OF MICE AND MOOSE: SMALL AND LARGE MAMMAL RESPONSES TO A GRADIENT OF FOREST HARVESTING INTENSITIES ACROSS INTERIOR BRITISH COLUMBIA

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Abstract

British Columbia's interior forests have been heavily logged, burnt and subject to beetle outbreaks for decades. The compounding effects of these disturbances on wildlife and their habitat must be considered. Partial retention forest harvesting may be a method that could mitigate some of the negative effects of clearcut harvesting on wildlife. However, tests of the effects of partial harvests on ecosystem patterns and processes in different contexts are needed. From December 2018 to June 2020, we conducted live trapping for small mammals and camera trapping for medium-to-large-bodied mammals to estimate species diversity, population density, habitat use, and behaviours across different forest harvesting practices. For large mammals, the experimental harvesting gradient was replicated in three study areas spanning a 900 km gradient (John Prince Research Forest, Alex Fraser Research Forest, and Jaffray, BC). For small mammals, we live trapped at the most northern site, John Prince, and we detected 7 species, with diversity highest in the control (mean Shannon Index = 1.01, SE = 0.14) and partial retention treatments (means = 0.99, 0.98; SE = 0.17, 0.17) and significantly lower in the seed tree treatment (mean = 0.63, SE = 0.17, p = 0.02). Population densities of North American deer mouse (Peromyscus maniculatus) and southern red-backed vole (Myodes gapperi) estimated with spatially explicit capture-recapture models highlight the importance of partial harvest practices that maintain sufficient cover to support higher densities of forest specialists. Analysis of medium- to large-bodied mammal diversity across all three locations suggested that the regional environmental context had a stronger effect on mammal communities than local-scale differences in harvesting practices. Vegetation productivity measured with the normalized difference vegetation index was a more important predictor of habitat use for ungulates than harvest treatment, potentially due to the importance of forage availability. Across both small and

large mammals, responses to forest harvesting were variable; several species used partial harvests more than clearcuts. Forest practices should consider broader implementation of partial harvests to provide suitable habitats for a wider range of species. More experimental approaches to forest operations are needed across larger spatial scales, such as adaptive management of forest harvest with rigorous wildlife monitoring to ensure ecological objectives are met.

Lay Summary

British Columbia's forests are disturbed by large-scale logging, fires, beetles, climate change and more. Clearcutting creates uniform open areas that are problematic for wildlife species that depend on forest cover. To promote forest management that supports wildlife and their habitat, novel forest harvesting practices need to be studied to determine what best practices can be employed for the future. We used camera trapping and live trapping to determine how mammals responded to forest harvesting methods that retained more tree cover than traditional clearcutting methods. We found that maintaining partial cover allowed for a more diverse small mammal community than did clearcut harvesting, and that partial retention treatments also provided valuable cover for several large mammal species. Forest harvesting best practices must be updated to further consider wildlife habitat. This thesis highlights the importance of large and small mammal responses to logging, which can inform larger scale forest management.

Preface

This thesis work was conducted as part of the Mother Tree Project. Chapters 2 and 3 use live trapping and/or camera trapping data sampled in a forest harvesting experiment developed by Dr. Suzanne Simard (UBC), Jean Roach (UBC/Skyline Forestry Consultants), Dr. Brian Pickles (University of Redding, UK) and Les Lavkulich (UBC). I designed the live trapping and camera trap surveys with advice from Cole Burton (UBC), Suzanne Simard, and Dexter Hodder (UNBC/Chuzghun Resources Corporation), Tom Sullivan (UBC) and Charley Krebs (UBC). I managed field work preparations and data collection, and field assistance was provided by: Katie Tjaden-McClement, Eddy Kapp, Gaurav Singh-Varma, Erin Tattersall, Cindy Hurtado, Alvaro Garcia-Olaechea, Cheng Chen, Joanna van Bommel (UBC), Steven Murdock and Lauren Runge (UNBC/Chuzghun Resources Corporation), Dancing Water Sandy and Helen Sandy (Williams Lake First Nation), Matthew Thompson (BA Blackwell & Associates), as well as Callem McDougall, Quinn Thompson, and Erin Pippus (friends). GIS data and maps were provided by Cathy Koot and David Hamilton for Alex Fraser Research Forest, Shannon Crowley and Dexter Hodder for John Prince Research Forest, and Allie Winter and Kori Vernier from Canfor for Jaffray. Katie Tjaden-McClement, Eddy Kapp, Anna Tsigounis, Eric Jolin and I processed all camera trap data. All wildlife monitoring was approved by the Canadian Council of Animal Care administered by UBC (Protocol #A19-0012). Live trapping was also approved by the Ministry of Forests, Lands, Natural Resource Operations and Rural Development (Protocol #PG19-492155).

Over the course of this project, I worked with members of the Williams Lake First Nation (T'exelc Nation) and discussed interim results along the way through community meetings and (during the COVID-19 pandemic) video calls with members of community. We went to the field together for camera trap checks and I have done my best to carry out the field work, analysis and interpretation of this chapter with a holistic perspective, influenced by the perspectives of those with whom I have worked.

Chapters 2 and 3 will be adapted as manuscripts co-authored by Cole Burton, Suzanne Simard and Dexter Hodder. I conducted all of the data organization and analysis and wrote the chapter drafts. All members of committee provided feedback, as did Wildlife Coexistence Lab postdoctoral fellows Chris Beirne and Cat Sun. Forest harvesting treatments were applied by Canfor, Alex Fraser Research Forest, and John Prince Research Forest/Chuzghun Resources Corporation or their contractors.

The "we" referred to in this document is me, Alexia Constantinou, MSc student, as well as my supervisors, Dr. Suzanne Simard and Dr. Cole Burton, committee member Dexter Hodder, and in cases when referring to data collection and field work, "we" includes the field assistants involved.

