancy modelling. I defined an individual sampling period as 15 days for moose, lynx, and coyote, and 7 days for snowshoe hare; this yielded detection probabilities that were adequate (> 0.2) for models to converge on precise occupancy estimates (Mackenzie and Royle 2005). Before occupancy analysis, I determined the most plausible detection model for each species by

fitting different combinations of site- and survey-specific covariates suspected to influence detection rates. Vegetation structure may alter the size of the camera detection zone, or influence animal behaviour in a way that affects probability of detection (Burton et al. 2015). Phenological changes in species behaviour may cause detection rates to vary across time. I considered tree density (overstory and understory), lateral cover, basal area, and date as potential detection covariates. I incorporated the best detection model into all subsequent occupancy models for the relevant species.

I developed a set of models to test *a priori* hypotheses about the influence of salvage logging and forest structure on species' occupancy (using the hypotheses and associated covariates outlined in Table 2.1 and Table 2.2) (Burnham and Anderson 2003). The candidate set of occupancy models included single-variable models as well as additive and interactive combinations of variables when biologically relevant (i.e. when interactive or additive effects were anticipated based on species' ecology). For example, lynx may select sites where snowshoe hares have the highest occupancy, but may avoid extremely dense habitats (Fuller et al. 2007); I therefore included the interaction between hare occupancy and understory tree density in lynx models. All continuous covariates were standardized by converting to z-scores (overall mean of 0 and standard deviation of 1), and correlated covariates ($r > 0.6$) were not included in the same models to avoid multicollinearity (Dormann et al. 2013). To test for trends in occupancy along longitudinal or latitudinal gradients, I ran models with first- and second-order polynomials of spatial coordinates (Borcard et al. 2011, Legendre and Legendre 2012). If spatial terms improved model performance, and were not explained by habitat covariates, the spatial terms were retained in candidate models.

I compared candidate models to each other, and to the null and global models, using Akaike's Information Criterion (AIC) or Quasi-AIC (QAIC). I removed models with uninformative parameters from the candidate set (i.e. complex models that received lower AIC than the simpler nested model) (Arnold 2010), as well as models that did not converge. I did not use AIC corrected for small sample size (AICc) because this produces biased estimates for non-Gaussian data, particularly for logistic models (Richards 2015). AIC weights were used to evaluate the relative strength of each candidate model. If no model received a weight $> 90\%$, I calculated parameter estimates and unconditional standard errors by averaging across a set of confidence models (the "confidence set") where Akaike weights summed to approximately 0.95 (Burnham and Anderson 2003).

I used graphical elements to show a) the size and direction of predicted covariate effects, b) the uncertainty associated with predicted effects, and c) the amount of variation explained by covariates (Figure 2.8, 2.9, and 2.11). First, I determined the predicted model-averaged effect when other covariates were held at mean values (i.e., the partial effects), as implemented by the `modAvg` function in *RPresence* (represented by solid lines in figures). To show uncertainty, I obtained model-averaged 95% confidence intervals via the Delta method (Cooch and White 2018): unconditional standard errors were estimated on the logit scale, then confidence intervals were calculated and back-transformed to the probability scale (represented by shaded regions). Lastly, I calculated model-averaged real site occupancy estimates (represented by points), which account for *all* covariate effects in the confidence set. Point scatter reflects the degree of unexplained variation; however, lines may not perfectly fit these points as they are not "real" data to which a model was fit. The effects of categorical variables (e.g. stand type and age) were

shown with mean site occupancy estimates (bars) and associated 95% confidence intervals (e.g. Figure 2.10).

I calculated occupancy model residuals (Warton et al. 2017) from the best-fitting (lowest AIC) model and tested for spatial autocorrelation using Moran's I correlograms of residuals (Tiefelsdorf 2000, Dormann et al. 2007). Methods have not been developed for calculating residuals from multi-state occupancy models (Warton et al. 2017), so I prepared correlograms from raw presence-absence data for the analysis of female moose with calves (e.g. Webb et al. 2014). I evaluated the fit of the most saturated model with 10,000 bootstrapping events and a chi-square goodness-of-fit test (MacKenzie and Bailey 2004), and QAIC values were used to compare models when overdispersion and a lack of fit were indicated (i.e. $\hat{c} > 1$). When QAIC was used for model selection, I inflated unconditional standard errors by the square root of the \hat{c} value (McCullagh and Nelder 1989, MacKenzie and Bailey 2004).

2.3 Results

Unsalvaged stands had higher basal area ($F_{2,87} = 99.4$, $P < 0.001$), canopy cover ($F_{2,87} = 153.8$, $P < 0.001$), and overstory tree density ($F_{2,87} = 109.4$, $P < 0.001$) than high-retention-logged stands, which in turn had higher values than low-retention-logged stands (Figure 2.6 A, B, and C). Understory tree density ($F_{2,87} = 21.85$, $P < 0.001$) and lateral cover ($F_{2,87} = 7.39$, $P = 0.001$) were highest in unsalvaged stands, whereas deciduous stem density was highest in low-retention logged stands ($F_{2,87} = 8.03$, $P < 0.001$) (Figure 2.6 D, E, and F). Unsalvaged stands also had the least amount of coarse woody debris ($F_{2,87} = 3.95$, $P = 0.02$) and the lowest shrub + herb + grass cover ($F_{2,87} = 10.15$, $P < 0.001$) (Figure 2.6 G and H). Understory tree density, lateral cover, and shrub + herb + grass cover did not differ between low and high retention stands, but they did increase with stand age ($t = -2.88$, $df = 26.9$, $P = 0.008$; $t = -2.89$, $df = 36.6$,

$P = 0.007$; $t = -2.13$, $df = 26.9$, $P = 0.04$, respectively) (Figure 2.7 A, B, and D). In contrast, deciduous stem density did not differ between new (0–10 year) and old (11–25 year) logged stands ($t = -1.6$, $df = 47.1$, $P = 0.12$) (Figure 2.7 C).

Camera monitoring was successful at 89 of 90 study sites (one camera malfunctioned at an unsalvaged site), resulting in a total of 5,905 camera trap days. Moose were detected at 49% of sites, and 26% of those sites had females with young-of-the-year calves (Figure 2.5A). Snowshoe hare, lynx, and coyote were detected at 63%, 34%, and 22% of sites, respectively (Figure 2.5 B, C, and D). Although wolves are the primary predators of moose in the study region, they were detected at only one site and could not be included in occupancy analyses.

The results of goodness-of-fit tests for occupancy models indicated overdispersion (i.e., more variation than predicted by occupancy models) for all species but lynx. For moose, snowshoe hare, and coyote, QAIC values were used to compare and rank candidate models. Model selection produced multiple supported models for each species (i.e., no one model had $> 90\%$ AIC or QAIC weight). To account for model selection uncertainty, I obtained parameter estimates and occupancy predictions via model averaging.

2.3.1 Moose

All Moose:

The best-fitting detection model for moose was the null model, indicating that forest structure and date did not have an influence on probability of detection. Model-averaged detection probability for moose was 0.24 and site occupancy ranged from 0.18 to 0.98.

Seven models were included in the confidence set predicting moose occupancy (Table 2.3). The top model (canopy cover + distance to water + coarse woody debris) received > 6 times more support than other models in the candidate set based on QAIC weights (QAIC weight of

top model/QAIC weight of alternative model). Canopy cover, distance to water, and coarse woody debris each appeared in four of seven models in the confidence set, and stand type (high-retention logged, low-retention logged, unsalvaged) appeared in three models. Only the partial regression coefficient for canopy cover had a confidence interval that did not overlap zero (Table 2.4). Moose occupancy declined with increasing canopy cover (Figure 2.8 A). Distance to water and coarse woody debris also tended to have a negative influence on moose occupancy, but confidence intervals overlapped zero, indicating either inconsistent effects or imprecise parameter estimates (Table 2.4, Figure 2.8 B and C). Moose occupancy was highest in low-retention logged stands, followed by high-retention logged stands and unsalvaged stands (Figure 2.8 D); however, confidence intervals were large (Table 2.4). Distance to edge, total edge, and linear disturbance density had no influence on moose occupancy.

The goodness-of-fit test on the global model indicated there was no lack of fit ($\chi^2 = 69.68$, $P = 0.11$), but data were overdispersed ($\hat{c} = 1.3$). No spatial autocorrelation was detected in model residuals; the p-value for the Moran's I test was > 0.05 for most lag distances up to the maximum of 35 km, and the x-intercept of the correlogram was 0 km (Figure A.1).

Female Moose with Calves:

Female moose with calves were detected at 11 sites (12 %). In multi-state models for females with calves, the null model was the best detection model for both parameters ρ_1 (probability of detection, given only adults are present) and ρ_2 (probability of detection, given females with calves are present), indicating that detection was relatively constant among surveys and sites. Model-averaged values of ρ_1 and ρ_2 were 0.25 and 0.22, respectively. The δ parameter (probability of identifying calves when present) was also constant at 0.39. Given that only canopy cover had significant effects on single-state occupancy (see above), ψ^1 models

(occupancy by all moose) were held constant as ψ^1 (canopy), while a suite of covariates for ψ^2 (occupancy by females with calves) were investigated.

Results of multi-state occupancy models were generally inconclusive. Consistent with the models for all moose, canopy cover had a significant negative effect on ψ^1 ; however, the direction of effect for all ψ^2 covariates could not be determined. Top models for females with calves included distance to water, stand type, forest cover, deciduous stem density, and stand age (Table 2.5), but confidence intervals were large and overlapped zero for all estimates (Table 2.6). The top model received 170 times more support than the null model which had a QAIC weight of 0.002, suggesting that covariates did influence occupancy by females with calves. More sites would likely be required to estimate the direction and size of these effects with confidence (Mackenzie and Royle 2005). Distance to water appeared in three of four confidence models (Table 2.5) and had an overall positive effect on females with calves (i.e. females with calves were more likely to occupy sites farther away from waterbodies), although confidence intervals overlapped zero (Table 2.6). Mean occupancy by females with calves was higher in unsalvaged and high-retention stands than in low-retention stands, in contrast to patterns of general occupancy from single-state models (Figure 2.8 D).

Goodness-of-fit tests have not been developed for multi-state occupancy models, but comparison with the null model suggested that covariates improved model fit. Strong spatial autocorrelation was not detected in raw presence/absence data (Moran's I statistic was < 0.35 at all lag distances, and $P > 0.05$ for most lag distances) (Figure A.1).

2.3.2 *Snowshoe hare*

The probability of detecting snowshoe hare increased with tree basal area (Table 2.4), and ρ (basal area) was the top-ranked detection model. Basal area was included as a detection covariate in all subsequent occupancy models. Estimated detection probabilities varied from 0.37 to 0.93 depending on basal area, while occupancy probabilities ranged from 0.29 to 0.97.

There were seven occupancy models in the confidence set, with models including single variables and additive combinations of overstory tree density, canopy cover, lateral cover, shrub + herb + grass cover, stand age, and stand type (Table 2.3). The top model (overstory trees + lateral cover) was 1.5 times more supported than the second-best model, and 15.5 times more supported than the last model in the confidence set. Both overstory tree density and canopy cover had a significant positive relationship with snowshoe hare occupancy (Table 2.4), approaching asymptotes at approximately 2000 tree/ha and 70 % canopy cover, respectively (Figure 2.9 A and B). Hare occupancy tended to increase with lateral cover but confidence intervals overlapped zero. In contrast, hare occupancy declined with increasing cover of shrubs, herbs, and grasses (Table 2.4, Figure 2.9 C and D). Snowshoe hare occupancy was significantly higher in unsalvaged stands than in logged stands of any retention level or age category; however, there was no apparent preference between low-retention and high-retention logged stands, or between logged stands aged 0–10 and 11–25 years (Figure 2.10).

Results of the goodness-of-fit test suggested that the model fit the data ($\chi^2 = 4724.12$, $P = 0.054$), but data were overdispersed ($\hat{c} = 1.41$). Weak but significant spatial autocorrelation was detected up to a lag distance of 1 km; however, the Moran's I statistic was < 0.3 within this distance range (Figure A.1). Given that spatial autocorrelation was weak, and that sites were

spaced at greater distances than snowshoe hare summer home range sizes (Feierabend and Kielland 2014), I did not adjust any models to account for spatial autocorrelation.

2.3.3 Lynx and coyote

Neither forest structure nor date influenced lynx or coyote detection. Occupancy probabilities for lynx were generally lower than those for snowshoe hare (Figure 2.10) and ranged from 0.18 to 0.94. Coyote occupancy was lower than both lynx and snowshoe hare (Figure 2.10), ranging from 0.01 to 0.88.

The confidence set for lynx included occupancy models with stand type, hare occupancy, stand age, and total edge, as well as the null model (Table 2.3). The best-fitting lynx model (stand type + easting) had similar support to the alternative model (hare occupancy + easting). Easting was present in all three top models, indicating large-scale spatial trends were present in the data. Easting was the only parameter with significant effects, and lynx occupancy declined from west to east (Table 2.4). Although lynx occupancy seemed positively related to snowshoe hare occupancy, confidence intervals overlapped zero (Table 2.4, Figure 2.11 A). Patterns of lynx and snowshoe hare occupancy were generally similar with respect to stand type and stand age, but relative use of unsalvaged stands was lower for lynx (Figure 2.10). Occupancy models were a good fit to the data ($\chi^2 = 58.59$, $P = 0.43$), and there was no overdispersion ($\hat{c} = 0.95$). Spatial autocorrelation was not detected (Figure A.1).

Only four models were included in the confidence set for coyote (Table 2.3). The top model (hare occupancy + northing) received > 2.3 times more support than any other model. Hare occupancy had a significant positive effect on coyote occupancy (Table 2.4, Figure 2.11 B). Coyote occupancy was higher in unsalvaged stands than logged stands, but preference for low-retention and high-retention stands was similar (Figure 2.10). Older logged stands (11–25 years)

were preferred over younger stands (0–10 years) (Figure 2.10). Coyote occupancy was lower than snowshoe hare occupancy in all stand types and age categories. All models in the confidence set included northing as a covariate, and coyote occupancy increased on a gradient from south to north (Table 2.4). Overstory tree density had a positive effect but confidence intervals were large, suggesting that effects were inconsistent (Table 2.4). Models were a good fit for the data ($\chi^2 = 61.69$, $P = 0.2597$) and there was minor overdispersion ($\hat{c} = 1.09$). Spatial autocorrelation was not present in the coyote dataset (Figure A.1).

2.4 Discussion

In summary, my predictions regarding the negative impacts of salvage logging were supported for snowshoe hare and their predators but not for moose. High stand retention did not mitigate the negative effects on snowshoe hare, lynx, or coyote, and may have reduced the value of logged stands for moose (although female moose with calves may have benefitted). Habitat use by snowshoe hares and their predators increased with time since logging, whereas moose did not show any preference for or avoidance of older logged stands.

2.4.1 Moose

Moose generally preferred salvage-logged stands over unsalvaged stands, and low-retention logged stands over high-retention stands, contrary to my predictions. This preference likely reflects selection for stands with low canopy cover and, consequently, high food availability. Covariates relating to concealment cover (e.g. lateral cover, overstory and understory tree density) were not important to moose. Linear disturbance density did not influence moose occupancy, despite previous findings that linear features improve access for predators and hunters (Rempel et al. 1997, Frair et al. 2008, Hebblewhite et al. 2009, Whittington et al. 2011).

Forest edges were not important, and moose were detected as often near stand edges as in the centre of logged stands, despite being more vulnerable to wolf predation when far from forest cover (Kunkel and Pletscher 2000).

Ungulates experience trade-offs between food and cover (Kie 1999, Mysterud and Ostbye 1999, Godvik et al. 2009). For moose, particularly non-reproductive adults, the benefits of high forage abundance may have outweighed the costs of elevated predation risk in salvage-logged stands. Moose may prefer clear-cuts in other regions of the boreal forest (Rempel et al. 1997, Anderson et al. 2018) due to abundant forage in regenerating cut blocks (Dussault et al. 2005b). Moose in my study area are shrub-specialists, with >80% of their summer diet being composed of shrubs (Jung et al. 2015). The results of my study hint at the importance of bottom-up constraints on moose populations in the northern boreal forest (Stephenson et al. 2006), even in summer when nutritious food is thought to be readily available (McArt et al. 2009). In the montane forests of southern British Columbia, Canada, clear-cut logging is attributed with artificially boosting moose populations by increasing early-seral vegetation (Serrouya et al. 2011), regardless of potential losses from improved hunter access along logging roads (Rempel et al. 1997).

Despite the importance of food, deciduous stem density— a variable which directly characterizes food availability (Franzmann 1981, Dussault et al. 2005b)— did not have a significant influence on moose occupancy. Perhaps my survey methods did not adequately account for the patchiness of shrubs within a given stand, so canopy cover was a better predictor of food availability than the actual food measurements. Alternatively, predation risk may be more important than food, but the ability to detect approaching predators was more relevant than hiding cover. Prey species may experience trade-offs between concealment cover and long-range

visibility, where vegetation characteristics that improve one feature detract from the other (Camp et al. 2013). If moose selected habitat for visibility, it would potentially explain the lack of preference for 11–25-year over 0–10-year stands. Although food was more abundant in older regenerating stands, predators would be more difficult to detect as shrubs were often >2 m tall. Group-living ungulates, including elk (Hebblewhite et al. 2005) and bighorn sheep (Greene et al. 2012), prefer habitat with long-range visibility for early predator detection; however, little evidence exists for more solitary ungulates such as moose. Poole et al. (2007) found that female moose preferred habitats with low tree densities, presumably due to improved predator detection.

As predicted, moose tended to avoid stands with large amounts of coarse woody debris, likely because downed logs increased the energetic costs of movement (Parker et al. 1984). Silvicultural practices that leave piles of slash in logged stands will likely decrease habitat value for moose. Moose (aside from females with calves) had higher occupancy in stands that were close to water bodies (rivers, lakes, and wetlands). Aquatic habitats are important foraging areas due to the high nutritional value of emergent vegetation and lowland shrubs (MacCracken et al. 1993).