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Glossary

AFRF: Alex Fraser Research Forest, northeast of Williams Lake, BC, managed by the University of British Columbia on the unceded territories of the T'exelcemc, Xatsu'll and Esketemc peoples.

BEC: Biogeoclimatic zones of British Columbia.

Clearcut: A timber extraction method where all standing trees are removed from the area.

Forest harvesting: The removal of trees for commercial timber purposes.

JPRF: John Prince Research Forest, most northern site of the Mother Tree Project, co-managed by the Tl'azt'en Nation and the University of Northern British Columbia.

Latitudinal gradient: Describes the climactic and positional differences between the most southern and most northern sites.

Location: Describes one of the three project sites that are spread across a latitudinal gradient with different climate conditions (JPRF, AFRF, Jaffray).

Partial harvesting/partial retention: A timber resource extraction method where some trees are removed, either in patches or strips.

Species composition: Refers not only to what species are in an area, but their relative abundances.

Species richness: A count of the number of wildlife species in a designated area or community.

Treatment: Describes one of the five types of forest harvesting methods that were sampled

(includes clearcut, 30% partial retention, 60% partial retention, seed tree and control forest).

Treatment gradient: Describes the four harvesting treatments and the control forest (a gradient from 0% to 100% canopy cover.

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I would also like to acknowledge that my field work was carried out on the territories of the Ktunaxa, Xat'sull, T'exelc, Tl'azt'en and Binche Nations. I owe the people of T'exelc Nation a huge debt of gratitude – the community meetings, field trips with elders, medicine walks and video calls we have shared have meant the world to me. I look forward to continuing to build this relationship.

Chapter 1: General Introduction

1.1 British Columbia's forests and wildlife

The effects of anthropogenic resource extraction on wildlife are of great concern in this era we call the Anthropocene (Caro et al., 2012; Crutzen & Stoermer, 2000). Globally, wildlife habitats are fragmented, and access to reliable food sources and intact home ranges are altered by a variety of activities including mining, oil and gas, and forest harvesting (Reglero et al., 2009; Laurance et al., 2001; Shackelford et al., 2018; Fisher & Burton, 2018). In British Columbia (BC), Canada, though the proportion of total forested area harvested each year is small (less than 1% of public forests are logged each year; MFLNRORD 2020), the cumulative effects of logging on wildlife can be significant (Shackelford et al., 2018). More than one third of the province's land base has been directly or indirectly modified by anthropogenic land use, and the largest proportion of this is from forest harvesting (7% of BC is under forest tenure; Shackelford et al., 2018). The viability of many wildlife species' populations in BC forests are hung in the balance between decision-makers weighing the value of timber extraction and maintenance of ecosystems and biodiversity (Bunnell et al., 1999). The effects of resource extraction on wildlife are worsened by, and play a role in increasing the prevalence of, other disturbances to BC's forests: fires, biotic disturbances like beetles, and climate change (Jenkins, 1990; Hessburg et al., 2019; Wang et al., 2012).

The increased amount of anthropogenic disturbance impacts biodiversity in BC, which serves as Canada's biodiversity hotspot. BC is home to a wide range of wildlife, including 137 native mammal species – the highest number of mammals anywhere in the country (E-Fauna BC, 2018). Overall, many populations of vertebrate species in the province have been on the decline since the 1990s when the Ministry of Environment (MoE) began tracking their Conservation Status Indices (Ministry of Environment, 2014; Westwood et al., 2019). A notable mammalian example is caribou (*Rangifer tarandus*), a federally protected species dependent on contiguous, undisturbed tracts of old-growth forest that has been undergoing precipitous population declines and multiple herd extirpations (Wittmer et al., 2007; Palm et al., 2020; Collard et al., 2020; Hebblewhite, 2017).

Clearcut timber harvesting constitutes the full removal of trees from a designated area. This practice expanded rapidly with major technological and machinery advances, and without government regulation, in British Columbia in the late 1880s (Hagerman et al., 2010). In BC, as clearcut forest harvesting continues to homogenize and fragment wildlife habitat and remove canopy cover, it alters the availability of energetically suitable habitat for the terrestrial mammal community. Energetically suitable habitat constitutes habitat that provides: 1) sufficient nutritional forage/prey (more herbivorous forage must be consumed to achieve the same amount of nutrients and protein provided by animal prey), 2) cover from predators, and 3) cover to prevent excess heat loss during winter/to intercept snow and shade to protect individuals from direct heat during the summer (Hudson, 2018; Humphries et al., 2004; Bunnell & DeMarchi, 1995). Large-scale clearcuts do not provide cover or a heterogenous crown that supports a wide variety of forage types. The decline in vertebrate populations and the effects of clearcutting on their habitats must be resolved quickly to mitigate further losses. This could be done through innovative and holistic forest management practices that consider multiple values of a forest, including placing emphasis on the biodiversity and habitat a forest provides, rather than overemphasizing the economic value of timber harvesting (see Menominee Forest Keepers and Menominee Tribal Enterprises, Mausel et al., 2017).

Forest harvesting in BC is dominated by clearcutting (B.C. Ministry of Forests, Mines and Lands, 2010) but there is a pressure to shift toward a "natural disturbance emulation

paradigm", which aims to harvest areas so they create a similar set of conditions as would be present after a natural disturbance such as fire (Bunnell, 1995; Fisher & Wilkinson, 2005; Galindo-Leal & Bunnell, 1995). Clearcutting is different from natural disturbance with respect to the legacy of organic materials left behind and the scale of the impact: uniform removal of trees is spatially and ecologically different than fire refugia, and there is more soil compaction via large machinery (Galindo-Leal & Bunnell, 1995; Froehlich, 1979). By contrast, partial harvesting maintains an overstorey of larger trees that provide stand characteristics that support species dependent on developed forest structure (Day et al., 2011). Retention of a portion of the overstory trees may mitigate the effects of forest harvesting on biodiversity, by maintaining structural diversity of mature forests (Fuller et al., 2004; McComb et al., 1993). In BC, partial harvesting is not applied frequently: 92% of harvesting is clearcutting, or clearcutting with small patches of trees left for wildlife (Beese et al., 2019). Moreover, where partial harvest is applied, the proportion of forest within a harvested area with any level of retention is usually well below 20% (Beese et al., 2019).