Results from the analysis of females with calves were ambiguous. Covariates relating to predation risk (tree density, lateral cover, percent forest cover, and linear disturbance density) were not important for females with calves, contrary to my predictions and evidence from previous work (Miquelle et al. 1992, Dussault et al. 2005b, McGraw et al. 2011, Oehlers et al. 2011). Nevertheless, females with calves avoided low-retention logged stands, in contrast to the habitat preferences of non-reproductive moose. Moose calves are more vulnerable to predation than adults are (Hayes et al. 2000), and females with calves may have avoided low retention stands to minimize predation risk, similar to the way they select against clear-cuts in other

regions (Poole et al. 2007, Bjørneraas et al. 2011). Females may benefit from protective tree cover by reducing the risk of calf mortality and, simultaneously, reducing their own anti-predator vigilance (White and Berger 2001). This allows them to spend more time foraging to meet the energetic demands of lactation and calf-rearing (White and Berger 2001). Divergent habitat preferences between reproductive females and non-reproductive moose were likely the result of different nutritional requirements and predation risk as opposed to active avoidance of other moose (Miller and Litvaitis 1992, Miquelle et al. 1992, Oehlers et al. 2011).

2.4.2 Snowshoe hare

Among the studied species, vegetation characteristics influenced the probability of detection only for snowshoe hare. I expected dense vegetation to reduce detection rates, but detection increased with tree basal area. Snowshoe hares may experience lower predation rates in densely-treed forests; thus, they also decrease their speed of movement, are more active, and spend more time in dense forests (Hodson et al. 2010a, Ewacha et al. 2014). These behavioural changes may have enhanced detection. Accounting for variable detection is advantageous, as it reduces negative bias in occupancy estimates (Mackenzie et al. 2002).

As anticipated, snowshoe hares showed a strong preference for unsalvaged stands with high overstory tree density, canopy cover and, to a lesser extent, lateral cover. Negative impacts of logging on snowshoe hares have been documented previously, but in a relatively restricted area of eastern Canada (Ferron et al. 1998, de Bellefeuille et al. 2001, Potvin et al. 2005, Hodson et al. 2010b). The value of intact forest and logged stands may converge with increasing retention (Hodson et al. 2010b, Ruel et al. 2013), time since harvest (Hodson et al. 2011), and decreasing cut sizes (Conroy et al. 1979). Snowshoe hares in my study area showed no preference for logged stands of one retention class over the other, perhaps because canopy cover was relatively

similar in these stand types. The residual trees in high-retention stands may have been inadequate to protect snowshoe hares from aerial predators.

Snowshoe hare habitat preferences are density-dependent (Hodson et al. 2010b) and may vary throughout the 10-year population cycle. Although evidence suggests that snowshoe hares in southwest Yukon prefer conifer forest (Hodges 2000), hares are more likely to use open habitat with minimal canopy cover during high phases of the cycle (O'Donoghue et al. 1998, 2001), and particularly during summer (Hodges 2000). My study was conducted largely in summer during a year that snowshoe hares were at the peak of their cycle (Boonstra et al. 2018). Nevertheless, hares strongly avoided logged stands and preferred densely-treed areas, suggesting these habitat preferences would be even more pronounced in winter and during cyclic population lows.

Unsalvaged stands had the highest canopy cover and tree densities but the lowest deciduous stem densities and shrub, herb, and grass coverage, likely imposing a trade-off between food and cover for snowshoe hares. Snowshoe hares apparently occupied stands with low predation risk rather than high food. Predation is likely the most significant constraint on snowshoe hare populations in the northern boreal forest (Hodges 2000). Snowshoe hare occupancy approached its asymptotic maximum in stands with high overstory tree density and canopy cover, suggesting that food may become limiting in very dense forests. The abundance and diversity of understory shrubs and herbaceous plants declines rapidly with increasing canopy cover in the boreal forest (Hart and Chen 2006).

The relationship between hare occupancy and cover was consistent with previous studies (Hodson et al. 2010a, 2011, Ewacha et al. 2014, but see Fuller and Harrison 2013). However, it was surprising that habitat use was largely driven by overhead cover (overstory tree density,

canopy cover) more so than understory cover (understory tree density, horizontal cover). Covariates relating to overhead cover ranked higher in model selection and had stronger relationships with hare occupancy. This suggests that evading aerial predators (e.g. goshawks and owls) may be more important than avoiding terrestrial predators (lynx and coyote) during spring and summer. Aerial predators may be more difficult for snowshoe hares to detect and avoid. Conversely, during winter, mammalian predation rates are higher than avian predation rates (Feierabend and Kielland 2015), perhaps explaining the elevated importance of understory cover found by many winter snowshoe hare studies (e.g. Wolfe et al. 1982, Hodges 2000, Wirsing et al. 2002, Fuller and Harrison 2013, Ewacha et al. 2014).

Amongst salvage-logged stands, snowshoe hares exhibited a slight but non-significant preference for older (11–25 years) over younger (0–10 years) stands. Logged stands of all ages had significantly lower occupancy than unsalvaged stands which were all >100 years old (Garbutt et al. 2006). This is contrary to findings from lower latitude studies, where early- and mid-successional stands (10–40 years old) supported more hares than mature coniferous forests (Koehler 1990, Fisher and Wilkinson 2005, Newbury and Simon 2005, Allard-duchêne et al. 2014). In Yukon, early- to mid-successional trembling aspen stands (8–15 years post-fire) had higher hare densities than mature aspen or spruce forests (Strong and Jung 2012). Latitude and forest type likely influence the rate of succession, and therefore the timing of peak snowshoe hare abundance. Succession in the spruce forests of southern Yukon may progress slowly, suggesting that salvage-logged stands will take a comparatively long time to recover their value for snowshoe hares.

2.4.3 Lynx and coyote

Hare occupancy was the strongest predictor of both lynx and coyote occupancy, whereas stand type, stand age, and other habitat attributes were of secondary importance. Snowshoe hares are the preferred prey of both lynx and coyote in the boreal forest, particularly during the high phase of the hare cycle (O'Donoghue et al. 1998, 2001). As predicted, the patterns of habitat use by lynx and coyote roughly paralleled those of snowshoe hare: all three species preferred unsalvaged stands over salvage-logged stands of either retention class. Lynx are generally thought to select habitat based on prey availability more so than land cover (Murray et al. 1994, O'Donoghue et al. 1998, 2001, Mowat and Slough 2003). Coyote also prefer habitats with abundant prey, and this may result in the selection of dense forest habitat in Yukon (Murray et al. 1994, O'Donoghue et al. 2001). This contrasts with their behaviour in eastern North America, where coyotes benefit from anthropogenic disturbance and favour clear-cuts over intact forest (Boisjoly et al. 2010, Crimmins et al. 2012).

Predators select habitat based on prey abundance, but habitat characteristics that affect prey encounter and capture success are also important (Gorini et al. 2012). I expected the strength of the relationship between lynx, coyote, and snowshoe hare occupancy to be influenced by understory vegetation, but no interactions were evident. Nevertheless, lynx had lower occupancy than snowshoe hare in unsalvaged stands (coyote occupancy was lower in all stand types). This is consistent with previous findings that snowshoe hares use denser habitats than lynx (O'Donoghue et al. 1998, 2001, Fuller et al. 2007), and suggests that dense unsalvaged forests may serve somewhat as refugia for hares. Lynx may have higher prey encounter rates (Fuller et al. 2007) and capture success (Parker et al. 1983) in mature forest, but this advantage declines after conifer trees exceed a density threshold (Fuller et al. 2007).

Lynx had higher occupancy in 11 – 25 year salvage-logged stands than in 0 – 10 year stands, consistent with previous findings that lynx prefer mid-successional stands and avoid new harvest blocks (Parker et al. 1983, Fisher and Wilkinson 2005, Fuller et al. 2007). I predicted that snowshoe hares would prefer old stands more than lynx or coyote would, as tall shrubs and saplings were expected to impede prey detection and capture, but lynx had the stronger preference. High shrub densities may allow lynx to get closer to ambush their prey, which improves hunting success (Parker et al. 1983). Coyote also preferred older over younger stands. Coyotes in eastern Canada may have higher hunting success in open habitats (Thibault and Ouellet 2005); however, coyotes in Yukon may improve their success by using dense vegetation as concealment cover (Murray et al. 1995).

2.4.4 Management implications

Anthropogenic climate change is predicted to heighten the potential for large scale bark beetle outbreaks and wildfires in North America (Bentz et al. 2010), and if so, salvage logging will become increasingly prevalent in these disturbed areas. In the northern boreal forest, where commercial logging is a recent development, there is growing interest in using biomass energy from beetle- and fire-killed trees to reduce petroleum consumption (P Brand Bioenergy Consulting 2009) and to expand the timber industry (Alsek Renewable Resource Council 2004). As post-infestation salvage logging is a relatively new practice, guidelines are still being developed and research is needed to inform forest management policies, particularly in the north.

The results of my study demonstrate that post-infestation salvage logging causes significant changes in habitat use by moose and snowshoe hares, both of which are ecologically important species in the boreal forest. Logging practices that maintain residual trees – even at high retention levels (>25 % typical in the study area) – do not provide adequate cover for

snowshoe hares and their predators, or female moose with calves. Higher retention levels may be required to mitigate negative impacts at the stand scale. Retaining patches of residual trees rather than individual trees may be most beneficial to snowshoe hares, as intact patches could provide refugia from predators.

Salvage logging in the northern boreal forest is occurring at a small scale (i.e., < 30 ha per cut) and these results are not necessarily transferrable to regions where salvage blocks are significantly larger and more widespread on the landscape. Habitat selection depends on landscape context and relative availability (Osko et al. 2004); moose, for example, avoided cut-blocks in Quebec where logging covered 22% of the landscape (Courtois et al. 2002). Extensive logging could ultimately cause snowshoe hare population declines, as open habitats are population sinks for hares (Griffin and Mills 2009). Moose and snowshoe hare may require ample residual forest to persist on a logged landscape (Potvin et al. 2005). Salvage logging practices that maintain small cut sizes interspersed with large patches of forest are likely the most sustainable for these species.

Forest succession proceeds slowly in northern climates, and it will be well over 25 years before logged stands recover to the point where they provide high quality habitat for snowshoe hare and their predators. My study highlights short-term effects of salvage logging, but long-term monitoring of mammals is equally critical. If salvage operations continue to expand in the northern boreal forest, it will be important to consider the scope and severity of logging cycles and long-term strategies for habitat recovery.

Table 2.1 Variable names, descriptions, and hypotheses (including predicted effect in parentheses) for site- and landscape-level habitat variables used in occupancy models for moose and snowshoe hare in beetle-affected and salvage-logged forests in Yukon, Canada.

Variable	Description	Species	Hypothesis and Prediction
<i>Site-level Covariates</i>			
Stand Type	Low-retention logged, high-retention logged, un-salvaged	Moose + Hare	Logging reduces cover and increases predation risk (-)
Stand Age	Early-seral (0-10 years) and mid-seral (11-20 years), un-salvaged (>100 years)	Moose + Hare	Cover and food availability improve over time (+)
Overstory Trees	Estimated stand density (trees/ha) of overstory trees (DBH >3 cm), measured along 40 m transects	Moose + Hare	Improves concealment cover and reduces predation risk (+)
Understory Trees	Estimated stand density (trees/ha) of understory trees (DBH <3 cm), measured along 40 m transects	Moose + Hare	Improves concealment cover and reduces predation risk, also a source of food (+)
Canopy	Estimated canopy cover (%) of stand, measured along three 40m transects	Moose + Hare	Reduces food availability (understory productivity) but increases overhead cover (+)
Deciduous Stems	Number of deciduous stems (stems/10m ²), including shrubs and trees <2 m tall	Moose	Increases food availability (+)
Lateral Cover	Percent cover (%), measured with a 2 m tall cover pole	Moose + Hare	Improves concealment cover and reduces predation risk (+)
Shrub Herb Grass Cover	Percent cover (%) of herbaceous plants, grasses, and shrubs in 0.5m ² circular plots	Hare	Increases food availability (+)
CWD	Total number of downed trees with diameter >4cm, intersecting three 40m transects	Moose + Hare	Increases energetic expense for moose (-), provides cover for hare (+)
<i>Landscape Covariates</i>			
Water	Distance (km) to nearest lake, river, or wetland	Moose	Drinking and foraging habitat (-)
Edge	Distance (m) from camera to nearest forest edge (e.g. edge of logged stand, road, pipeline)	Moose + Hare	Edges are high quality habitat: high food availability and close proximity to protective cover (-)
Total Edge	Total forest edge distance (m) within a 500 m radius of camera	Moose	Edges are high quality habitat (+)
Linear Density	Linear disturbance density (km/km ²) within 500 m of camera	Moose	Improved access for hunters and predators (-)

Table 2.2 Variable names, descriptions, and hypotheses (including predicted effect in parentheses) for site- and landscape-level habitat variables used in occupancy models for lynx and coyote in beetle-affected and salvage-logged forests in Yukon, Canada.

Variable	Description	Hypothesis and Prediction
<i>Site-level Covariates</i>		
Stand Type	Low-retention logged, high-retention logged, un-salvaged	Prey avoid logged areas due to lack of cover, predators follow prey (-)
Stand Age	Early-seral (0-10 years) and mid-seral (11-20 years), un-salvaged (>100 years)	Prey prefer older stands with more cover and food, predators follow prey (+)
Understory Trees	Estimated stand density (trees/ha) of understory trees (DBH <3 cm), measured along 40 m transects	Prey prefer stands with dense understory (+), but predators avoid extremely dense stands where prey are hard to catch (asymptotic relationship)
Overstory Trees	Estimated stand density (trees/ha) of overstory trees (DBH >3 cm), measured along 40 m transects	Prey prefer stands with dense trees (+), but predators avoid extremely dense stands where prey are hard to catch (asymptotic relationship)
Lateral Cover	Percent cover (%), measured with a 2 m tall cover pole	Prey prefer stands with dense lateral cover (+), but predators avoid extremely dense stands where prey are hard to catch (asymptotic relationship)
Hare Occupancy	Model predicted snowshoe hare occupancy, from separate model	Predators follow their primary food source, snowshoe hares (+)
<i>Landscape Covariates</i>		
Forest Cover	Percent cover (%) of forest within a 500 m radius of camera	Prey prefer forest cover, and predators respond to prey abundance at the landscape scale (+)
Edge	Distance (m) from camera to nearest forest edge (e.g. edge of logged stand, road, pipeline)	Prey accumulate near edges, and predators follow prey (-)
Total Edge	Total forest edge distance (m) within a 500 m radius of camera	Edges are high quality habitat for prey, and predators follow prey (+)

Table 2.3 Confidence set of occupancy (ψ) and detection (ρ) models (QAIC or AIC weights sum to ~ 0.95) for moose, snowshoe hare, lynx, and coyote in beetle-affected and salvage-logged forest in Yukon, Canada. Quasi-Akaike's Information Criterion (QAIC), delta QAIC, QAIC weight, and number of parameters (K) are shown for each candidate model (lynx values are in AIC units). Occupancy covariates are defined in Table 2.1 and 2.2. Null models are indicated with (.).

Species/Model	QAIC	Δ QAIC	QAIC weight	K
<i>Moose</i>				
ψ (Canopy + CWD + Water), ρ (.)	244.56	0	0.658	5
ψ (Canopy + CWD), ρ (.)	248.14	3.58	0.1099	4
ψ (Stand Type + CWD + Water), ρ (.)	249.46	4.9	0.0568	5
ψ (Canopy + Water), ρ (.)	249.73	5.17	0.0496	4
ψ (Stand Type + CWD), ρ (.)	250.67	6.11	0.031	4
ψ (Canopy), ρ (.)	250.99	6.43	0.0264	3
ψ (Water + Stand Type), ρ (.)	251.15	6.59	0.0244	4
<i>Snowshoe Hare</i>				
ψ (Overstory Trees + Lateral Cover), ρ (Basal Area)	533.09	0	0.3169	5
ψ (Canopy + Lateral Cover), ρ (Basal Area)	533.98	0.89	0.2146	5
ψ (Canopy), ρ (Basal Area)	534.17	1.08	0.2001	4
ψ (Overstory Trees), ρ (Basal Area)	534.40	1.31	0.1671	4
ψ (Stand Age), ρ (Basal Area)	537.51	4.42	0.0326	4
ψ (Lateral Cover + Shrub Herb Grass), ρ (Basal Area)	537.51	4.90	0.0222	5
ψ (Stand Type), ρ (Basal Area)	538.49	5.40	0.0205	4
<i>Lynx</i>				
ψ (Stand Type + Easting), ρ (.)	256.98	0	0.3705	4
ψ (Hare Occupancy + Easting), ρ (.)	257.55	0.57	0.2786	4
ψ (Easting), ρ (.)	258.07	1.09	0.2149	3
ψ (Stand Age), ρ (.)	261.45	4.47	0.0396	3
ψ (Hare Occupancy), ρ (.)	262.93	5.95	0.0189	3
ψ (.), ρ (.)	263.48	6.5	0.0144	2
ψ (Stand Type + Total Edge), ρ (.)	263.53	6.55	0.014	4
<i>Coyote</i>				
ψ (Hare Occupancy + Northing), ρ (.)	165.04	0	0.5451	4
ψ (Stand Type + Northing), ρ (.)	166.73	1.69	0.2341	4
ψ (Stand Age + Northing), ρ (.)	167.78	2.74	0.1385	4
ψ (Overstory Trees + Northing), ρ (.)	170.04	5	0.0447	4

Table 2.4 Model averaged parameter estimates, unconditional standard errors (SE), and 95% confidence intervals (CI) for moose, snowshoe hare, lynx, and coyote detection (ρ) and occupancy (ψ) in beetle-affected and salvage-logged forest in Yukon, Canada. Covariates following ρ and ψ intercepts are detection and occupancy parameters, respectively. Estimates were calculated by averaging across the set of confidence models where QAIC or AIC weights summed to 0.95. Occupancy covariates are defined in Table 2.1 and 2.2. Significant coefficient estimates (CI's do not overlap zero) are listed in bold.