Across the province, there are differences in the size of harvesting cut blocks, the "remoteness" of logging operations, aesthetic requirements and ecosystem types (as defined by biogeoclimatic ecozones, Sachs et al., 1998; Beese et al., 2019; Haeussler, 2011). In December 2020, the Forest Practices Board (a third-party auditing board for investigating complaints about forest management) released the results of an investigation stating that the Prince George Biodiversity Order is outdated, based on 20 years of shifting conditions due to vast salvage logging and diminishing old forests (Forest Practices Board, 2020). The interior of the province, where this investigation was undertaken, has a larger maximum clearcut size than coastal regions (sizes dependent on natural disturbance cycles) and there is less public pressure to stop clearcutting (Beese et al., 2019). Over 70% of BC's forest harvesting occurs in the interior of the

province (Ministry of Forests, Lands, Natural Resource Operations and Rural Development, 2020) – so there is a need to better understand the effects of different forest harvesting methods on the diverse terrestrial mammal community.

1.2 Climate change

In British Columbia, the impacts of forest harvesting on wildlife are compounded by environmental and climate change. Climate and human influences are two main factors altering biodiversity, and also acting synergistically, creating landscape-level changes for species (Hansen et al., 2001). When individual plant, fungal, bacterial and animal species are faced with changing climate or other environmental conditions, they respond uniquely, resulting in complex changes to ecosystems, as they do not shift as intact assemblages (Hansen et al., 2001). The current biogeoclimatic ecosystem classification (BEC) system in BC is based on historical climatic conditions that shaped today's forests, and as such will eventually be not be able to indicate habitat suitability for a given mammal species under future climates (Mahony et al., 2018). Moreover, each wildlife species responds individually to changing climate, and it will be difficult to project their presence in shifting and novel ecosystems. For now, the BEC system will serve as a valuable framework for forest classification and provide a solid baseline for understanding the effects of future climate climatic conditions on habitat suitability (Forest Service British Columbia Research Branch, 2018).

There is an abundance of scientific literature illustrating the severity of climate change and the necessity for changing industrial carbon footprints (Intergovernmental Panel on Climate Change [IPCC], 2018a; Mawdsley et al., 2009; Hannah et al., 2002). In 2018, the IPCC published a special report about the impacts and importance of limiting global temperature increase to 1.5° Celsius; increases in temperature above this threshold would limit biodiversity and cause species losses, extinctions, and decreases in ecosystem services (IPCC, 2018b). In western and northern Canada, air temperatures have already risen by 2 degrees Celsius since 1950, which is associated with "unambiguous declines in snow cover depth, persistence, and spatial extent" (DeBeer et al., 2016). This average rise in air temperature is most pronounced in western and northwestern Canada, with increases between 1.5 and 3 degrees Celsius from 1950 (DeBeer et al., 2016).

Forests, though they are resilient and complex adaptive systems, are not immune to the effects of climate change. Having wide diversity within and between functional groups encourages ecological resistance (Noss 2001). Strategies for climate adaptation in the face of precipitous global declines of wildlife is critical, and management recommendations are lacking at the local scale (LeDee et al., 2020). Additionally, progress in preparing local natural resource managers in climate change adaptation is lacking, if not non-existent (LeDee et al., 2020). Fragmented forest landscapes are more vulnerable to climate change, and it is imperative that the effects of land-use intensification activities, which are exacerbated by climate change, are mitigated with progressive, local management strategies (Noss, 2001), including alternative forest harvest practices. Testing the responses of the mammal community to these alternative and more novel harvesting methods will allow for localized mitigation methods to be implemented.

1.3 Indigenous peoples and wildlife

Large-scale alterations to a landscape, like resource extraction, affect not only ecological processes, but also the cultural ones that are tied to the land (Garibaldi & Turner, 2004). British Columbia contains within its borders 203 unique First Nations, speaking over 57 languages (British Columbia Assembly of First Nations, 2018). Many Nations have cultural, spiritual and historic relationships with certain wildlife species, considered to be part of kin networks (Fraser, 2018). Some species (wildlife or plant) can be defined as cultural keystones – species that are disproportionately important to the culture or community because of their importance in

medicine, diet or in providing materials like hides and furs (Garibaldi & Turner, 2004). For example, the Kitcisakik Algonquin people in Quebec have been calling for sustainable management of white pine (*Picea strobus*), a cultural keystone tree species, because overharvesting, fire suppression and plantation failures have caused a severe decline in the abundance of the species (Uprety et al., 2017). Similarly, Downing and Cuerrier (2011) describe caribou as a wildlife cultural keystone species in Inuvialuit, and how climate change disruption of ecological processes disturbs First Nations and Inuit hunting, food security, cultural identity and human health.

Governance of forest management in BC is undergoing significant change, particularly on unceded First Nations territories, and this is rooted in calls to action from the Truth and Reconciliation Committee (Truth and Reconciliation Commission of Canada, 2015). First Nations people of BC have acted as responsible stewards of the land since time immemorial, but they have been marginalized and systematically displaced on the landscape with provincial and federal forestry policies and colonization (Hasegawa, 2001). New examples are more frequently emerging of Indigenous peoples reclaiming and re-establishing sustainable management of their forest resources – like the Menominee peoples in Wisconsin, USA implementing a continuous forest inventory and heavily managing their territory for sustainable timber and biodiversity goals (Mausel et al., 2017).