Species/Parameter	Estimate	SE	95% Lower CI	95% Upper CI
<i>Moose</i>				
ρ intercept	-1.09	0.48	-2.03	-0.15
Ψ intercept	1.83	1.39	-0.9	4.56
Canopy	-1.85	0.94	-3.69	-0.01
Water	-1.49	0.86	-3.18	0.2
CWD	-1.84	1.02	-3.85	0.16
Stand Type	-1.82	1.18	-4.12	0.49
<i>Snowshoe Hare</i>				
ρ intercept	0.04	0.11	-0.18	0.26
Basal Area	0.65	0.12	0.42	0.88
Ψ intercept	0.84	0.51	-0.15	1.84
Overstory Tree Density	1.6	0.73	0.17	3.04
Canopy	1.19	0.44	0.33	2.04
Lateral Cover	0.55	0.35	-0.13	1.23
Shrub Herb Grass Cover	-0.68	0.33	-1.3268	-0.0332
Stand Type	1.13	0.42	0.3068	1.9532
Stand Age	1.07	0.39	0.3056	1.8344
<i>Lynx</i>				
ρ intercept	-1.27	0.24	-1.73	-0.8
Ψ intercept	-0.68	1.09	-2.82	1.45
Stand Type	0.99	0.58	-0.14	2.12
Hare Occupancy	2.96	2.01	-0.99	6.91
Easting	-0.0014	0.00067	-0.0027	-0.000087
Stand Age	0.83	0.51	-0.17	1.83
Total Edge	0.51	0.37	-0.22	1.24
<i>Coyote</i>				
ρ intercept	-1.04	0.30	-1.62	-0.46
Ψ intercept	-4.00	1.84	-7.61	-0.38
Hare Occupancy	6.16	2.04	2.16	10.16
Stand Type	1.38	0.47	0.46	2.30
Stand Age	1.14	0.43	0.30	1.98
Overstory Tree Density	0.91	0.50	-0.07	1.89
Northing	0.002	0.0008	0.00043	0.0036

Table 2.5 Confidence set of multi-state moose occupancy models, where QAIC weights sum to ~0.95, in beetle-affected and salvage-logged forest in Yukon, Canada. Quasi-Akaike's Information Criterion (QAIC), delta QAIC, QAIC weight, and number of parameters (K) are shown for each candidate model. Models include two occupancy states: (ψ^1) probability of occupancy regardless of age, and (ψ^2) probability of females with calves, given that a site is occupied. p = probability of detection when state=1, p = probability of detection when state=2, and δ = probability that calves are successfully identified. Occupancy covariates are defined in Table 2.1 and 2.2. Null models are indicated with (.).

Multi-State Occupancy Model	QAIC	Δ QAIC	QAIC weight	K
ψ^1 (Canopy), ψ^2 (Water + Stand Type), $\rho_1(\cdot)$, $\rho_2(\cdot)$, $\delta(\cdot)$	375.8	0	0.3398	8
ψ^1 (Canopy), ψ^2 (Water + Forest Cover), $\rho_1(\cdot)$, $\rho_2(\cdot)$, $\delta(\cdot)$	375.94	0.14	0.3168	8
ψ^1 (Canopy), ψ^2 (Water), $\rho_1(\cdot)$, $\rho_2(\cdot)$, $\delta(\cdot)$	376.77	0.97	0.2092	7
ψ^1 (Canopy), ψ^2 (Deciduous Stems + Stand Age), $\rho_1(\cdot)$, $\rho_2(\cdot)$, $\delta(\cdot)$	378.29	2.5	0.0974	8

Table 2.6 Model averaged parameter estimates, unconditional standard errors (SE), and 95% confidence intervals (CI) for moose multi-state models. Models include two occupancy states: (ψ^1) probability of occupancy regardless of age, and (ψ^2) probability of females with calves, given that a site is occupied. p = probability of detection when state=1, p = probability of detection when state=2, and δ = probability that state 2 is successfully identified, where state 1 = only adults present, and state 2 = females with calves present. Estimates were calculated by averaging across the set of confidence models where QAIC or AIC weights summed to 0.95. Covariates are defined in Table 2.1 and 2.2. Significant coefficient estimates (confidence intervals do not overlap zero) are in bold.

Parameter	Estimate	SE	95% Lower CI	95% Upper CI
<i>Probability of occupancy (ψ^1)</i>				
ψ^1 intercept	1.12	0.67	-0.1932	2.4332
Canopy	-0.981	0.44	-1.8434	-0.1186
<i>Probability of calves, given occupancy (ψ^2)</i>				
ψ^2 intercept	2.19	5.99	-9.55	13.92
Water	4.86	3.22	-1.46	11.17
Stand Type	1.2	2.18	-3.0728	5.4728
Forest Cover	-1.37	1.01	-3.3496	0.6096
Deciduous				
Stems	-2.1	3.15	-8.274	4.074
Stand Age	6.32	6.8	-7.008	19.648
<i>Probability of detection and correct identification (ρ_1, ρ_2, δ)</i>				
ρ_1 intercept	-1.09	0.27	-1.6192	-0.5608
ρ_2 intercept	-0.25	0.38	-0.9948	0.4948
δ intercept	-0.4	0.55	-1.478	0.678

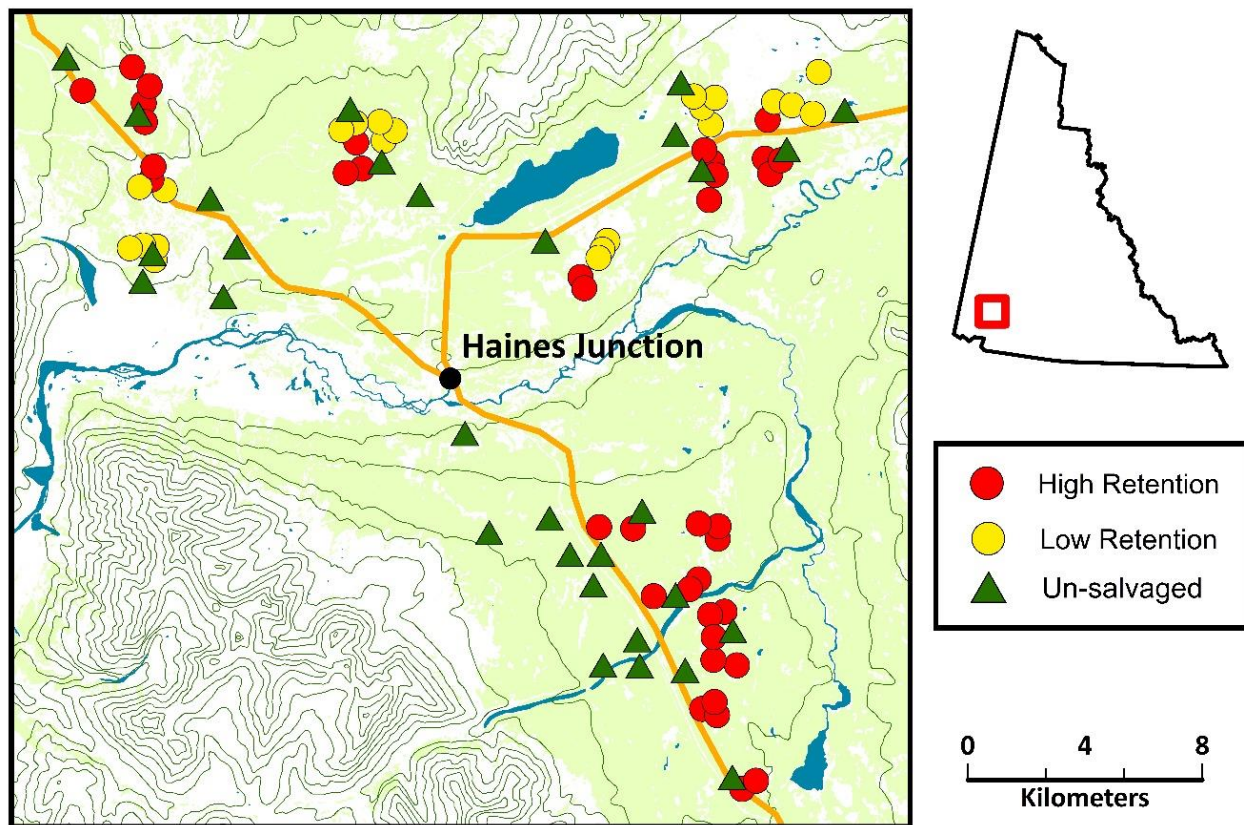


Figure 2.1 Map of study sites in southwest Yukon, including high-retention logged (n=38), low-retention logged (n=22), and un-salvaged spruce beetle sites (n=30). Contour intervals are 140 m.

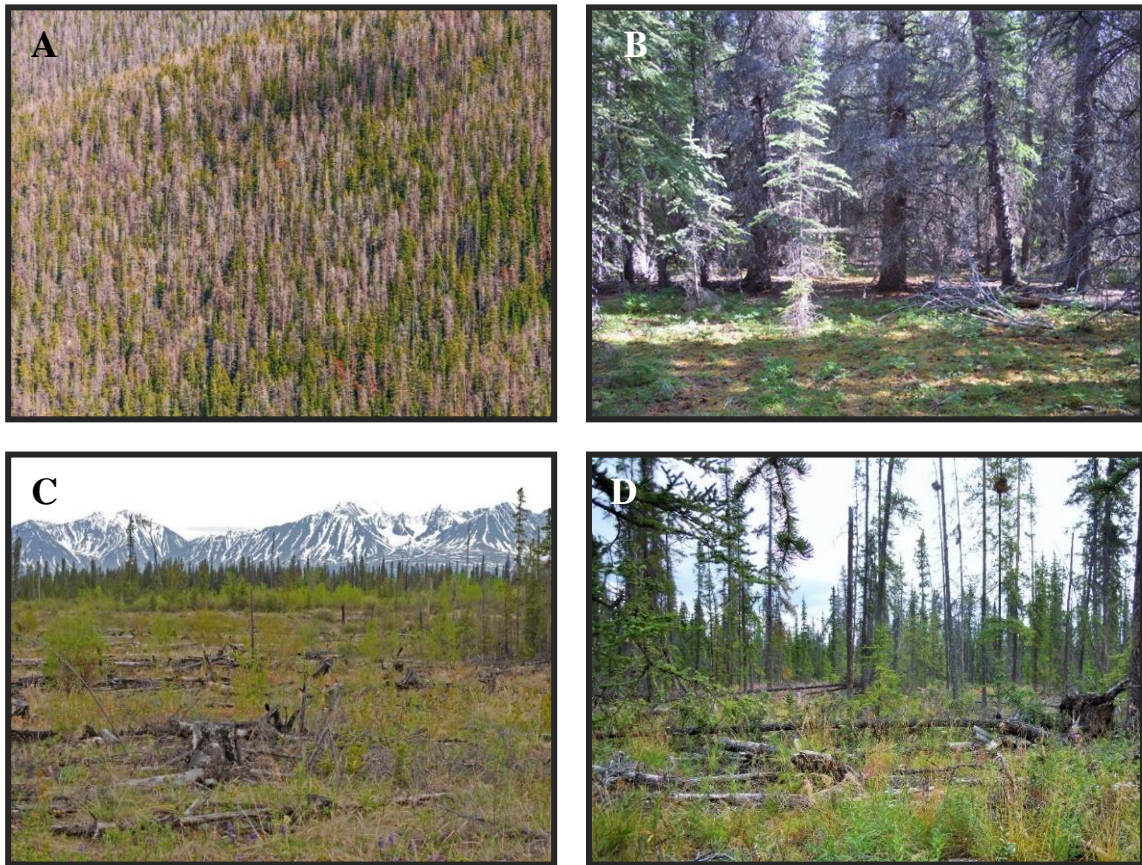


Figure 2.2 Photos of an aerial view of spruce bark beetle infestation (A); spruce beetle affected stand (B); low-retention logged stand (C); and high-retention logged stand (D).

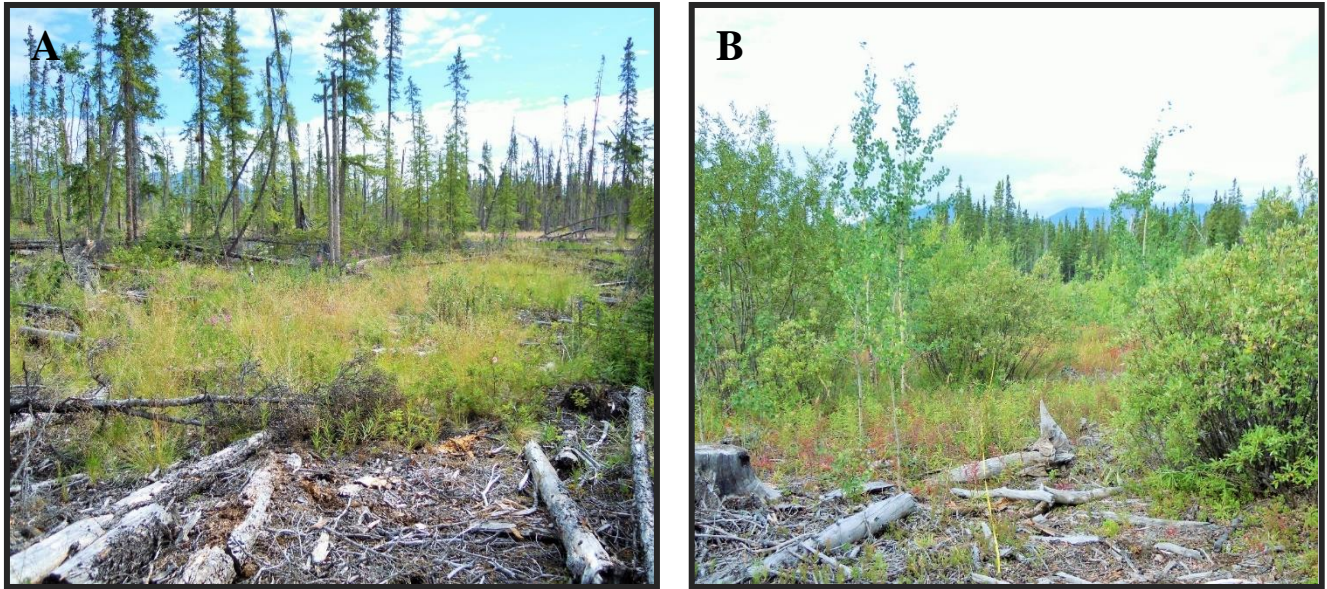


Figure 2.3 Photos of salvage-logged stands of two different age categories: 0 – 10 years post-harvest (A), and 11-25 years post-harvest (B).

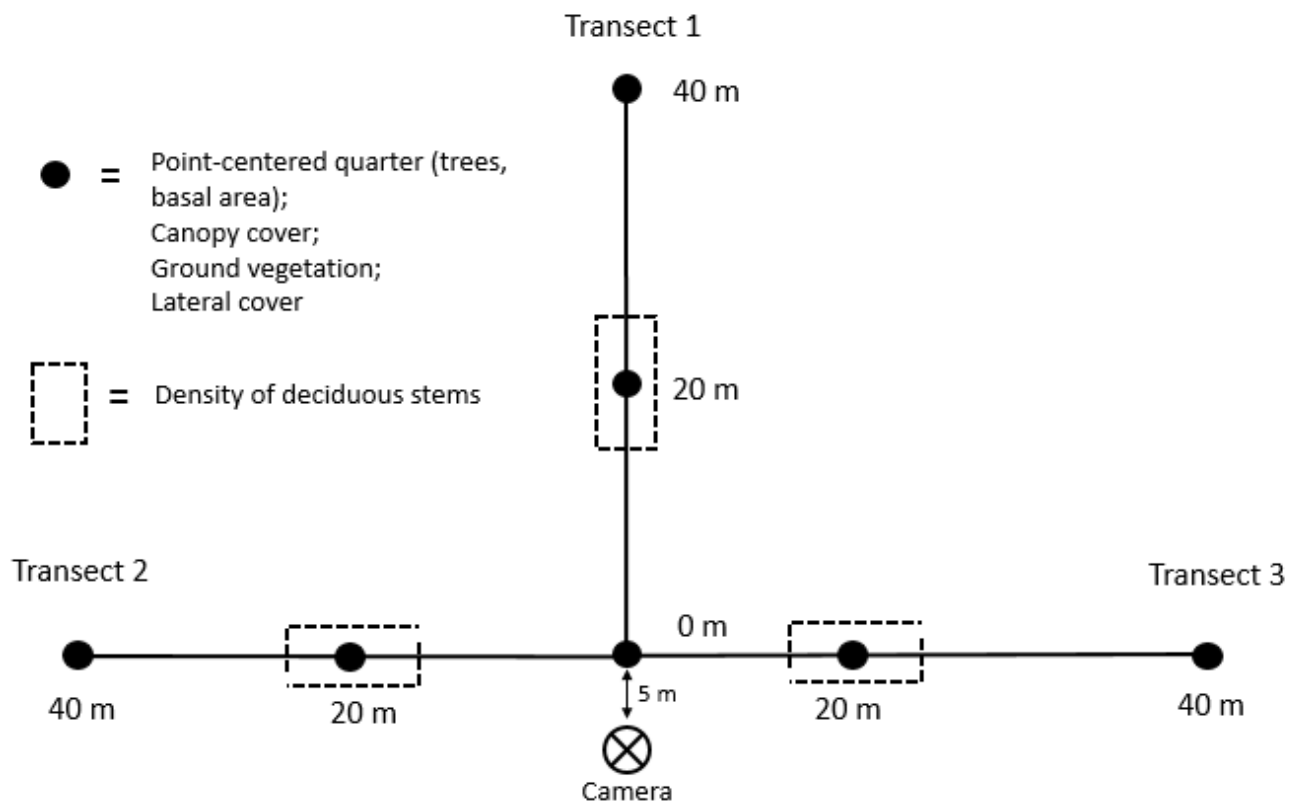


Figure 2.4 Transect layout for vegetation and forest structure surveys. Coarse woody debris was also measured by recording the number of pieces intersecting each transect.



Figure 2.5 Examples of wildlife photographs captured with Reconyx Hyperfire cameras from May-October 2016 near Haines Junction, Yukon, including moose (A), snowshoe hare (B), lynx (C), and coyote (D).

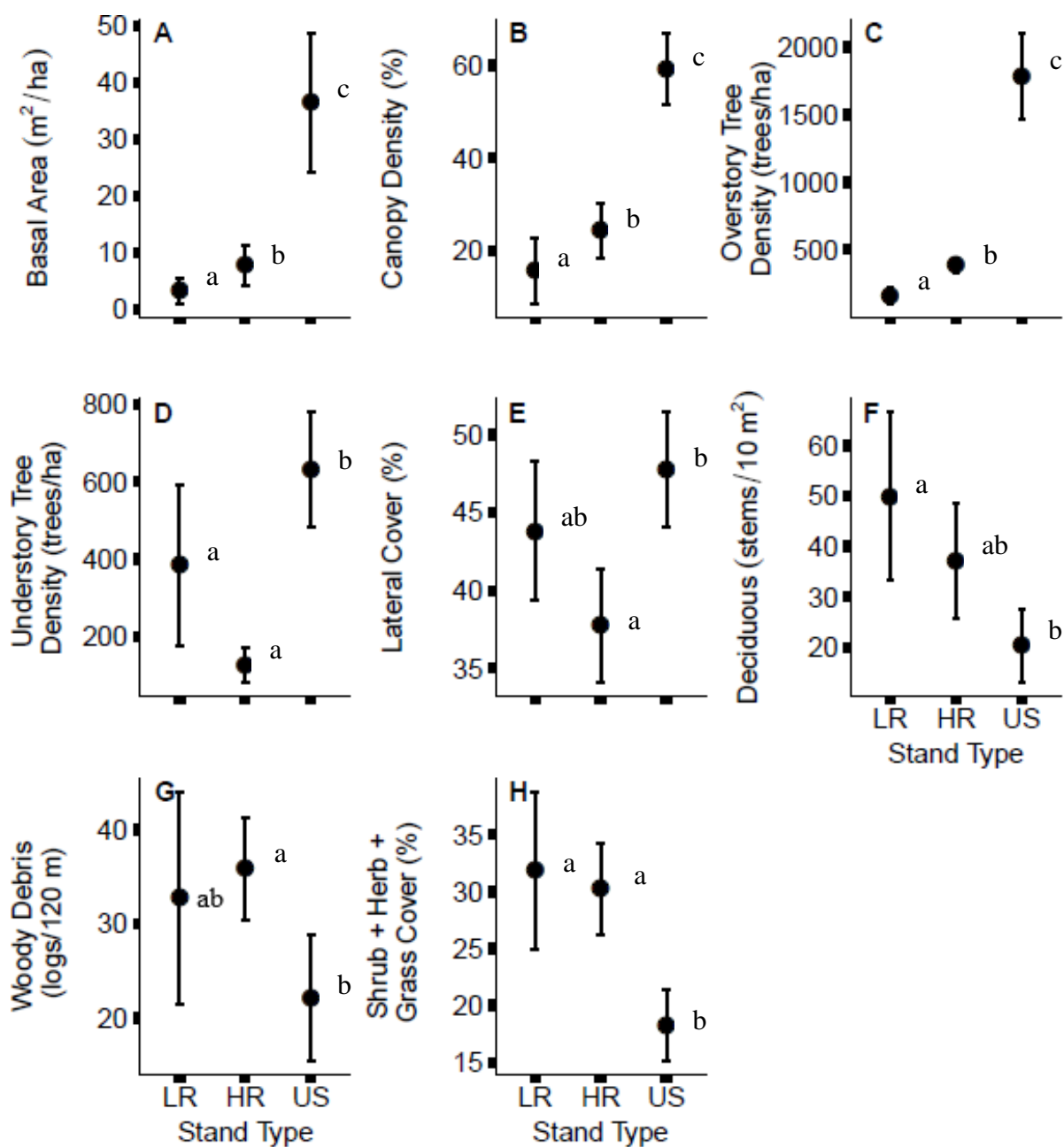


Figure 2.6 Comparison of mean vegetation and forest structure measurements between low-retention salvage-logged (LR), high-retention salvage-logged (HR), and unsalvaged beetle-affected stands (US) in southern Yukon, Canada, including: basal area (A), canopy cover (B), overstory tree density (C), understory tree density (D), lateral cover (E), deciduous stem density (F), course woody debris (G), and shrub + herb + grass cover (H). Error bars represent 95% confidence intervals. Lower case letters indicate means that are significantly different (Tukey's HSD, $P < 0.05$).

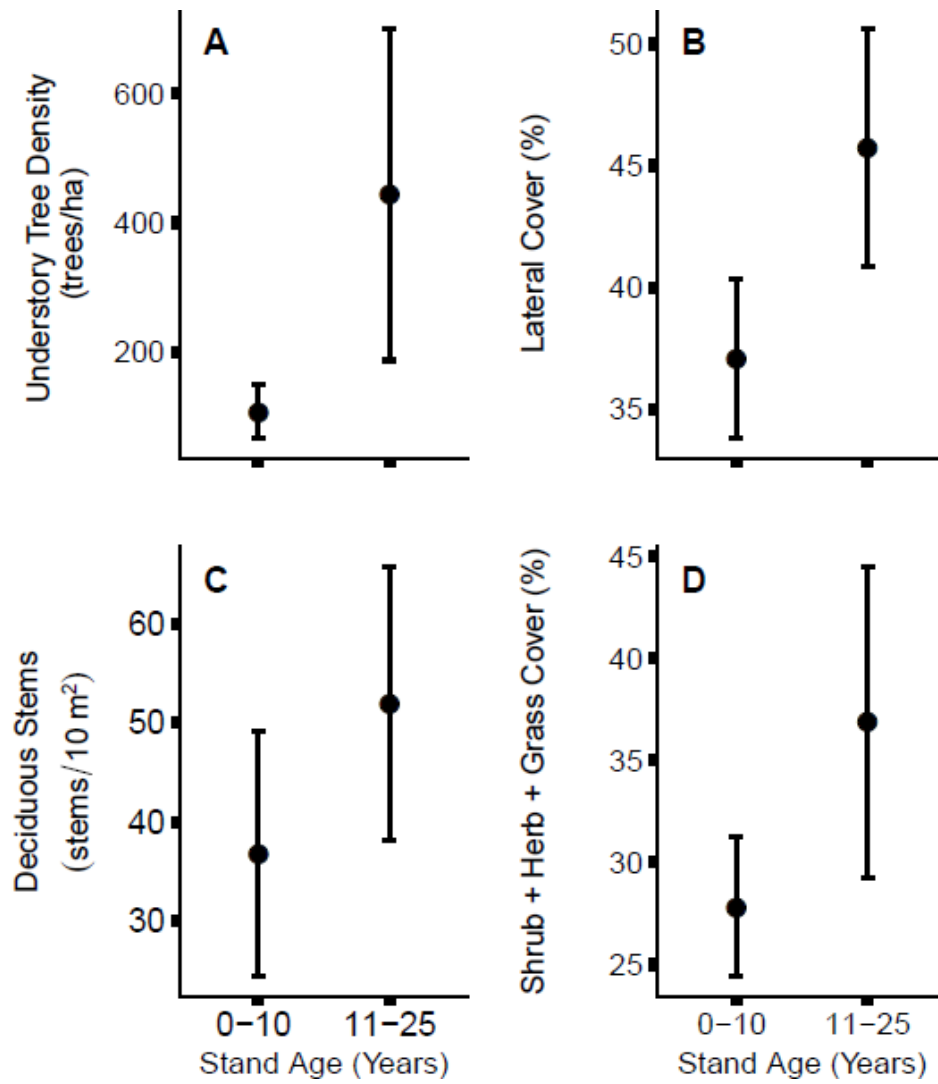


Figure 2.7 Comparison of mean vegetation and forest structure measurements between young salvage-logged stands (0-10 years post-harvest) and old salvage-logged stands (11-25 years post-harvest) in southern Yukon, Canada, including: understory tree density (A), lateral cover (B), deciduous stem density (C), and shrub + herb + grass cover (D). Error bars represent 95% confidence intervals.

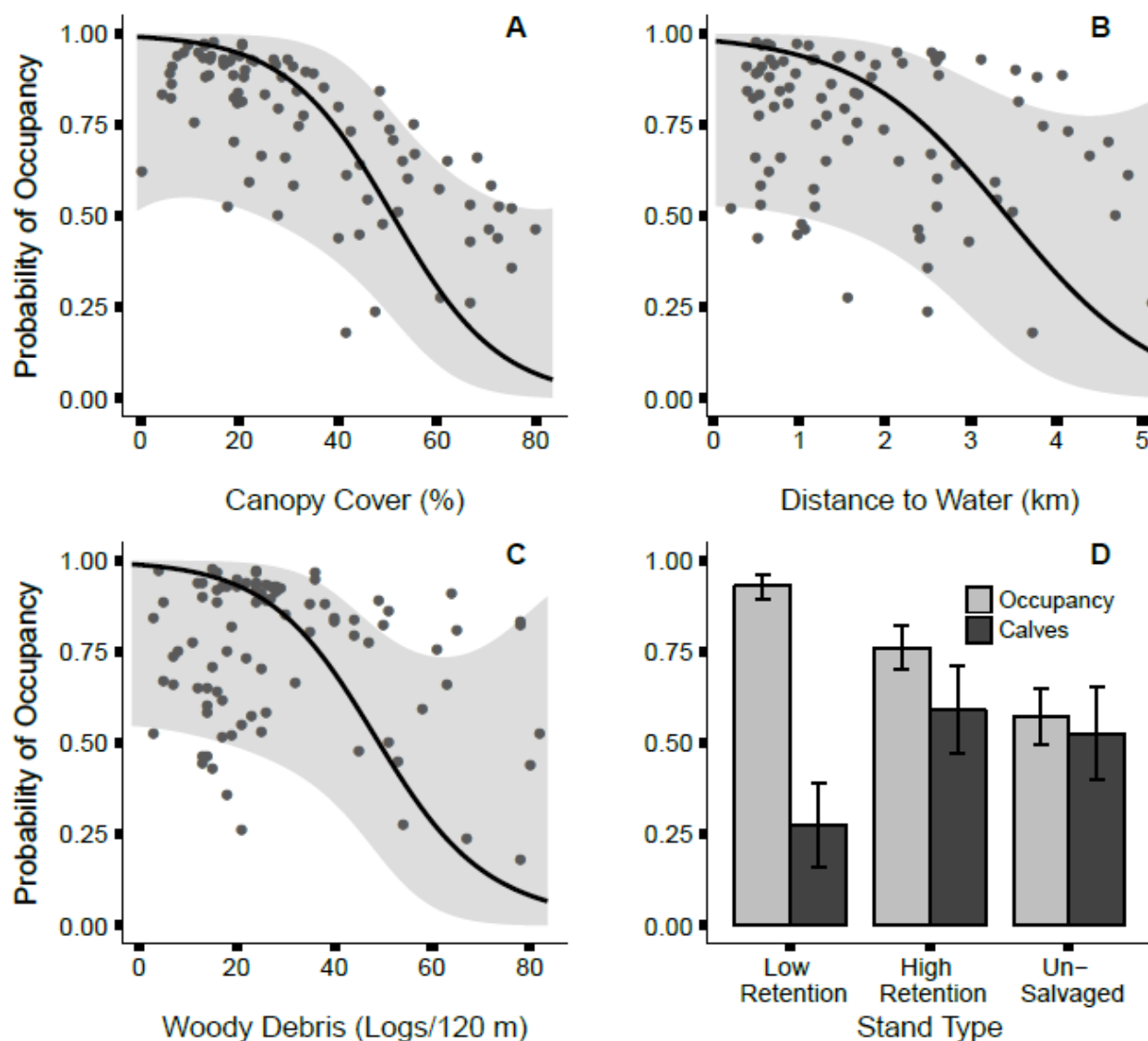


Figure 2.8 Model-averaged estimates of moose occupancy as a function of canopy cover (A), distance to water (B), woody debris (C), and stand type (D) in southwest Yukon, Canada. Panel D shows results of multi-state occupancy models, with general occupancy (ψ_1) in light gray, and occupancy by females with calves in dark gray (ψ_2). Occupancy estimates (points and bar plots) and predicted relationships (lines) were obtained by model-averaging across the confidence set of models where QAIC weights summed to 0.95. Lines show predicted covariate effects, when all other covariates are held constant at their mean. Shaded regions and error bars are unconditional 95% confidence intervals.

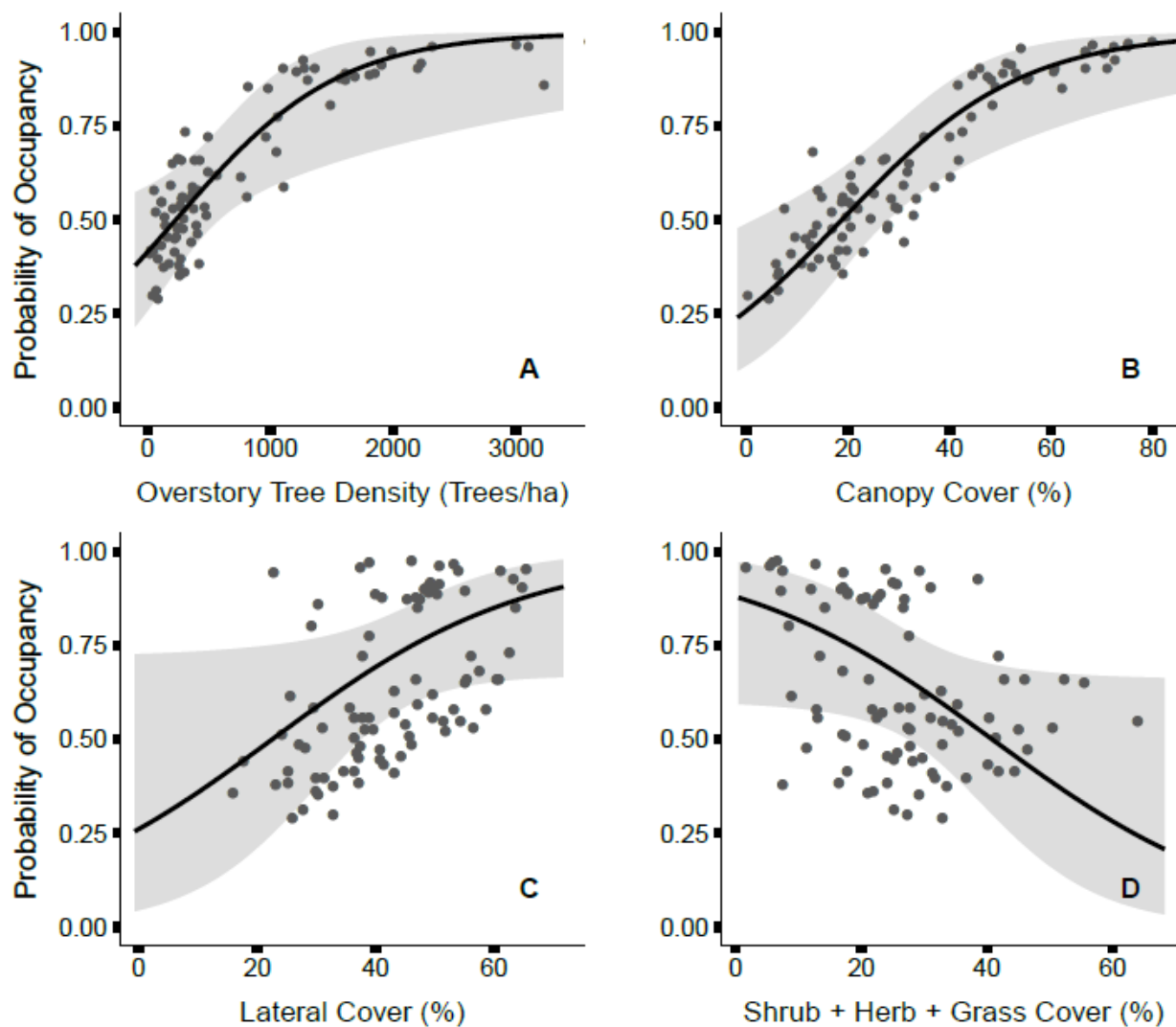


Figure 2.9 Model-averaged estimates of snowshoe occupancy as a function of overstory tree density (A), canopy cover (B), lateral cover (C), and shrub + herb+ grass cover (D) in southwest Yukon, Canada. Occupancy estimates (points) and predicted relationships (lines) were obtained by model-averaging across the confidence set of models where QAIC weights summed to 0.95. Lines show predicted covariate effects, when all other covariates are held constant at their mean. Shaded regions are unconditional 95% confidence intervals.