Government agencies and industry leaders are beginning to recognize that forest management should not be undertaken without consideration and inclusion of First Nations' cultural values, and when possible, traditional ecological knowledge. Legal duty to consult with and accommodate First Nations where possible, when a proposed action or decision may affect claimed or proven Aboriginal rights and title or treaty rights (Province of British Columbia, n.d.), is critical to reconciliation. Two key examples of this shift in attitude toward First Nations'

epistemology in BC are: (1) the new Wildlife Advisory Council to the Minister of Forests, Lands, Natural Resource Operations and Rural Development, and (2) the First Nations-BC Wildlife Forum "formed in response to the Province's Improving Wildlife and Habitat Conservation Initiative as an innovative way to obtain perspectives from First Nations across British Columbia on wildlife stewardship issues" (Ministry of Forests, Lands, Natural Resource Operations and Rural Development, 2020a & 2020b).

Over recent years, conservation and resource-based research has also been undergoing significant change. Collaborative conservation and land-based research with First Nations has grown, weaving together multiple worldviews. Two-eyed Seeing has emerged as an example of an "ethic of knowledge coexistence" where one eye has the strengths of an Indigenous worldview and ways of knowing, while the other has the strengths of mainstream ways of knowing (Reid et al., 2020; Bartlett et al., 2012). A critical aspect of this approach is the responsibility bestowed upon the participants to act upon the knowledge by which they have been transformed (Reid et al., 2020).

Co-management of resources between First Nations and provincial or federal government is still uncommon and is always centred around a resource – as the goal of co-management agreements is to address a "resource in crisis, threatened by competing interests" (Goetze, 2005). A landmark event and agreement between colonial and Indigenous governments occurred after the "War in the Woods" in Clayoquot Sound on Vancouver Island, between the Nuu-chah-nulth people and the Province of BC (Goetze, 2005). This was one of the first places and times where colonial government worked together with local peoples to develop innovative sustainable forest harvesting methods. Out of this panel came a recommendation to retain patches of forest in logged areas – and so variable retention was described, and later, in 1994, was incorporated into the Forest Practices Code (Beese et al., 2019; Ministry of Forests, Lands, Natural Resource

Operations and Rural Development, 2020). These discussions also led to the designation of the Great Bear Rainforest, 6.4 million hectares of co-governed forest on the central-north coast of BC, with objectives focused on protecting old growth forests and biodiversity (Howlett et al., 2009).

Given this context of reconciliation and appreciating and incorporating multiple ways of knowing, over the course of this thesis research, I worked closely with the John Prince Research Forest (co-managed by Tl'azt'en Nation) and T'exelc (Williams Lake) First Nations. One of the concurrent aims of this project beyond wildlife research was respectful engagement with the peoples upon whose territories this project was conducted, even though it was not necessarily in direct partnership with any one community. I continue to work with the T'exelcemc First Nations to assemble the project information into a format that highlights cultural keystones that the community is interested in, as well as the effects of natural resource harvesting on those species. Additionally, throughout the results and discussion, Dakelh names are included in parentheses for species that are found on the traditional territories of the Tl'azt'en Nation. I have been slowly working towards learning animal names and basic phrases, with language resources and information provided by the Carrier Linguistic Society and Nak'albun Elementary School (Carrier Linguistic Society, 2013).

1.4 Thesis objectives and hypotheses

To explore how newer, ecologically focused forest harvesting methods differ from clearcut harvesting in their effects on wildlife, I assessed the diversity, densities, habitat use and behaviours of small and large mammals in BC's interior. My aim was to examine the effects of a gradient of forest harvesting treatments on the local-scale responses of small and large mammals and in so doing I asked the overarching question: do partial harvesting methods that provide a mixture of canopy cover better support use by a higher diversity of wildlife species than does

clearcutting? I did this by: 1) live trapping small mammals and analyzing their diversity and densities across a gradient of forest harvesting treatments at one location (JPRF), and 2) using camera trapping to examine the habitat use, diversity and behaviours of large mammals across the harvesting gradient replicated at different latitudes. Each study site has three replicates of the forest harvesting gradient, with each treatment unit approximately four hectares in size (see section 1.5.1 below for further details). In these small, replicated plots, I was able to analyze patterns of habitat use by the entire terrestrial mammal community using multiple field and analytical methods.

In my second chapter, I used live trapping to estimate the effects of forest harvesting on the species diversity of small mammals and the density or habitat use of four focal small mammal species. Small mammals are a tiny portion of biomass (mice and voles only making up 4% of the ecosystem biomass, Boonstra et al., 2004) relative to large mammals in boreal forests but as a group have a disproportionately large effect on their ecosystems (Villette et al. 2016, Krebs et al. 2014). For the purposes of this project, I defined small mammals as species that are approximately 100 grams in weight or smaller. This part of the study was conducted at the most northern site of my project (JPRF), where a small mammal community analysis had never been undertaken.

My overarching hypothesis for the small mammal community study was: partial retention forest harvesting methods would create heterogeneous open- and closed-canopy conditions that would support a more diverse small mammal community than clearcut harvesting. For individual species, I hypothesized the following: 1) red squirrels (*Tamiasciurus hudsonicus*), as a treedependent species, would be present almost entirely within closed-canopy treatments, and 2) the deer mouse (*Peromyscus maniculatus*) and 3) common shrew (*Sorex cinereus*) would occur more frequently in the clearcuts or open canopy treatments. There was conflicting literature regarding

the response of 4) southern red-backed vole (*Myodes gapperi*) to clearcutting (reviewed in Chapter 2), so I hypothesized that they would be most dense in the partial harvesting treatments.