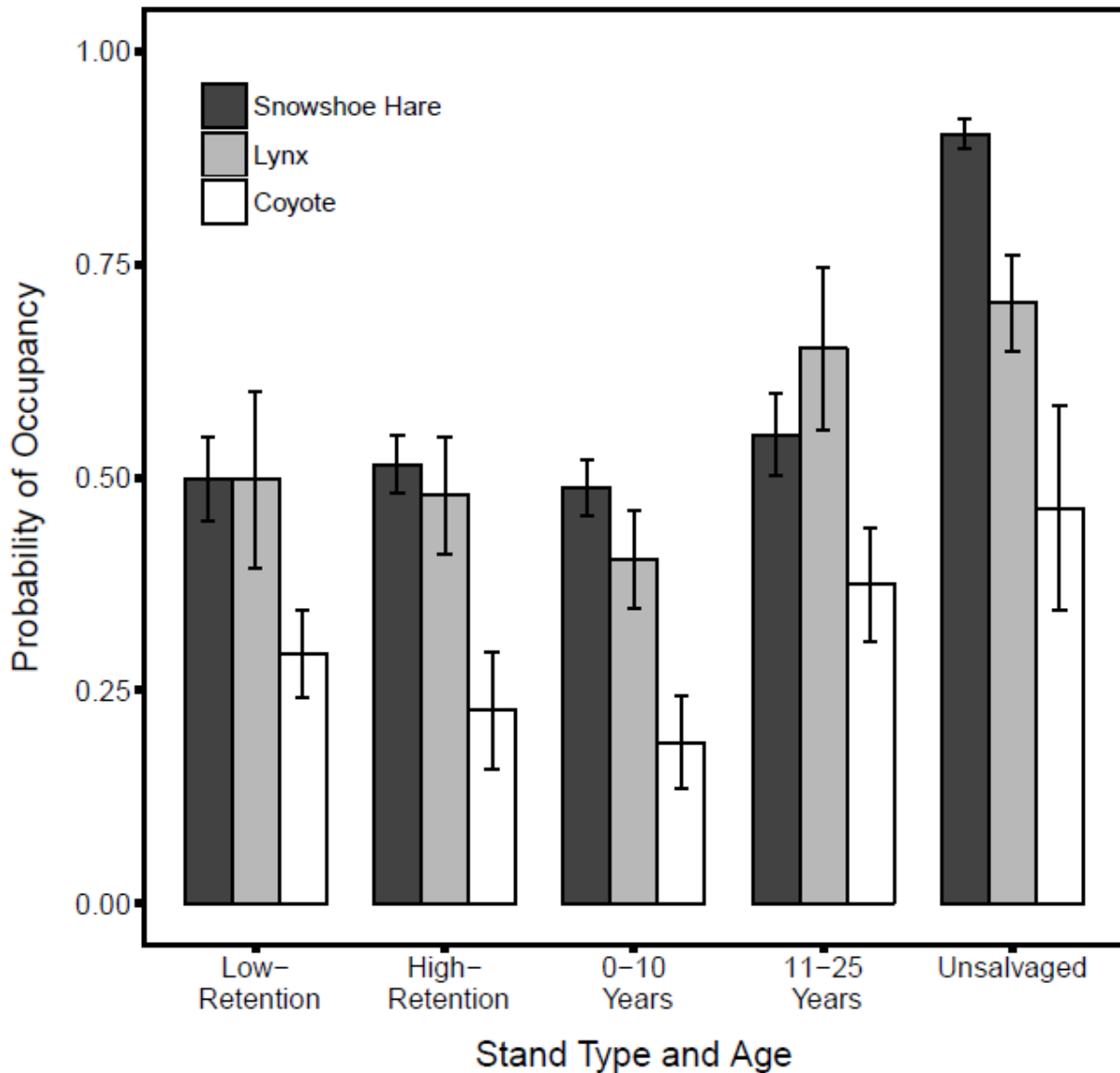


Figure 2.10 Mean estimates of snowshoe hare, lynx, and coyote occupancy in salvage logged stands of different retention levels (low/high) and ages (0-10 years and 11-25 years post-harvest), and in un-salvaged forest stands in southwest Yukon, Canada. Estimates were obtained by model averaging real parameters across the confidence set of models where QAIC weight summed to 0.95. Error bars represent 95% confidence intervals.

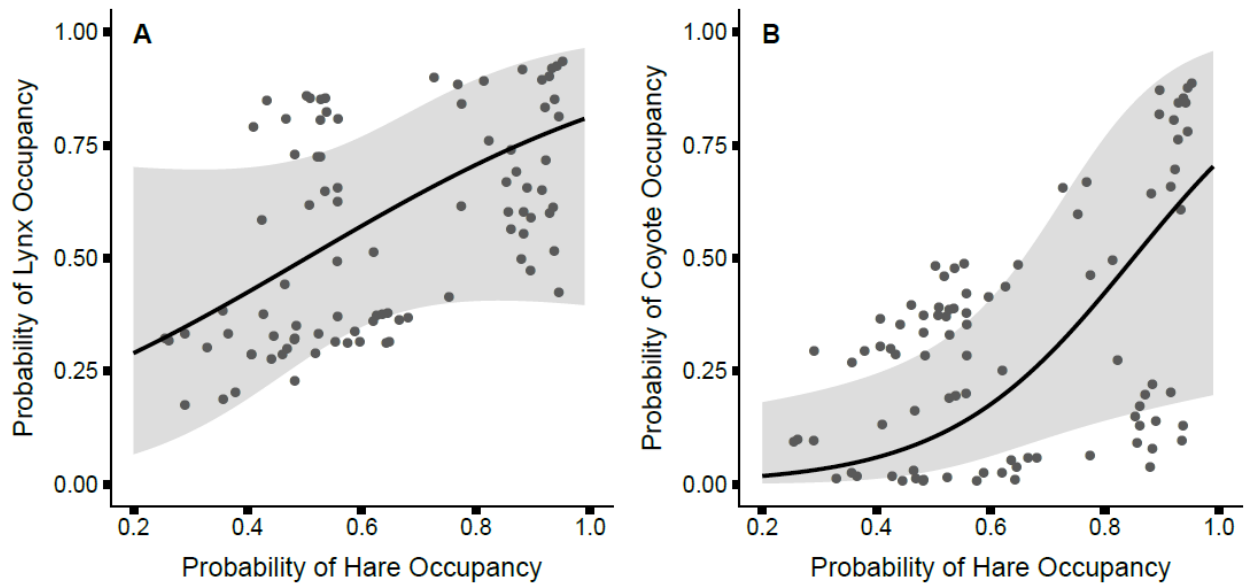


Figure 2.11 Model-averaged estimates of lynx (A) and coyote (B) occupancy versus predicted snowshoe hare occupancy in beetle-affected salvage logged and un-salvaged stands in southwest Yukon, Canada. Occupancy estimates (points) and predicted relationships (lines) were obtained by model-averaging across the confidence set of models where QAIC weights summed to 0.95. Lines show the predicted effects of snowshoe hare occupancy, while accounting for effects of all other covariates. Shaded regions represent unconditional 95% confidence intervals.

Chapter Three: Effects of Salvage Logging on Little Brown Bat (*Myotis lucifugus*) Occupancy Near its Northern Range Limit

3.1 Introduction

Bark beetles are a major disturbance agent in the boreal forest where they cause substantial tree mortality and changes to forest structure (Veblen et al. 1991). The largest infestations on record have occurred in recent decades, including mountain pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*Dendroctonus rufipennis*) outbreaks in western North America (Berg et al. 2006, Werner et al. 2006, Raffa et al. 2008). The extent and severity of these recent outbreaks has been attributed to climate warming (Dale et al. 2001, Berg et al. 2006, Bentz et al. 2010, Fettig et al. 2013). Beetle-killed timber is often harvested (a practice known as “salvage logging”) to minimize economic losses and reduce wildfire risk, yet this is an increasingly controversial management strategy. Salvage logging is claimed to aid forest recovery (Sessions et al. 2004) and improve wildlife habitat (Beguín et al. 2015), and is occasionally used as a management tool in parks and protected areas (Shore et al. 2003, Mehr et al. 2012, Thorn et al. 2018). Alternatively, evidence suggests that salvage logging may disrupt post-disturbance succession, reduce ecosystem services, remove biological legacies (e.g. snags), and alter wildlife habitat (reviewed in Hutto 2006, Lindenmayer and Noss 2006, Noss et al. 2006, Schmiegelow et al. 2006). The impacts of post-infestation salvage logging have been documented for cavity-nesting birds (Drever and Martin 2010, Edworthy et al. 2011) and passerines (Kroll et al. 2012), but few published studies have examined consequences for mammals (reviewed in Saab et al. 2014). Among mammals, bats are particularly sensitive to disturbances that alter forest structure (Medellín et al. 2000, Hayes and Loeb 2007). They have low reproductive rates (Barclay et al.

2004) so their populations are slow to recover from declines caused by habitat loss or degradation (Jones et al. 2009).

Forest-dwelling bats may select habitat based on stand structural complexity (Jung et al. 1999, Loeb and O’Keefe 2006, Müller et al. 2013), known as clutter (Fenton 1990). Vegetative clutter is an important ecological constraint for bats (Schnitzler and Kalko 2001). Clutter interferes with echolocation — making prey detection and location difficult — and reduces flight efficiency (Simmons et al. 1988, Fenton 1990, Schnitzler and Kalko 2001). Nevertheless, cluttered habitats (e.g. dense forests) typically have the highest insect densities, conferring advantages to insectivorous bats that can tolerate clutter (Kalcounis and Brigham 1995, Müller et al. 2012). Furthermore, forests provide protective cover that may reduce the risk of predation by owls and other aerial predators (Rydell et al. 1996, Russo et al. 2007), although the significance of predation for bats is widely debated (Speakman 1991, Speakman et al. 2000, Baxter et al. 2006, Lima and O’Keefe 2013). Thus, habitat selection by forest-dwelling bats involves a trade-off between clutter, food, and predation risk which may influence how bats respond to salvage logging.

While bark beetle infestations cause a gradual decrease in clutter as trees decay and collapse over decades (Randall et al. 2011, Kortmann et al. 2017), salvage logging causes an immediate and pronounced change in the structure of remnant forest, particularly if live trees are also harvested. Insect abundance may be reduced by logging activity (Jokimäki et al. 1998, Deans et al. 2005) and bats may be exposed to predation risk (or perceived predation risk) in logged areas due to increased illumination, especially at high latitudes (Russo et al. 2007, Talerico 2008, Randall 2009). However, high densities of aerial insects tend to aggregate at forest edges created by logging (Jokimäki et al. 1998, Deans et al. 2005) and bats may

preferentially forage or commute along edges (Grindal and Brigham 1998, 1999). The habitat guild (open, edge, or closed) and foraging mode (aerial hawking, gleaning) (Fenton 1990, Schnitzler and Kalko 2001) to which a bat belongs may be indicative of how it will respond to salvage logging (Mehr et al. 2012). Bat species that forage by hawking aerial insects tend to prefer open or edge habitats, and some exhibit a preference for logged areas (Grindal and Brigham 1998, 1999, Hogberg et al. 2002, Patriquin and Barclay 2003). While these species could benefit from salvage logging, closed-habitat species that glean non-aerial prey from the surfaces of vegetation are more tolerant of clutter (Arlettaz et al. 2001) and may avoid logged areas (Patriquin and Barclay 2003, Clarke et al. 2005). Negative effects on closed-habitat species may be mitigated by silvicultural practices that maintain residual trees (Hogberg et al. 2002). However, open-habitat species may prefer the most heavily-logged stands (Patriquin and Barclay 2003). To date, two studies have examined the consequences of post-infestation salvage logging for bats. Only open-habitat species benefitted from salvage logging in central European forests, whereas other guilds were unaffected (Mehr et al. 2012). In southwest Yukon, bat activity was lower in salvage-logged stands compared to beetle-affected, but unlogged forests (Randall 2009).

Bats at high latitudes face unique challenges, and there is mounting evidence that individuals at northern range limits are behaviourally, morphologically, and physiologically distinct from those at the core of their range (Talerico 2008, Lausen et al. 2009, Randall 2009, Reimer 2013, Boyles et al. 2016, Kaupas and Barclay 2018, Shively et al. 2018). Cold temperatures limit the flight of aerial insects near the beginning and end of the active season for bats (Talerico 2008), and short summer nights reduce available time for nocturnal foraging (Reimer 2013). The little brown bat (*Myotis lucifugus*) is an insectivorous species that is widely distributed across North America. This species typically prefers open and edge habitats (Barclay

1991, Segers and Broders 2014) and forages by aerial hawking (Fenton and Barclay 1980). Near its northern range limit in the boreal forest of Canada and Alaska, little brown bats may compensate for cold temperatures and short nights by gleaning as well as hawking prey to exploit a greater diversity of prey — most notably spiders (*Araneae*) (Talerico 2008, Boyles et al. 2016, Kaupas and Barclay 2018, Shively et al. 2018). Little brown bats at high latitudes may have developed divergent morphological (Talerico 2008) and acoustic characteristics (Lausen et al. 2009) that allow them to hunt in cluttered forest habitats where insects are most abundant (Grindal and Brigham 1999). Alternatively, northern bats may use cluttered forests because they provide canopy cover and protection from predators during the extended daylight hours (Talerico 2008, Randall 2009). Protective forest cover allows bats to emerge from roosts earlier while remaining relatively safe from predators (Rydell et al. 1996, Russo et al. 2007), thereby increasing total foraging time (which is a limiting factor at high latitudes; Reimer 2013). Given these constraints and adaptations, northern bats may respond to post-infestation salvage logging in unique ways compared to individuals further south.

My study evaluated the impacts of post-infestation salvage logging on habitat use by the little brown bat in southwestern Yukon, where it occurs near the northern limit of its geographic range. The little brown bat was recently listed as Endangered in Canada, largely due to a fungal disease known as white nose syndrome, and research on anthropogenic impacts is important to national recovery efforts (Environment Canada 2015). There are substantial knowledge gaps regarding the ecology of little brown bats in the boreal forest, including their response to forest disturbance (Jung et al. 2014).

Specifically, my objective was to compare the effects of different salvage logging practices on little brown bats by assessing three stand types: a) salvage-logged stands with low

structural retention (< 250 stems/ha); b) salvage-logged stands with high structural retention (≥ 250 stems/ha); and c) beetle-affected stands that were not logged (“unsalvaged”) and still had high densities of standing timber (> 1000 stems/ha). If little brown bats at high latitudes select habitat that maximizes insect abundance and minimizes predation risk, then unsalvaged stands will be preferred. If clutter avoidance is most important, then bats will select low retention salvage-logged stands, and habitat use will vary inversely with the density of standing timber. However, if clutter, food, and predation are all significant constraints, high retention stands with intermediate tree densities may provide the optimal habitat to satisfy these conflicting requirements. Note that logging may diminish roosting habitat for tree roosting species (Crampton and Barclay 1998), but this is an unlikely mechanism for salvage-logging impacts in Yukon, as little brown bats at high latitudes generally roost in buildings and other anthropogenic structures (Slough and Jung 2008).

Given the constraints on northern bat populations, and the behavioural and morphological adaptations that allow little brown bats to exploit clutter, I predicted that bats would prefer unsalvaged stands over salvage-logged stands of either retention level. I also predicted that high retention stands would be preferred over low retention stands. However, the behaviour and diet of bats at high latitudes may be contingent on seasonal variations in temperature (Kaupas and Barclay 2018), prey availability (Talerico 2008), and night length (Reimer 2013). Little brown bats in Yukon are more likely to avoid openings (e.g. logged and burned stands) near solstice when nights are short and never fully dark (Randall 2009). I predicted that habitat use in response to salvage logging would vary throughout the active season for bats. In spring and early summer temperatures are cool, aerial insect densities are low, and nights are short; thus, bats should exhibit the strongest preference for unsalvaged stands. In late summer, temperatures and

prey densities are higher and nights are longer, so bats may use salvage-logged stands during this period.

3.2 Methods

3.2.1 Study area

I conducted research near the town of Haines Junction (60.7522°, -137.5108°, elevation 599 m) in southwestern Yukon, in the Boreal Cordillera ecozone of Canada (Smith et al. 2004). Forests are characterized by homogenous white spruce (*Picea glauca*) overstories with willow (*Salix* spp.) understories and a groundcover of moss and ground shrubs (Smith et al. 2004, Garbutt et al. 2006). Trembling aspen (*Populus tremuloides*) stands are rare but present in previously logged or burned areas. The average age of overstory spruce in the study area is 170 years (Hawkes et al. 2014). The climate is dry and cool; average annual precipitation is 250–300 mm/year, and mean July temperatures vary from 7–12°C (Smith et al. 2004).

From 1990 to 2005, a severe infestation of spruce bark beetles affected over 360,000 ha of forest in this region (Garbutt et al. 2006, Hawkes et al. 2014). On average, forest stands had $32\% \pm 21.1$ SD tree mortality caused by spruce bark beetles (Randall et al. 2011), and almost no forests in the region were unaffected by beetles (Garbutt et al. 2006). Salvage logging began in the 1990's and is ongoing. Stands with the highest beetle mortality were generally selected for logging, although existing road access, community fire risk, recreational value, and fish and wildlife habitat were also considered during stand selection (Alsek Renewable Resource Council 2004, Resource Assessment Technical Working Group 2006). At the time of study, salvage logging affected less than 5% of the forest landscape in the area, and many high mortality stands had not been logged. An average of 25% stand retention was required in designated High Wildlife Value Areas, which comprised over 86% of the region (Resource Assessment Technical

Working Group 2006). Nevertheless, stand retention varied extensively across the study area. Clear-cut logging (i.e. near complete removal of live and beetle-killed trees) was practiced in areas where reducing fire risk was a high priority, or where windthrow was an issue. Retention levels exceeded 25% in some stands where trees were selectively removed on an individual basis. Most logging occurred on a relatively small scale (cuts were < 30 ha). Aside from post-infestation logging and associated roads, there were few anthropogenic disturbances on the landscape. This provided a unique opportunity to study salvage logging in relative isolation, without the confounding influence of other human impacts.

3.2.2 Study species

Little brown bats are the most abundant bat species in Yukon and are the only known species across most of the territory (Slough and Jung 2008). During spring and summer, reproductive females congregate in large maternal roosting colonies, but males and non-reproductive females typically roost alone or in small groups (Fenton and Barclay 1980). Almost all known maternity colonies in Yukon are located in buildings or artificial bat houses, except for two roosts in rock crevices (Slough and Jung 2008). Randall et al. (2014) found that reproductive females roosted in buildings in Haines Junction. There are two large maternity colonies in the centre of town — one in a housing complex and one in a Parks Canada building (with some bats in nearby bat houses) — but there are likely many other buildings with bats (personal communication with residents of Haines Junction). The roosting behaviour for males and non-reproductive females in the study area is largely unknown.

Little brown bats primarily eat aerial insects such as dipterans and lepidopterans (Fenton and Barclay 1980), but they can also glean non-aerial arthropods (Ratcliffe and Dawson 2003). In addition to forests, important foraging areas include clearings, edges, and water bodies

(Barclay 1991, Krusic et al. 1996, Broders et al. 2006) where little brown bats feed on aerial insects with aquatic larvae (e.g. chironomids, Fenton and Barclay 1980). During foraging bouts, reproductive female little brown bats are constrained by the distance from their maternal roosting colony, particularly when lactating (Henry et al. 2002). In Yukon, females fly up to 6 km nightly to reach foraging areas, whereas males tend to roost in close proximity to foraging areas (Randall et al. 2014).

3.2.3 Study design

My study design included 90 sites, with 60 salvage logged stands and 30 unsalvaged stands (Figure. 2.1, Figure. 2.2). I categorized salvaged stands as high retention if post-harvest overstory tree densities were 250–820 trees/ha ($n = 38$), and low retention if densities were 20–249 trees/ha ($n=22$). While I use “retention” as a descriptive term, tree densities prior to salvage logging were unknown so these categories more accurately reflected tree densities at the time of my study rather than true retention (i.e., what remained after logging). These categories also aligned with silvicultural prescriptions; low-retention stands were prescribed for fuel abatement, whereas high-retention stands were logged for timber value (with preservation of wildlife habitat as a priority).