In my third chapter, I examined large mammal responses to forest harvesting treatments across the full latitudinal gradient in climatic conditions that stretched from the southeast corner to the north central region of the province. There is concern about the negative effects of forestry on native species and on the biodiversity of the community (Fuller et al., 2004). However, these analyses are lacking for the large mammal community as a whole in BC, particularly for carnivores, and research into alternative harvesting methods is also lacking (Fuller et al., 2004; Fisher & Wilkinson, 2005). Climate is an important factor limiting the distribution and abundance of mammals and other wildlife species. In order to examine potential interactions between climate and forest harvesting on mammal responses, I chose three study areas that included the most northern and southern extremes, thus representing the extreme conditions for Douglas fir interior forests sampled by the Mother Tree Project. I used camera trapping to compare large mammal community diversity among locations and harvesting treatments, as well as species' habitat use and behaviours within each treatment.

My first hypothesis was that there would be similar species richness but different species compositions between harvesting treatments. With such a wide range of ungulates, carnivores, mesocarnivores, generalists and specialists sampled, I did not expect one forest harvesting method to have overall more frequent usage by the whole community, but rather that some species would use treatments with more forest cover while others would use open canopy treatments more (Table 3.1). My second hypothesis focused on ungulate species. I anticipated that the variation in mammal responses would be explained by differences between generalist and specialist species' preferences for more open and closed canopy treatments, respectively. My final hypothesis for this chapter was that individual animal behaviour is related to or explained

by harvesting treatment (i.e., the amount of canopy cover). To do this, I used a novel approach of characterizing behaviours from camera trap images. I defined different classes of behaviour including travelling, foraging, bedding down, intra-species interactions (like feeding juveniles or rutting), and inspecting the cameras. I predicted that any behaviour other than travelling would be demonstrated in treatments with more canopy cover (less anthropogenic habita disturbance), because of the increased shelter and concealment (from predators or for stalking prey), less energetic losses to open canopy through radiation, and concealment of young (Wilson et al., 2020).

In my fourth chapter, I reflected on the strengths and management implications of the study, as well as ways to improve upon the limitations of the project. I also recommended further areas of study, as there is a vast amount of work to be done to grapple with resource extraction and its implications for wildlife in BC's interior.

1.5 General Methods

1.5.1 Project Design & Harvesting methods

This project addresses the need for assessments of multispecies responses to alternative harvesting methods across a variety of biogeoclimatic regions in BC. Having a repeated, experimental design across a latitudinal gradient in the interior allowed for valuable comparisons between multiple locations. I conducted this thesis work within the Mother Tree Project (MTP), which is investigating forest renewal practices that will protect biodiversity, carbon storage and forest regeneration as climate changes (Simard et al., 2020; Mother Tree Project, 2020). The focus of the MTP is to compare the effects of clearcutting and partial retention methods on a range of ecosystem goods and services across the large latitudinal range of interior Douglas-fir dominated forests in British Columbia. The partial retention treatments were designed to protect "Mother Trees", so named for the key role they play as hubs of mycorrhizal networks that

facilitate natural regeneration (Beiler et al. 2010; Simard et al. 2012). The MTP spans a 900-km latitudinal gradient across the interior of the province, including nine climatic regions within the distribution of interior Douglas-fir (Simard et al., 2020). Douglas-fir forests in the interior of BC are economically valuable and at high risk of being affected by climate change, and as such are of considerable concern and interest (Simard et al., 2020; Hamman & Wang, 2006). For my project, I selected the furthest ends of the climatic gradient: Jaffray (in the east Kootenays), the hottest and driest site at the southern end; John Prince Research Forest, the coolest and wettest stite at the northern end (in the North Central region of BC), and Alex Fraser Research Forest (in the Cariboo) as a midpoint of the latitudinal gradient.

My project design followed that of the larger MTP, with a two-way factorial design. At each of the three climatic project locations (described in 1.4.2), there were five forest harvesting treatments and three replications of each harvesting treatment (Fig. 1.1, 1.2). Each treatment unit was three-to-five-hectares in size, with a one-hectare NFI measurement plot positioned centrally to avoid edge effects. For the purposes of this project, Jaffray, Alex Fraser and JPRF will all be referred to as locations or sites, while individual treatments will be referred to as experimental or treatment units. A group of all five experimental units is a replicate.



Figure 1.1: Location of the three study areas in the interior of British Columbia. Sites boxed in red are the only study areas for this project. The other sites, noted as 'selected sites' in the legend, indicate the other locations of the Mother Tree Project (reproduced with permission from Mother Tree Project, 2020).

Prior to my project, at the centre of each treatment unit, a National Forest Inventory (NFI) plot was measured before and after harvesting as part of the Mother Tree Project (National Forest Inventory Task Force, 2020). The NFI protocol is being applied across Canada, resulting in a systematic, statistical sampling of all forest types through time (NFI Task Force, 2020). The plots carried out in the MTP treatment units included sampling of soil, tree heights and diameters, tree health, signs of wildlife, substrate sampling, coarse and fine woody debris, and sampling of mosses, herbs, shrubs and woody materials in microplots.

The harvesting treatments represented a gradient of increasing retention: clearcut (0% retention through complete canopy removal); seed tree (10% retention; 30% retention (30% of basal area retained in discrete patches): ; 60% retention (60% of basal area retained with thinning

from below and with discrete portions removed in strips) and uncut forest (100% retention, with an intact, natural canopy; Fig. 1.1). A similar gradient to this project's design of control forest, seed tree, partial retention methods, and full clearcut has been used in other small mammal studies, including in Douglas fir forests (Sullivan & Sullivan, 2001; Fuller et al., 2004; Huggard et al., 2000). The control and clearcut treatments represent opposite ends of the harvesting spectrum, from an entirely intact canopy and understory to none. The order of the harvesting treatments in figures in this thesis is: clearcut, seed tree, 60% retention, 30% retention and control. The 30% retentions are placed next to controls because they have an understorey that has not been disturbed (in the patches) by logging machinery. Additionally, as the 60% retentions were by basal area rather than % of area, they do not necessarily have more canopy cover than the 30% retentions.



Figure 1.2: Visualization of the Mother Tree Project harvesting treatments, with control forest at the top (100%), followed by the two partial harvesting treatments (60% and 30%), the seed tree treatment (10%) and the clearcut (0%). The percentages describe the amount of canopy left behind after harvest, and in the case of the control, the untouched canopy.

The seed tree treatment retains single trees for natural seed regeneration and mimics an industry tradition of leaving behind single trees for natural seed regeneration (a.k.a. Mother Trees). Seed tree retention is a method used by the forestry industry to boost the publicly perceived aesthetics of the harvested area (Gibe, 2005) and as one way to better balance economic and ecological values in managed landscapes (Halpern et al., 2005). Both the 30% and 60% retention treatments are examples of variable retention silvicultural systems that retain portions of the overstorey to provide seed and protect the natural regeneration below (Day, Koot & Wiensczyk, 2011). In both variable retention systems, legacy logs and snags preserve biodiversity at those sites, and multiple rounds of thinning can create a more economically sustainable management plan (Day, Koot & Wiensczyk, 2011). The 30% retention treatment included clusters of trees meant to represent a 'family' of related trees that were linked via mycorrhizal connections (Pickles et al. 2017; Asay et al. 2020); the patches also protect trees against potential blowdown while providing an economically worthwhile harvest. The 60% retention treatment retained the full suite of species and structures originally present in the stand while conserving the maximum potential mycorrhizal connections between trees (Simard et al. 2012). This treatment also allows for analysis of mycorrhizal connections between various tree species and genotypes and among non-related species. The large patch treatment will also protect mother trees while providing a good opportunity for a second harvest in the coming decades once the harvested gaps have regenerated.



Figure 1.3 Examples of the forest harvesting gradient. The top row is control forest where 100% of natural canopy cover is maintained (CON, a) and 30% patch retention where the patches are untouched by machinery and the understory is intact (30P, b). The middle row shows 60% partial retention which is harvested in strips (60P, c) and seed tree retention with largest Douglas-fir every 25 metres maintained (SEED, d). The last photo is the clearcut treatment where all canopy is removed (CC, e). Photos taken at JPRF in 2018. Photos taken by Jean Roach and the Mother Tree Project crew.

1.5.2 Study systems

1.5.2.1 Jaffray

The Jaffray site is in the traditional, ancestral and unceded territory of the Ktunaxa First Nation. This location is within the Kootenay dry, mild variant of the Interior Douglas fir biogeoclimatic (BEC) zone (IDFdm2) of BC, at an average elevation of 1050 metres (MacKillop et al., 2018). The stands are comprised of approximately 80% Douglas fir, 20% western larch (*Larix occidentalis*), and <1% lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosae*) (Jean Roach and MTP crew, unpublished data, 2018). The climate is characterized by winter temperatures averaging between -1°C and -6.5°C, and summer temperatures averaging 15°C. Jaffray has low precipitation, generally less than 50mm each month (The Weather Network, 2018a). In May-June 2017, the study area was logged as part of the MTP. Before logging, the sites had on average 882 stems per hectare with a sparse understory. The herb and shrub plant community is dominated by pinegrass (*Calamagrostis rubescens*) and heart-leaved arnica (*Arnica cordifolia*).

1.5.2.2 Alex Fraser Research Forest

The Alex Fraser Research Forest (AFRF), near Williams Lake, is managed by the Faculty of Forestry at UBC, and occurs on the traditional, ancestral and unceded territory of the T'exelcemc, Xatsu'll and Esketemc First Nations (Alex Fraser Research Forest, n.d.). AFRF covers three biogeoclimatic zones – the Sub-Boreal Spruce (SBS), the Interior Cedar Hemlock (ICH) and the Interior Douglas fir (IDF) zones, with one replicate of the harvesting treatments in each BEC zone. Generally, the Williams Lake area has slightly lower temperatures throughout the year and more precipitation every month than the Jaffray area. The SBS subzone is dry and warm (SBSdw1), the ICH subzone is moist and cool (ICHmk3), and the IDF subzone is cold and dry (IDFdk3) with the greatest precipitation in the ICH and the warmest temperatures in the IDF. The SBS and ICH forests are dominated by even-aged "mixed stands of Douglas-fir, lodgepole pine and trembling aspen [*Populus tremuloides*]" (Alex Fraser Research Forest, n.d.). In 2017, the SBS zone at the research forest was impacted by a large fire that destroyed the understory and forest floor but left most trees alive but with some exterior damage. The IDF forests are dominated by uneven-aged stands of Douglas fir and lodgepole pine (Alex Fraser Research Forest, n.d.), with rich communities of shrubs and herbs in the understory.

1.5.2.3 John Prince Research Forest

John Prince Research Forest (JPRF) lies northwest of Fort Saint James on the Binche Keyoh (traditional and current territory of the Binche Whut'en First Nation) and is comprised of 16,500 hectares of boreal forest. It is co-managed by UNBC and the Tl'azt'en Nation (Crowley & Hodder, 2017). JPRF is mostly contained between two large lakes, Pinchi and Tezzeron, as well as crisscrossed by many streams leading to these lakes (Crowley & Hodder, 2017). This area is in the dry, sub-boreal subzone of the SBS biogeoclimatic zone (SBSdw3; John Prince Research Forest, n.d.). Snow depths reach up to 1.2 metres over winters, where temperatures can reach -40 degrees Celsius and remain below -10 degrees Celsius for extended periods (John Prince Research Forest, n.d.). Temperatures can reach 30 degrees Celsius during the short, moist summers (John Prince Research Forest, n.d.).