All study sites were located within a 25 km radius of the town of Haines Junction. The region is topographically and climatically diverse, but this relatively small study area allowed for minimal variation in elevation and climate. Unsalvaged sites were randomly selected (with some concessions for accessibility), but salvage logged sites were selected to achieve adequate sample sizes for each retention category. The minimum distance between sites was 300 m (about 10 times the maximum distance detected with the ultrasonic detectors), with an average of $741 \text{ m} \pm 484 \text{ SD}$ between neighbouring sites.

3.2.4 Bat surveys

I monitored bat presence by recording echolocation calls with eleven Anabat SD1 and II ultrasonic detectors (Titley Scientific, Ballina, NSW, Australia) from 7 June to 27 August, 2016. Acoustic monitoring is a common and non-invasive method of determining bat habitat preferences (e.g. Grindal and Brigham 1998, 1999, Hogberg et al. 2002, Patriquin and Barclay 2003). I selected bat detector locations randomly within each salvage-logged or unsalvaged stand. I mounted detectors on tripods 1.5 m above the ground, with microphones tilted at a 45° angle from the ground (Weller and Zabel 2002). Bat detectors were directed towards forest openings to reduce vegetative obstruction and improve detection rates (Weller and Zabel 2002).

Most sites (60 %) were surveyed once during the early summer period (7 June to 15 July) and again during the late summer period (16 July to 27 August) to account for activity changes in response to shifting day length, insect abundance, and bat reproductive phenology (juvenile bats become volant in mid-July; Slough and Jung 2008). The remaining sites (40 %) were surveyed only during one of the sampling periods due to logistical constraints. Sites were monitored for 3–6 consecutive nights during one or both sampling periods, for a maximum of 12 sampling nights per site. Bat detectors were programmed to record continuously each night, from 30 minutes before sunset to 30 minutes after sunrise.

I manually processed all echolocation files using Analook W Version 4.1 software (Titley Scientific, Ballina, NSW, Australia). I considered a site to be occupied on a given sampling night if at least one bat pass was recorded, and I defined a bat pass as ≥ 2 echolocation calls in rapid sequence (Thomas 1988, Randall et al. 2011). I identified bat calls produced by *Myotis* species based on characteristic call frequencies and patterns of frequency change over time (Fenton and Bell 1981). *Myotis* species are difficult to distinguish due to overlap in call characteristics.

Nevertheless, little brown bats were the only confirmed bat species in southwestern Yukon until recent years, and recordings of other species are extremely rare (Slough and Jung 2008, Slough et al. 2014). Furthermore, little brown bats are the only confirmed species of *Myotis* in the study area; thus, I assumed all *Myotis* calls were little brown bats. Non-myotis species were not included in the analysis.

3.2.5 Habitat and climate

I took forest measurements at each site to characterize local stand structure in terms of value to bats (i.e. clutter, prey, and predation risk) (Table 3.1). I collected forest structure data along three perpendicular 40-m transects that originated at the bat detector location (Figure 2.4). I determined tree species composition, tree density (trees/ha), and basal area (m^2/ha) using the point-centred-quarter method (Cottam and Curtis 1956), taking measurements at the central point and at the 20-m and 40-m locations on each transect (seven locations total). I only counted trees if the diameter at 1.3 m (DBH) was ≥ 5 cm. At each of the locations described above, I used convex spherical densiometers to record canopy cover (%) in each cardinal direction.

Bats respond to habitat characteristics at local- and landscape-scales (Ford et al. 2006, Loeb and O'Keefe 2006, Duff and Morrell 2007, Bender et al. 2015). Land cover data with adequate resolution were not available for the study area, so I developed a land cover product through classification of Sentinel-2 satellite images at 20-m resolution (European Space Agency Copernicus Program). I used supervised maximum-likelihood classification techniques in ArcGIS version 10.4.1 (ESRI, Redlands, California) to distinguish three classes: forest, open, and water. Classification accuracy was 90 % — this was verified with a combination of ground surveys and aerial imagery at 100 random locations throughout the study area. I calculated total

forest edge (m) within a 500-m radius of each site using Fragstats version 4.2.1 (University of Massachusetts, Amherst, Massachusetts). I measured the distance from the detector to the nearest permanent water body (lakes, wetlands, and streams) and to the nearest stand edge (i.e., edge of forest patch or logged stand) with the Point Distance tool in ArcGIS. I also measured the distance between each site and a central point in the town of Haines Junction, where several maternal roosting colonies were located in buildings (Randall et al. 2014). Vector data were provided by the Yukon Department of Environment. Hypotheses regarding the influence of landscape-scale variables on little brown bats are outlined in Table 3.1.

Weather variables (e.g. temperature, precipitation) influence bat emergence and foraging activity (Erickson and West 2002, Talerico 2008). I obtained hourly weather data from the local Haines Junction weather station (Government of Canada 2016). Bats at northern latitudes typically emerge from their roosts shortly after sunset (Talerico 2008, Reimer 2013), so I used temperature values recorded at sunset. I classified precipitation events using two categories: significant precipitation (> 2 mm from sunset to sunrise) or non-significant precipitation (< 2 mm). I obtained sunset and sunrise times (National Research Council Canada 2016) and calculated night length based on the hours of darkness between civil twilight.

3.2.6 Statistical analyses

I compared vegetation and forest structure among stand types (low retention, high retention, and unsalvaged) with ANOVAs and post-hoc Tukey's HSD tests in R version 3.4.3 (www.r-project.org). I \log_{10} transformed basal area and tree density to meet assumptions of normality and homoscedasticity. I analyzed acoustic bat data using single-season occupancy models with the R package *RPresence* (version 2.12.6, Mackenzie and Hines 2017). Occupancy models allow the use of presence/absence data to assess landscape-level patterns in habitat use

while accounting for imperfect species detection (Mackenzie et al. 2002, 2006) and they are increasingly common in bat studies (Ford et al. 2006, Yates and Muzika 2006, Gorresen et al. 2008, Weller 2008, Bender et al. 2015). Models incorporated the effects of site-specific covariates on occupancy (ψ), as well as site- and survey-specific covariates that were suspected to influence detection rates (ρ). My results should be interpreted as relative habitat use rather than patch occupancy because bat home-range sizes are larger than the spacing between detectors (Randall et al. 2014), and bats could move readily among sites (Mackenzie et al. 2006, Efford and Dawson 2012).

Before developing candidate occupancy models, I determined the most plausible detection model by fitting combinations of site- and survey-specific covariates suspected to influence bat detection. I considered basal area, temperature, precipitation, night length, sampling period (early versus late), and Julian day as detection variables (rationale outlined in Table 3.1), and incorporated the best detection model into all subsequent occupancy models.

I developed a set of models to test *a priori* hypotheses about the influence of salvage logging and forest structure on bat occupancy (using the hypotheses and associated covariates outlined in Table 3.1) (Burnham and Anderson 2003). The candidate set of occupancy models included single-variable models as well as additive and interactive combinations of variables when biologically relevant (i.e. when interactive or additive effects were anticipated based on species' ecology). For example, juvenile bats may forage close to their roosting colonies (Buchler 1980) and may have lower clutter tolerance than adult bats (Adams 1996). To account for this, I tested the effect of the interaction between basal area and distance to town on occupancy. All continuous covariates were standardized by converting to z-scores (overall mean of 0 and standard deviation of 1), and correlated covariates ($r > 0.6$) were not included in the

same models to avoid multicollinearity (Dormann et al. 2013). Tree density and basal area were highly correlated ($r = 0.8$). I only retained basal area, as it is a structural characteristic commonly used by forest managers. To test for trends in occupancy along longitudinal or latitudinal gradients, I ran models with first- and second-order polynomials of spatial coordinates (Borcard et al. 2011, Legendre and Legendre 2012). If spatial terms improved model performance, and were not explained by habitat covariates, the spatial terms were retained in candidate models.

To test my predictions regarding temporal shifts in bat use of salvage-logged and unsalvaged stands, I ran two separate occupancy models for data collected in the early and late sampling periods (in addition to the full models described above). For data from each sampling period, I ran a small subset of single-variable occupancy models. I included stand type, basal area, canopy cover, and distance to town as covariates.

I compared candidate models to one another — and to the null and global models — using Akaike's Information Criterion (AIC). I removed models with uninformative parameters from the candidate set (i.e., complex models that received lower AIC than the simpler nested model) (Arnold 2010), as well as models that did not converge. I did not use AIC corrected for small sample size (AICc) because this produces biased estimates for non-Gaussian data, particularly for logistic models (Richards 2015). AIC weights were used to evaluate the relative strength of each candidate model. If no model received a weight $> 90\%$, I calculated parameter estimates and unconditional standard errors by averaging across a set of confidence models (the “confidence set”) where Akaike weights summed to approximately 0.95 (Burnham and Anderson 2003). I model-averaged 95 % confidence intervals via the Delta method (Cooch and White 2017): unconditional standard errors were estimated on the logit scale, then confidence intervals

were calculated and back-transformed to the probability scale as implemented with the `modAvg` function in *RPresence*. Refer to section 2.2.6 for additional details.

I calculated occupancy-model residuals (Warton et al. 2017) from the top-performing model (lowest AIC) and tested for spatial autocorrelation using Moran's I correlograms of residuals (Tiefelsdorf 2000, Dormann et al. 2007). I evaluated the fit of the most saturated model with 10,000 bootstrapping events and a chi-square goodness-of-fit test (MacKenzie and Bailey 2004), and I used quasi-AIC (QAIC) values to compare models when overdispersion and a lack of fit were indicated (i.e. $\hat{c} > 1$). When QAIC was used for model selection, I inflated unconditional standard errors by the square root of the \hat{c} value (McCullagh and Nelder 1989, MacKenzie and Bailey 2004).

3.3 Results

Unsalvaged stands had higher basal area ($F_{2,87} = 99.4$, $P < 0.001$), canopy cover ($F_{2,87} = 153.8$, $P < 0.001$), and overstory tree density ($F_{2,87} = 109.4$, $P < 0.001$) than high-retention-logged stands, which in turn had higher values than low-retention-logged stands (Figure 2.6 A, B, and C). Bats were present at 77 of 90 sites (85.6 %). I recorded 773 bat passes across 613 sampling nights, and 99.7 % of passes were *Myotis* bats (assumed to be *M. lucifugus*). The remaining 3 bat passes (0.3 %) were not from the genus *Myotis* and were excluded from the analysis. The best-fitting detection model included sampling period and received a QAIC weight of 0.94; support for all other detection models was negligible (Table 3.2). The probability of detection was significantly higher during the late sampling period (Figure 3.1 A).

The confidence set of occupancy models (QAIC weights summing to 0.95) included basal area, distance to water, UTM coordinates, edge distance, total edge, and canopy cover, but no interaction terms (Table 3.3). The top two models (Basal Area + Water and Basal Area +

UTM) had a combined QAIC weight of 0.56. All other models had a < 10 % chance of being the best model in the set (i.e. QAIC weights <0.10). The goodness-of-fit test on the global occupancy model indicated there was no lack of fit ($\chi^2 = 3113.1$, $P = 0.27$), but there was minor overdispersion ($\hat{c} = 1.02$). No spatial autocorrelation was detected in model residuals; the Moran's I p-value was > 0.05 for most lag distances up to the maximum of 35 km, and the x-intercept of the correlogram was 0 km (Figure A.1).

Contrary to expectations, basal area had a negative effect on little brown bat occupancy (Table 3.4), particularly beyond a threshold of approximately 40 m²/ha (Figure 3.1 B). However, this relationship was disproportionately influenced by two sites with low occupancy and very high basal area (Figure 3.1 B); when these sites were excluded from the analysis, the effect of basal area was still negative but not significant (confidence intervals overlapped zero). Bat occupancy weakly declined with increasing distance to edge (Table 3.4, Figure 3.1 E), although this was largely explained by the influence of an extreme value (i.e., one site that was > 400 m farther from an edge than any other). Distance to water and canopy cover had an overall negative influence on occupancy, and total edge generally had a positive influence, but relationships were not significant (Table 3.4, Figure 3.1 C, D, and F). Both low retention and high retention salvage-logged stands tended to have higher occupancy values than unsalvaged stands, but confidence intervals overlapped zero, suggesting no effects of stand type. Both easting and northing had a positive influence on occupancy.

Occupancy models for the early and late sampling periods produced different outcomes, suggesting there was temporal variation in habitat preferences. The distance-to-town-model was the top model for early period data, with a QAIC weight of 0.61; conversely, in the late period basal area was the top model with a QAIC weight of 0.62. Basal area had a weak (but negative)

influence on occupancy during the early period ($\beta = -0.47$, $SE = 0.40$), and a much stronger negative influence during the late period ($\beta = -1.72$, $SE = 1.11$) (Figure 3.2 A). The threshold response noted above was only present during the late period. Occupancy declined strongly with increasing distance to town during the early period ($\beta = -0.86$, $SE = 0.40$), but not during the late period ($\beta = 0.02$, $SE = 0.66$) (Figure 3.2 B). The effects of stand type were not significant in either the early or late period; nevertheless, relative use of stand types varied from early to late (Figure 3.3). During the early period, high-retention-salvage-logged stands had higher occupancy (0.71 ± 0.12) than low-retention (0.56 ± 0.14) or unsalvaged stands (0.53 ± 0.13). During the late period, low retention and high retention stands had similar occupancy probabilities (0.95 ± 0.13 and 0.99 ± 0.13 , respectively), which were higher than occupancy in unsalvaged stands (0.87 ± 0.11).

3.4 Discussion

I predicted that bats would favour unsalvaged stands, particularly during early summer, yet bats showed no strong preferences based on stand type. There was some evidence of higher occupancy in high retention salvage-logged stands relative to unsalvaged stands, but effects were non-significant. There was no difference in occupancy between high retention and low retention stands. These results contrast with those of a study from the same region, which concluded that bats prefer beetle-affected forests over logged areas (Randall 2009).

My predictions about salvage logging were based on the hypothesis that bats seek habitat with abundant food and low predation risk. The importance of predation to bats is largely unknown (Speakman 1991, Speakman et al. 2000, Baxter et al. 2006, Lima and O'Keefe 2013). However, food may be limiting at high latitudes during the early active season (i.e., May and

June) when cool temperatures constrain the flight of aerial insects (Talerico 2008) and bats seek alternate prey such as spiders (Kaupas and Barclay 2018, Shively et al. 2018). This behaviour has been used to explain why little brown bats at high latitudes preferentially forage in forests (Talerico 2008, Randall 2009) rather than open and edge habitats like their southern counterparts (Barclay 1991, Krusic et al. 1996, Segers and Broders 2014). My study was conducted in 2016, which was an exceptionally warm year in the Yukon (Government of Yukon 2017). Little brown bats are more likely to consume spiders — as opposed to aerial prey — below an average daily temperature of 10°C (Kaupas and Barclay 2018), yet during June 2016 only 8 days fell below this threshold (Government of Canada 2016). In contrast, there were twice the number of < 10°C days in June 2006, the year of Randall's (2009) study. Warm temperatures in 2016 may explain why bats did not favour unsalvaged stands; this would imply that different habitat preferences could be observed in cooler years. This is mere speculation, as I did not quantify insect abundance or bat diet in response to temperature and stand type.

Little brown bats rarely occupied unsalvaged stands with basal areas exceeding a threshold of 40 m²/ha (although few stands were this dense). Species of bats adapted to forage in open and edge habitat may avoid densely treed stands because clutter makes flight and prey detection difficult (Fenton 1990, Kalcounis and Brigham 1995, Schnitzler and Kalko 2001). Clutter thresholds have similarly been observed for bats in USA and Australia (Blakey et al. 2016). In a previous study in the same region of southwestern Yukon, little brown bats likewise avoided dense forest (Randall et al. 2011), despite evidence that bats at high latitudes are more clutter-adapted than southern conspecifics (Talerico 2008). An alternative explanation for the observed threshold is that bats are simply harder to detect in dense habitats (O'Keefe et al. 2014).

However, detection models indicated that tree density and basal area had very weak effects on

detection rate. Another study in the boreal forest found that tree density did not affect the detectability of 40 kHz sound (Patriquin et al. 2003, but see Jung et al. 1999), which is a characteristic frequency for little brown bat calls (Fenton and Bell 1981).

In the northern boreal forest, the number of daylight hours varies widely throughout the spring and summer, which may influence bat activity and habitat preferences. In addition, juvenile bats become volant in mid-July (Slough and Jung 2008), which could significantly increase the population of flying bats during the late sampling period. I predicted more use of logged stands by bats during the late period than the early period. Although there were no seasonal shifts in the use of different stand types (i.e., occupancy was similar in all stand types regardless of sampling period), the shape of the relationship with basal area changed from early to late. During the late period, basal area had a much stronger negative influence on occupancy, and a clutter threshold was evident (Figure 3.2 B). There are two possible explanations for this shift, which are not mutually exclusive. In late summer the nights are significantly longer and darker, and bats may perceive lower risk of predation by aerial predators (Rydell et al. 1996, Speakman et al. 2000, Talerico 2008, Randall 2009), resulting in a higher likelihood of occupying open habitats. This would imply that predator avoidance plays a role in bat habitat selection in the northern boreal forest. Alternatively, newly volant juveniles are unskilled fliers and avoid cluttered habitat (Adams 1996), which could explain the threshold relationship with basal area in the late period.

During the early period, but not the late period, bat occupancy was largely dictated by distance from major roosting colonies in the town of Haines Junction rather than basal area. This contrast likely reflects phenological events. In the northern boreal forest, reproductive female little brown bats are lactating from approximately late June to late July (Slough and Jung 2008,

Reimer 2013, Boyles et al. 2016). Lactating bats may return to their maternal roosts several times a night to nurse, which imposes constraints on nightly foraging distances (Henry et al. 2002). Juveniles and female bats disperse from their maternal roosting colonies later in summer (Fenton and Barclay 1980); thus, they are no longer bound to a central location.