The forests in JPRF are naturally diverse, with a variety of species including Douglas fir, lodgepole pine, white spruce and some deciduous species such as trembling aspen and paper birch (*Betula papyrifera*; John Prince Research Forest, n.d.). The understory is dominated by a diverse suite of shrub species. This type of forest experiences, and geographic area is characterized by, stand-replacing wildfires occurring roughly every 100-200 years (John Prince Research Forest, n.d.).

Chapter 2: The effects of harvesting methods on small mammals in northern British Columbia

2.1 Introduction

2.1.1 Small mammals as ecosystem influencers

Small mammals make up just 4% of vertebrate biomass in boreal forests – a tiny portion relative to large mammals – but they have disproportionately large effects on ecosystems (Villette et al. 2016, Krebs et al. 2014; Boonstra et al., 2001). They serve a number of roles as prey for a wide variety of species, are crucial spore dispersers, encompass all different diet types, and include both diurnal and nocturnal species; a healthy forest ecosystem depends on small mammals (Fuller et al. 2004; Sullivan et al., 1990; Maser et al., 1978). They also contribute to biodiversity and influence food webs. The abundance and diversity of small mammals in temperate and boreal forests can be ecological indicators of changes to forest structure and function (Klenner & Sullivan, 2008). Small mammals alter plant communities through processes such as seed predation and dispersal, and their population dynamics are affected by forest management (Klenner & Sullivan, 2008). Small mammals (in this work, considered to be species <100 grams) are the most diverse group of mammals globally, as well as in British Columbia. In BC, this genetically broad group spans four taxonomic orders and a total of 52 species (E-Fauna BC, 2020).

2.1.2 Forest management and small mammals

Despite their ecological importance, very few small mammals are included among the 85 species listed as Identified Wildlife in the Forest and Range Practices Act (included are the water shrew species, *Sorex bendirii* and *Sorex palustris brooksi*, under the federal Species at Risk Act; *Forest and Range Practices Act*, 2002). This means that, broadly, natural resources harvesting it is not required to directly consider other small mammal species at any point in the planning phases or execution of forest management in the province. Research indicates that partial forest
harvesting methods could be management techniques that promote small mammal habitat use within harvested areas (Steventon et al., 1998). Partial harvesting can help create a heterogeneous landscape that supports small mammal species that use and inhabit mature forest, as well as more meadow-dependent species, by leaving intact forest adjacent to cleared areas, similar to patterns of natural disturbances (Steventon et. al, 1998). Fuller et al. (2004) compared mice, shrew and vole abundances across partial and clearcut harvests and determined that partial harvesting supported mice and voles in similar densities to uncut forest stands, which was greater than clearcut stands. They concluded that retaining forest structural traits could be important for maintaining small mammal populations and, by extension, benefit the species that prey upon small mammals. In another study, vole species persisted in variable retention treatments, and maintenance of residual conifer trees (particularly in patches with 30% retention) was critical for southern red-backed voles (Sullivan & Sullivan, 2001).

While these previous BC-focused studies have demonstrated effects of harvesting treatment on small mammals over time in different conifer forests of BC (Sullivan & Sullivan, 2001; Klenner & Sullivan, 2003; Klenner & Sullivan, 2008; Sullivan & Sullivan, 2018), the vast majority of those studies were focussed on southern BC, where average temperatures are hotter and there is less precipitation than the northern interior (Moore et al., 2010). Research on the effects of partial harvesting versus clearcutting on small mammals is limited in the northern parts of the province. Partial harvesting is also seldom implemented in the interior of BC, where clearcuts are larger and more common than on the coast (Beese et al., 2019).

2.2 Expected species' responses to forest harvesting methods

Small mammal species typical of BC interior forests have different (and in some cases, unclear) responses to forest harvesting. Deer mice and southern red-backed voles have been the most frequently trapped species in live trapping studies in the interior of BC (Klenner &

Sullivan, 2008, Sullivan & Sullivan, 2001). By using E-Fauna BC (Klinkenberg [E-Fauna], 2020) and other available literature, I put together a potential species pool of small mammals that I expected could be live trapped in the sub-boreal spruce BEC zone in the Nechako region of BC, where my most northern site, John Prince Research Forest, occurs (see Section 1.5.2.3 for site details). This table was then narrowed down to include only the species that were successfully trapped after the field season (Table 2.1).

I investigated small mammal species for which previous studies indicated a range of habitat preferences; these species ranged from open habitat generalists to closed forest specialists (Table 2.1). I examined four focal species that spanned a range of habitat preference and life history traits, from open-canopy, fecund generalists (deer mice) to complete canopy dependent, arboreal species (red squirrel). I aimed to study the responses across this group of species as they are some of the most proliferate species of each of these categories, and were such in this study (Sullivan et al., 1999; Sullivan & Sullivan, 2001; Villette et al., 2016).

I expected the red squirrel (*Tamiasciurus hudsonicus*) to exclusively use treatments with crown cover. This species is a conifer seed specialist and builds its nests arboreally. These life history traits, combined with studies finding fewer red squirrel tracks in clearcuts (Fisher & Wilkinson, 2005), led to my expectation that there would be higher densities of red squirrels with increasing crown cover.

For southern red-backed voles (*Myodes gapperi*), there has been disparity in the literature. Kirkland (1990) reviewed a wide range of studies and found an initial positive response of southern red-backed voles to forest harvest, while Sullivan (1999) showed that cover in control (unharvested) forests supported more voles. Based on these conflicting results, I hypothesized that there would be similar densities of voles in closed (control) and open (clearcut)

treatments, with highest densities in the partial retention treatments (both the 30% and 60% partial retentions provide open and closed canopy cover).