I observed spatial trends in bat occupancy, even after accounting for the influence of distance to waterbodies. Bat occupancy increased along a gradient from south to north, and from west to east (i.e., occupancy was highest in the northeast of the study area). I suspect these trends were attributed to the presence of Pine Lake — the largest waterbody in the region — in the northeast. Little brown bats often forage over water (Barclay 1991, Krusic et al. 1996, Broders et al. 2006) and Pine Lake is a particularly important foraging area for local bats (Randall et al. 2011), presumably because of its size and proximity to the town of Haines Junction (Randall et al. 2014). Furthermore, bats have been documented in rock crevices near Pine Lake (Slough and Jung 2008). Although many species of bats are thought to seek landscapes with edge habitat (Ford et al. 2006, Duff and Morrell 2007, Bender et al. 2015), little brown bats in my study did not appear to benefit from edges created by logging and linear disturbances at the landscape scale (i.e., total edge). There was some evidence that bats preferred to be closer to edges (perhaps because aerial insects accumulate near edges; Jokimäki et al. 1998), but this trend was mainly caused by a single site that was disproportionately far from any edge.

3.4.1 Management implications and future work

To summarize, little brown bats were largely unaffected by post-infestation salvage logging in southwest Yukon. Small-scale salvage logging (e.g. < 30 ha cuts in my study area) may be sustainable for little brown bats in the northern boreal forest and could even improve summer habitat, particularly for juvenile bats requiring uncluttered areas to forage. My

conclusions, however, were based on a single season of data when temperatures were unusually warm. Diet and habitat use by little brown bats may vary with temperature; thus, different results could be observed in cooler years.

My study has addressed the short-term (< 25 years) effects of salvage logging, yet logged stands can eventually regenerate as dense forests that may be unsuitable for some species of bats (Law and Chidel 2002, Blakey et al. 2016), particularly if clutter thresholds are exceeded. Bat habitat use in salvage-logged stands should be re-assessed in 20 or more years, when young forests have replaced the early- and mid-successional stands.

My study considered the effects of salvage logging on foraging and commuting habitat for bats, but not roosting habitat. In northern climates, reproductive female little brown bats typically roost in buildings (Slough and Jung 2008), as trees at high latitudes may be unsuitable for maternity colonies (Parker et al. 1997); thus, I suspect salvage logging would have little to no impact on maternal roosting habitat. However, male bats may roost in trees (Randall et al. 2014), and decaying beetle-killed trees may be particularly suitable roosts (Vonhof and Barclay 1996, Crampton and Barclay 1998). Additional work is required to determine impacts of post-infestation salvage logging on roosting habitat.

Table 3.1 Variable names, descriptions, and hypotheses (including predicted effect in parentheses) for site- and landscape-level habitat variables used in occupancy and detection models for the little brown bats (*Myotis lucifugus*) in salvage-logged and unsalvaged forests in Yukon, Canada.

Variable	Description	Hypothesis and Prediction
<i>Detection Covariates</i>		
Period	Sampling period: Early (June 1 – July 15) or late (July 17 – August 27)	Pups become volant after mid-July = increased probability of detection (early –, late +)
Date	Julian date	Bat activity increases through summer (+)
Basal Area	Basal area (m ² /ha) of stand (analogous to clutter)	Sound transmission may be reduced in densely vegetated/cluttered stands (–)
Night length	Hours of darkness between civil twilight	Greater chance of detecting bats when nights are longer (+)
Effort	Number of nights sampled	Greater chance of detecting bats with longer sampling periods (+)
Temperature	Temperature at sunset on a given sampling night	Higher temperatures increase likelihood of bats leaving roost (+)
Rain	Significant precipitation events	Bats less likely to leave roosts (–)
<i>Site-level Occupancy Covariates</i>		
Overstory Tree Density	Estimated tree density (trees/ha), measured along three 40 m transects	Reduces flight efficiency but reduces predation risk and increases prey density (+)
Basal Area	Estimated basal area (m ² /ha) of stand, measured along three 40m transects	Reduces flight efficiency but reduces predation risk and increases prey density (+)
Stand Type	3 categories: low-retention logged, high-retention logged, or un-salvaged	Logging increases predation risk and reduces prey density (low retention –, high retention –, un-salvaged +)
Canopy	Estimated canopy cover (%) of stand, measured using a canopy densitometer along three 40m transects	Provides darkness and protection from predators (+)
Edge Distance	Distance (m) from bat detector to nearest forest edge (e.g. edge of logged stand, road, pipeline)	Forest edges are easy to navigate and have high prey density, so bats fly near edges (–)
<i>Landscape-scale Occupancy Covariates</i>		
Water	Distance (km) to nearest lake, river, or wetland	Bats use waterbodies as foraging/drinking habitat (–)
Total Edge	Total forest edge distance (km) within a 500 m radius of bat detector	Forest edges are easy to navigate and have high prey density, so bats prefer areas with lots of edge (+)
Distance	Distance to the town of Haines Junction	Female bats use maternity roosts in buildings in town, particularly when lactating (–)

Table 3.2 Full set of detection (ρ) models for little brown bats (*Myotis lucifugus*) in beetle-affected and salvage-logged forests in southwest Yukon, Canada. Quasi-Akaike's Information Criterion (QAIC), delta QAIC, QAIC weight, and number of parameters (K) are shown for each model. Covariates are defined in Table 3.1. The null model is indicated with (.).

Model	QAIC	ΔQAIC	QAIC weight	K
ψ (.), ρ (Period)	534.52	0	0.9395	3
ψ (.), ρ (Date)	541.32	6.8	0.0314	3
ψ (.), ρ (Night Length)	542.18	7.66	0.0204	3
ψ (.), ρ (Night Length + Basal Area)	543.88	9.36	0.0087	4
ψ (.), ρ (Effort)	570.24	35.72	0	3
ψ (.), ρ (Basal Area + Effort)	570.29	35.77	0	4
ψ (.), ρ (Basal Area)	572.36	37.84	0	3
ψ (.), ρ (.)	572.84	38.32	0	2
ψ (.), ρ (Temperature)	573.4	38.88	0	3
ψ (.), ρ (Rain)	574.02	39.5	0	3

Table 3.3 Confidence set of occupancy (ψ) models (QAIC weights sum to ~0.95) for little brown bats (*Myotis lucifugus*) in beetle-affected and salvage-logged forests in southwest Yukon, Canada. Quasi-Akaike's Information Criterion (QAIC), delta QAIC, QAIC weight, and number of parameters (K) are shown for each candidate model. Covariates are defined in Table 3.1. UTM is a function of spatial coordinates (easting + northing).

Model	QAIC	Δ QAIC	QAIC weight	K
ψ (Basal Area + Water), ρ (Period)	672.31	0	0.354	5
ψ (Basal Area + UTM), ρ (Period)	673.38	1.07	0.207	6
ψ (Stand Type + Water), ρ (Period)	674.88	2.57	0.098	6
ψ (Edge Distance + Water + UTM), ρ (Period)	675.25	2.94	0.081	7
ψ (Basal Area), ρ (Period)	675.59	3.28	0.069	4
ψ (Total Edge + Water), ρ (Period)	675.77	3.46	0.063	5
ψ (UTM), ρ (Period)	676.84	4.53	0.037	5
ψ (Canopy + Water), ρ (Period)	677.25	4.94	0.030	5
ψ (Edge Distance + Water), ρ (Period)	677.51	5.20	0.026	5

Table 3.4 Model averaged parameter estimates, unconditional standard errors (SE), and 95% confidence intervals (CI) for little brown bat (*Myotis lucifugus*) detection (ρ) and occupancy (ψ) in southwest Yukon, Canada. Covariates following ψ and ρ intercepts are occupancy and detection parameters, respectively. Estimates were calculated by averaging across the set of confidence models where QAIC or AIC weights summed to 0.95. Occupancy covariates are defined in Table 3.1. Significant coefficient estimates (confidence intervals do not overlap zero) are listed in bold.

Parameter	Estimate	SE	95% Lower CI	95% Upper CI
ρ intercept	-0.83	0.47	-1.75	0.08
Period	1.37	0.20	0.98	1.76
Ψ intercept	4.03	1.67	0.76	7.3
Basal Area	-1.44	0.66	-2.72	-0.15
Water	-1.46	1.03	-3.48	0.55
Easting	0.003	0.0007	0	0.01
Northing	0.003	0.0008	0	0.01
Stand Type (High Retention)	4.20	3.57	-2.80	11.20
Stand Type (Low Retention)	2.75	1.87	-0.92	6.42
Total Edge	2.63	1.38	-0.06	5.32
Edge Distance	-0.88	0.44	-1.75	-0.02
Canopy	-1.29	0.67	-2.60	0.02

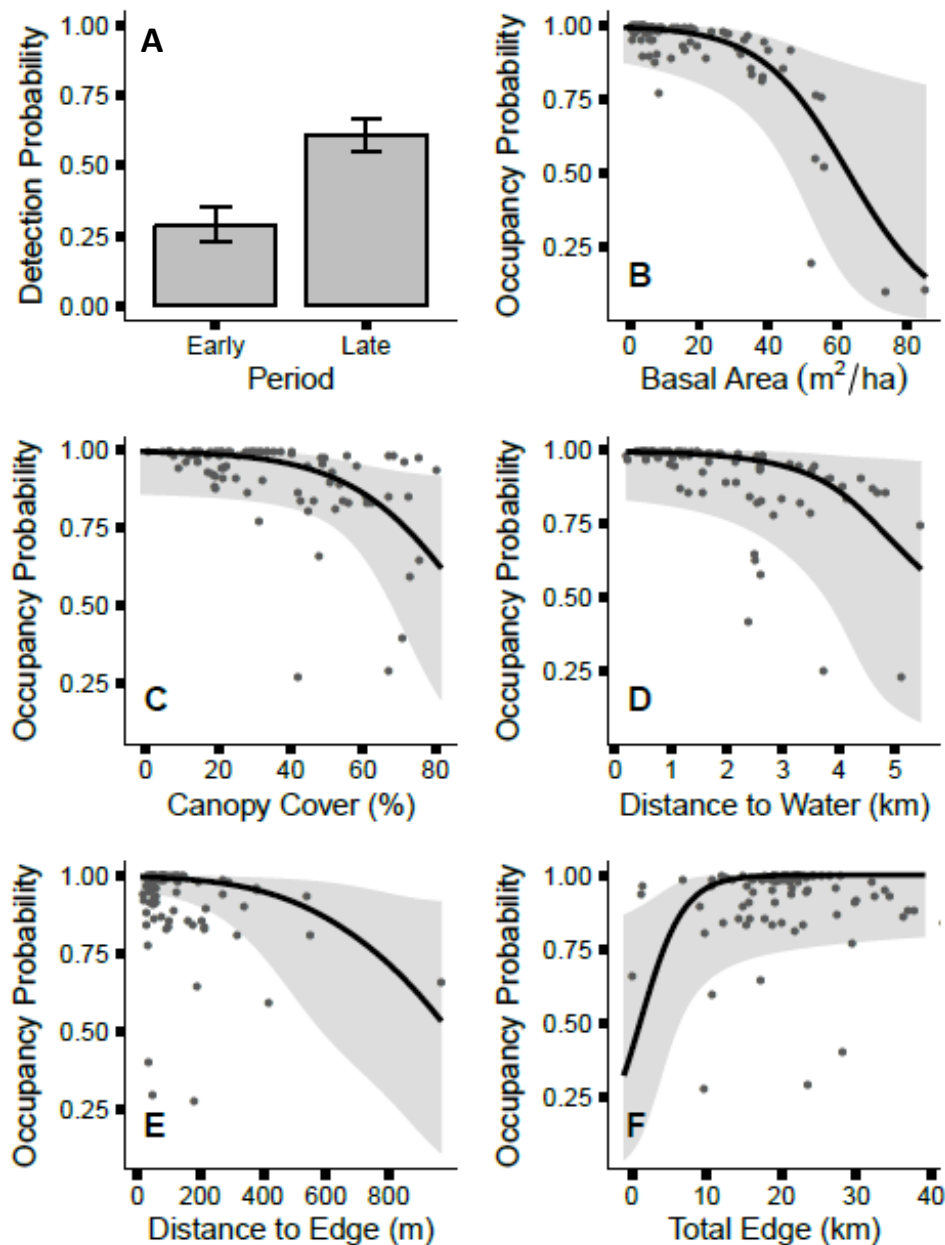


Figure 3.1 Model-averaged predictions of little brown bat (*Myotis lucifugus*) detection and occupancy in bark-beetle affected and salvage-logged forests in southwest Yukon, Canada, including the probability of detection in early and late sampling periods (A), and the probability of occupancy as a function of tree basal area (B), canopy cover (C), distance to water (D), distance to forest edge (E), and total edge (F). Occupancy estimates (points) and predicted relationships (lines) were obtained by model-averaging across the confidence set of models where QAIC weights summed to 0.95. Lines show predicted covariate effects, when all other covariates are held constant at their mean. Shaded regions are unconditional 95% confidence intervals, calculated via the delta method.

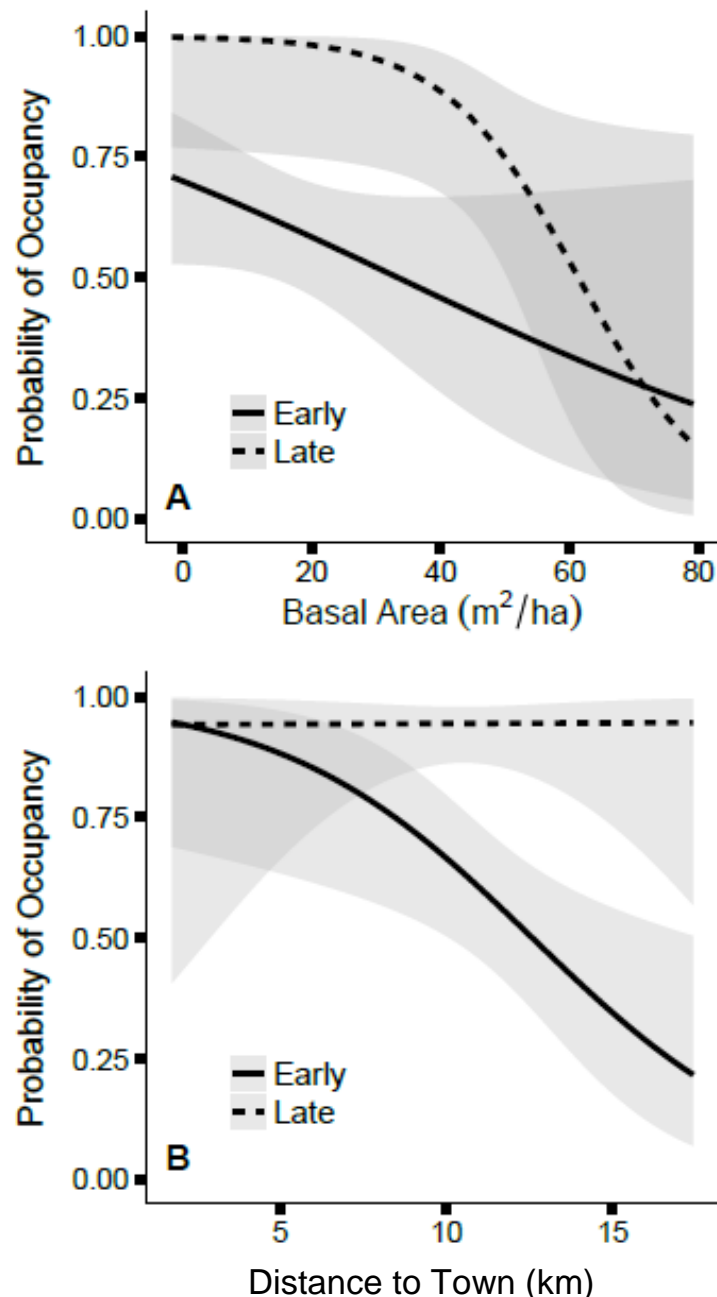


Figure 3.2 Model-averaged predictions of little brown bat (*Myotis lucifugus*) occupancy as a function of tree basal area (A) and distance to town (B) in beetle-affected and salvage-logged stands in southwest Yukon, Canada, during the early (1 June – 15 July) and late (16 July – 31 August) sampling periods. Predicted relationships were obtained by model-averaging across the confidence set of models where QAIC weights summed to 0.95. Lines show predicted covariate effects, when all other covariates are held constant at their mean. Shaded regions are unconditional 95% confidence intervals, calculated via the delta method.

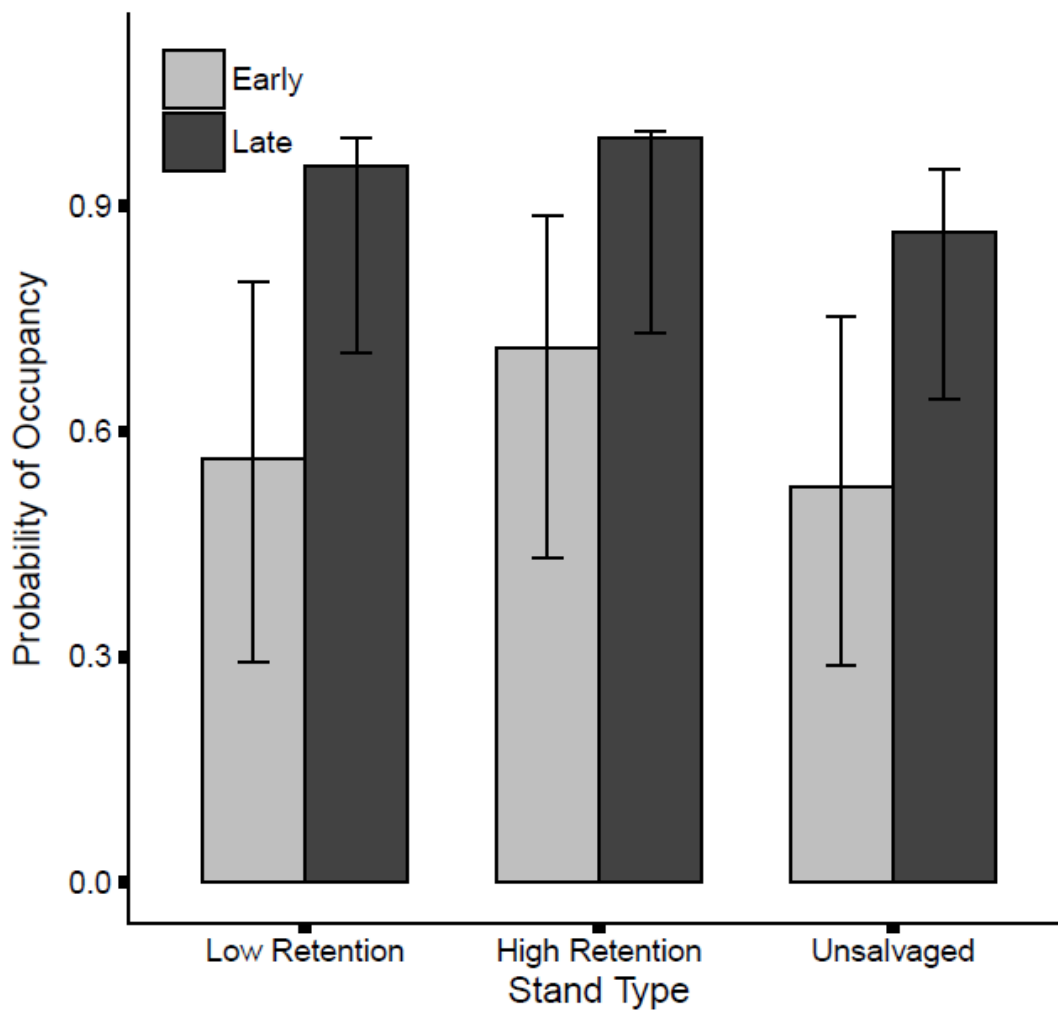


Figure 3.3 Predicted estimates of little brown bat (*Myotis lucifugus*) occupancy in salvage-logged stands of different retention levels (low/high) and in unsalvaged forest stands in southwest Yukon, Canada. Predicted values were averaged across the confidence set of models where QAIC weight summed to 0.95. Error bars represent unconditional 95% confidence intervals.

Chapter Four: Summary and Conclusions

Few studies have examined the effects of salvage logging on mammals, particularly at high latitudes where logging is a relatively new practice. My results indicate that mammalian species have different responses to the structural changes caused by salvage logging, possibly as a consequence of trade-offs imposed by limited resource availability. Terrestrial herbivores (moose [*Alces americanus*], snowshoe hare [*Lepus americanus*]) experience trade-offs between food and cover, while predators (lynx [*Lynx canadensis*], coyote [*Canis latrans*]) must balance prey abundance with accessibility. For little brown bats (*Myotis lucifugus*), vegetative clutter may prevent them from accessing habitats with the highest food and lowest predation risk.

In summary of my research, moose had higher occupancy in salvage-logged stands (with the possible exception of females with calves) while snowshoe hares, lynx, and coyote preferred unsalvaged stands. This was largely explained by canopy cover, which may have influenced food availability for moose and predation risk for snowshoe hare. Habitat use by lynx and coyote generally paralleled that of their primary prey, snowshoe hare; however, lynx had comparatively low occupancy in unsalvaged stands where hunting may have been difficult. Little brown bat occupancy appeared to be unaffected by salvage logging, despite the potential for high predation risk and low prey abundance in logged stands. Bats avoided very dense unsalvaged stands, perhaps because clutter was a deterrent.

High-retention logging practices appeared to have few benefits for these species. Compared to low retention stands, high retention stands had less food and lower moose occupancy, although females with calves may have benefitted from the cover provided by residual trees. Among salvage-logged stands, snowshoe hare, lynx, coyote, and little brown bats had no apparent preference for one retention level over the other. Habitat use by lynx and coyote

increased with time since logging, but salvage-logged stands of all ages (up to 25 years post-logging) had low value to snowshoe hares. Moose did not discriminate between older and younger logged stands.

4.1 Study Limitations and Suggestions for Future Research

There are several limitations associated with occupancy modelling. Occupancy can be used to infer patterns of relative habitat use, but it does not necessarily relate to abundance of individuals. Further, “habitat use” does not always imply habitat quality, as there are situations where species may select suboptimal habitat (e.g. due to site fidelity or competitive interactions; Johnson 2007). Occupancy modelling requires large sample sizes to achieve precision, although less so for abundant species with high detection rates (Shannon et al. 2014). Consequently, occupancy estimates were relatively precise for snowshoe hare — an abundant species in the boreal forest — but estimates had larger confidence intervals for other species, sometimes preventing reliable inference. Lastly, there may be a mismatch between species occupancy and performance in a given habitat. Moose, for example, may have high occupancy in logged stands, but may experience higher mortality from predation or hunting in these stands (Rempel et al. 1997). Research on the consequences of salvage logging for mammal performance, fitness, and demography is lacking (Saab et al. 2014), but would be invaluable for predicting population-level responses.

Point sampling devices such as wildlife cameras and acoustic bat detectors have several disadvantages. I selected a single point to represent each salvage-logged or unsalvaged stand, but habitat use for smaller mammals such as snowshoe hares may be dictated, to some extent, by patchiness within stands (Fuller and Harrison 2013). I surveyed many stands ($n = 90$) and

randomly selected point locations within stands; thus, my study design was likely adequate to characterize habitat use at the stand-level, but I did not quantify or control for the variation introduced by within-stand habitat selection. Further, there were limitations imposed by the spatial scale at which I conducted my study. My study area may have been too small (~20 km radius) and my sites too closely spaced to detect patterns of habitat use on a landscape-scale. Stand-level habitat characteristics (e.g. canopy cover) were generally more important predictors of occupancy than landscape-scale characteristics (e.g. total edge), perhaps because of this design limitation. For species with large home ranges, such as moose and little brown bats, my study was better suited to assess relatively fine-scale (i.e., stand-level) habitat use.

This was a single-year study (conducted over a relatively brief four-month period), but the Yukon experiences broad variation in annual temperatures (Government of Yukon 2017). Given that ambient temperatures have an influence on diet and habitat selection by little brown bats at high latitudes (Kaupas and Barclay 2018), a multi-year study capturing a variety of spring and summer temperatures would provide a broader perspective. Although my study was conducted in spring and summer, winter is often thought to be the limiting season for snowshoe hares (Feierabend and Kielland 2015) and moose (with respect to nutrition; Dussault et al. 2005). However, the quality and quantity of summer forage has an impact on the winter condition of moose (Stephenson 1995). Snowshoe hares cannot readily shift home ranges, particularly at high population densities (Boutin 1980, Boutin et al. 1985), and thus stand-level patterns of habitat use may be similar between seasons. Nevertheless, I advise caution in extrapolating my summer results to other seasons, and suggest additional research in winter.

4.2 Management Recommendations

Multi-species research is needed to guide the development of forest management policies that are sustainable for biodiversity. Science-based management strategies that focus on the needs of one species — even an “indicator species” — may occur to the detriment of others (Simberloff 1998, Lindenmayer et al. 2007). All species in my study have been proposed as indicators to monitor forest health or vertebrates in general (moose, snowshoe hare and lynx: McLaren et al. 1998; coyote: Bayne et al. 2004; little brown bats: Jones et al. 2009), yet managing one would not necessarily benefit the whole.

Given the conflicting requirements of species in my study, a balanced approach to managing beetle-affected forests is required. Low-retention logging provides food resources for moose, while high-retention logging could provide the canopy cover required by snowshoe hares (to the benefit of lynx and coyote) with adequate retention levels. Little brown bats will likely use logged stands of either retention level, possibly benefitting from reduced clutter. Thus, a mosaic of stands with different retention levels will likely benefit the most species; this reflects current practice in southwest Yukon where some stands are heavily logged for fuel abatement, while others are partially logged to preserve wildlife habitat. The caveat is that standard retention levels (25 % on average) are not high enough for snowshoe hares; I recommend retaining more individual trees, or more extensive patches of trees. Based on other work, higher retention levels are likely to benefit small mammals (Sullivan et al. 2010), although data on other mammalian taxa (e.g. mustelids, ursids) are still lacking. Above all, my results suggest that beetle-affected forests have higher value than salvage-logged stands for several ecologically important species, and some unsalvaged forests should be maintained on the landscape.

The results of my study also highlight the importance of studying forestry impacts at high latitudes where logging is a relatively new practice, and where forests and wildlife may respond to anthropogenic disturbance in unexpected ways. Snowshoe hare, in particular, responded differently than conspecifics in the southern boreal forest, where they prefer regenerating cut blocks over mature forest (Fisher and Wilkinson 2005). However, this may reflect the comparatively slow pace of succession at high latitudes more so than any behavioural divergence. Harvest regimes that accelerate the rate of coniferous regeneration (e.g. shelterwood harvest; Man and Lieffers 1999) would be advantageous. Forest succession will continue to change the value of these salvage-logged stands for moose, snowshoe hare, lynx, coyote, and little brown bats; I recommend a re-assessment of these stands in 20-40 years to determine longer-term impacts.

A key motivation for salvage logging is to extract the maximum volume of dead wood before the value is lost to decay (Schmiegelow et al. 2006, Saint-Germain and Greene 2009). Beetle-affected forests are often logged to prevent wildfires (Shore et al. 2003, Hood et al. 2017), although much evidence suggests that beetle outbreaks do not increase fire risk (reviewed in Romme et al. 2006, Black et al. 2013). Another common belief is that burned and beetle-affected forests are ecologically damaged and should be logged (McFarlane et al. 2006, Steelman and McCaffrey 2011, McGrady et al. 2016), despite improved scientific understanding of the value of natural disturbances (e.g. Attiwill 1994, Hutto 2008, Lehnert et al. 2013, Thom and Seidl 2015). For all of these reasons, salvage logging is exempt from standard operating procedures for cut sizes and retention levels in many provinces and territories (Schmiegelow et al. 2006, Saint-Germain and Greene 2009), or timber dues are reduced to provide incentives for salvage logging (e.g. Government of Yukon 2010). My results demonstrate that salvage logging causes

substantial ecological change, even when stands are partially logged. Some mammal species benefit from this change or are unaffected, while others experience short-term habitat loss, and the length of time needed for habitat recovery is unknown. A more regulated and cautious approach to salvage logging is warranted, and more research is required to inform policy improvements.

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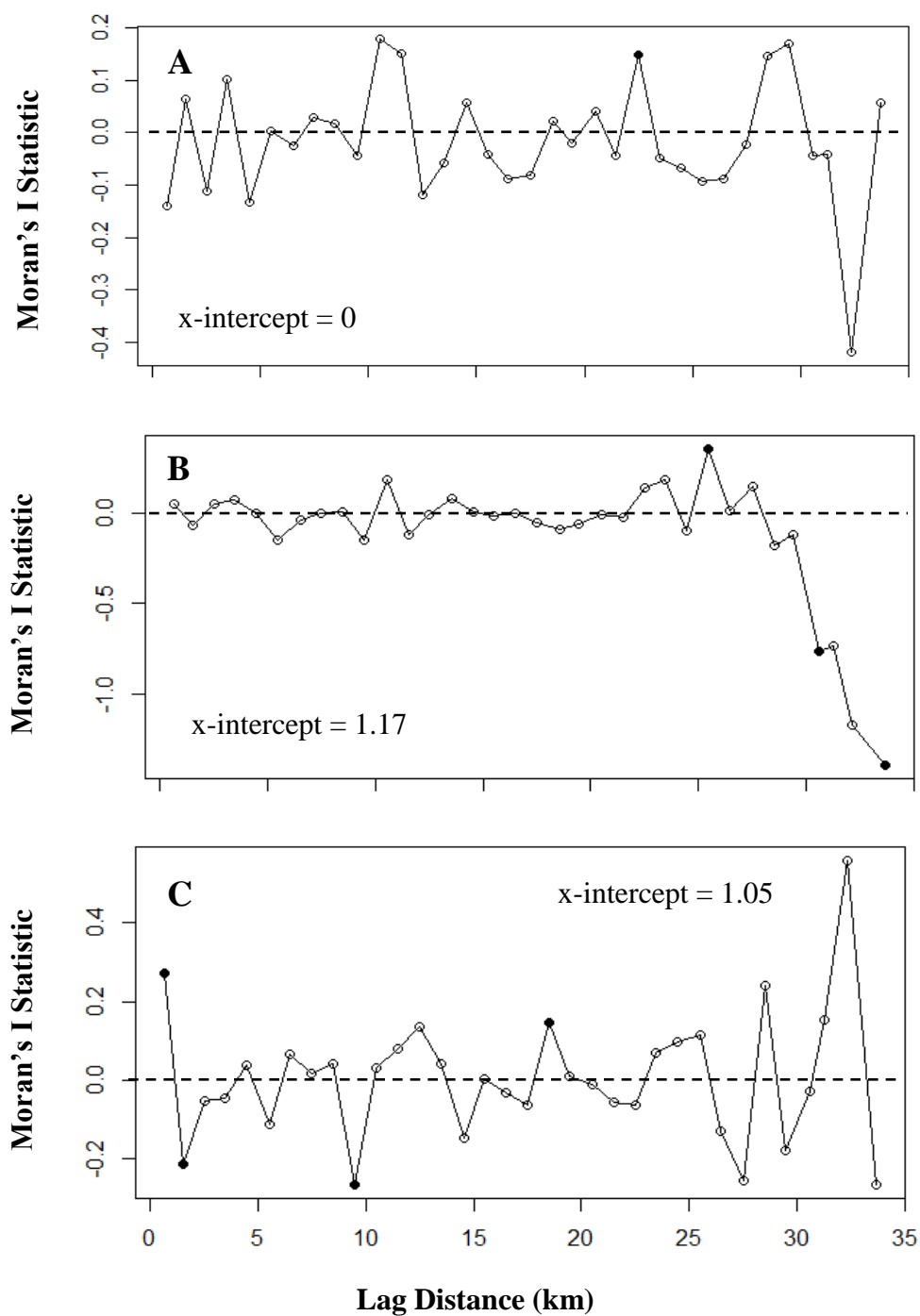
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Appendix A: Moran's I Spatial Correlograms



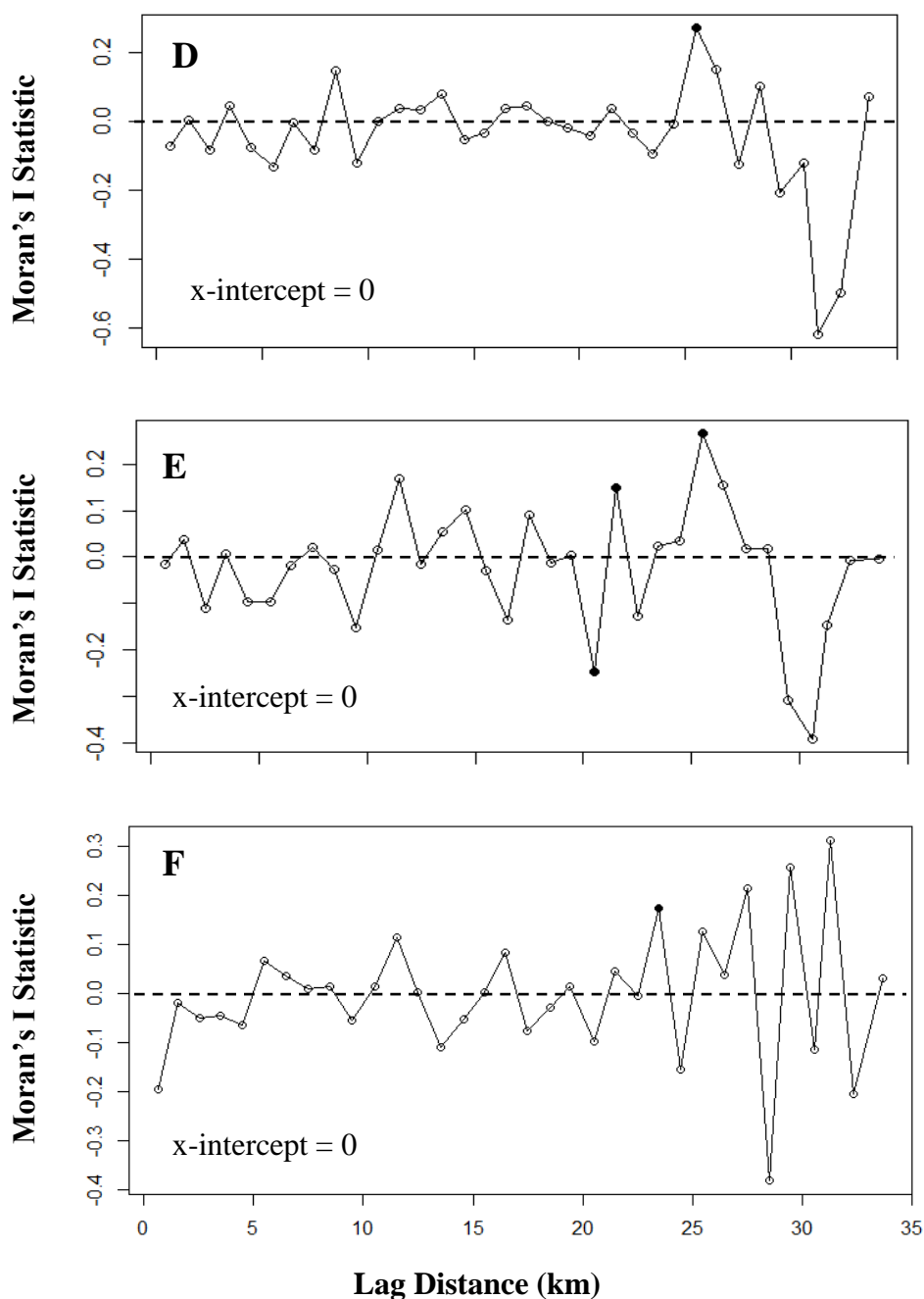


Figure A.1 Moran's I spatial correlogram, showing the results of spatial autocorrelation (Moran's I) tests across consecutive 1 km distance classes (lag distance) on the residuals of occupancy models for A) all moose, B) females moose with calves, C) snowshoe hare, D) lynx, E) coyote, and F) little brown bats. Moran's I statistic values range from -1 to 1, and the x-intercept represents the distance at which sites are no more similar than expected by chance. Closed circles represent significant spatial autocorrelation (i.e. $P < 0.05$). Dotted lines show zero correlation, for reference.