Previous studies suggest that the North American deer mouse is most abundant in clearcuts where they forage on seeds (Sullivan, 1979). However, a few studies (the exception, rather than the norm) have found higher deer mouse abundance with more crown cover, where greater cover was associated with higher overwinter survival (Fisher & Wilkinson, 2005). I expected deer mouse density to increase with increasing canopy removal and disturbance, at least during the summer season during which we sampled. Similarly, previous studies suggest that common shrews (*Sorex cinereus*) respond neutrally or positively to clearcut harvesting (Sullivan et al. 1999; Fisher & Wilkinson, 2005). Overall, I expected to find the highest densities of deer mice and common shrews in clearcut and seed tree plots, with decreasing densities as crown cover increased.

At JPRF, we expect increased habitat heterogeneity in the partial retention treatments (mixture of closed and open-canopy, and in the 30% patch retention, this includes an intact understorey), relative to the clearcut and control forest. The main objectives of this chapter are: (1) to estimate and compare the densities of focal small mammal species across the range of forest harvesting treatments at JPRF, (2) to determine if species show preferences for particular forest harvesting treatments, and (3) to test the hypothesis that partial harvest treatments provide better habitat for the entire small mammal community than clearcuts, with variation in response among generalists/specialists.

Table 2.1 Small mammal species' expected responses to clearcut forest harvesting based on literature review. This table includes only the species that were live trapped at John Prince Research Forest. A more complete list is included in Appendix Table A7, which includes any species that could have been captured during live trapping, based on their expected ranges and habitat associations. The 'Expected Response to Harvesting' column has my hypotheses for individual species' responses to clearcut harvesting, referring to existing peer-reviewed literature.

Common Name	Scientific Name	Literature-Based Species' Responses to Clearcut Harvesting	Literatures Source(s)	Overall Prediction
Meadow vole	Microtus pennsylvanicus	Abundance of meadow voles after harvest	Kirkland (1990), Fisher & Wilkinson (2005)	Positive
Southern red- backed vole	Myodes gapperi	Significant disparity between study results: initial positive response to harvest with potential steep drop-off after a few summers, versus results showing forest supported more voles	Kirkland (1990), Sullivan (1999)	Preference for partial retention
North American deer mouse	Peromyscus maniculatus	Disparity between study results: more studies show abundant in clearcuts (forage on seeds/insects found in new clearcuts) but more cover is associated with higher overwinter survival. Conflicting reports of clearcut effect on recruitment.	Summary: Fisher & Wilkinson (2005)	Preference for partial retention in winter – positive for summer sampling
Heather vole	Phenacomys intermedius	Occupies mossy meadows, shrubby areas in forests	BC CDC (1993)	Positive
Red squirrel	Tamiasciurus hudsonicus	Conifer seed specialist, less tracks in clearcuts, cut blocks as occasional summer forage areas	Fisher & Wilkinson (2005)	Negative
Common shrew	Sorex cinereus	Disparity between study results: no response, positive response to harvesting	Sullivan et al. (1999), Fisher & Wilkinson (2005)	Short-term positive

2.3 Methods

2.3.1 Study Area: John Prince Research Forest



Figure 2.1: Orthographic map of John Prince Research Forest, showing camera trap locations and replicate outlines. The numbers identify the three replicates, each outlined in red. In replicate one, from left to right the treatments are: 60% partial retention, 30% patch retention, seed tree, clearcut and control forest.

2.3.2 Small mammal sampling

Live trapping is a well-used and accepted method to evaluate small mammal species richness, composition and abundance (De Bondi et al., 2010; Kelt, 1996; Sullivan et al., 2001). To estimate species richness and population densities of small mammals, we set up Longworth (14 x 6.5 x 8.5") and Tomahawk (6 x 6 x 19") live traps (Longworth Small Mammal Trap, Oxford, UK; Tomahawk Live Trap, Hazelhurst, WI) on a one-hectare 7x7 grid covering the central measurement plot (NFI plot) in each forest harvesting treatment. We set up the experimental grid following the methods of Sullivan et al. (1999) and Steventon et al., (1998). The two types of traps were alternated along the gridlines, with Longworth traps targeting the

smallest mammals (voles, shrews and mice) and Tomahawk traps targeting slightly larger species (squirrels). We used an alphanumeric grid to label traps (lines A to G north-south, and 1 to 7 east-west). Lines A, C, E and G were Longworth traps (28 traps), while lines B, D and F were Tomahawks (18 traps total). This provided a total of 230 traps distributed across five treatments (46 stations per treatment) with 14.29-metre spacing between traps within each grid.





Replicates of the forest harvesting treatments were trapped sequentially, moving the traps from one block to the next after five trapping sessions. A trapping session was defined as each morning or afternoon check of every single trap in each treatment. We set traps on day one, pre-baited for days two and three (locked open, baiting with apples, carrots and oats), then on the evening of the third day set them to "trapping mode" – to automatically shut after an animal

triggered the trap closure mechanism. Trapping was carried out in the early morning and evening of days four and five, and the morning of day six. In total, there were 4,410 active trap-nights across 245 traps in June (June 4 – 22) and August (August 5 – 21) of 2019 (three nights/trap, 49 traps/treatment, five treatments, three replicates, two months).

We weighed each trapped animal, determine its sex and reproductive stage, and evaluated if there were any injuries from the handling and trapping process (following standards outlined by Jewell & Fullagar, 1966; Seddon et al., 2014; Powell & Proulx, 2003). We also attached one unique numbered ear tag to the right ear of each individual to track capture histories for mark-recapture analysis before releasing the animals back to the wild. All methods were approved by the UBC Animal Care Committee (protocol A19-0012) and a permit was obtained from the Ministry of Forests, Lands and Natural Resources Operations (Wildlife Act: Permit PG19-492155).



Figure 2.3: Longworth small mammal trap next to a stump at John Prince Research

Forest. Traps were covered in woody debris and foliage to prevent them from becoming too hot if exposed to sunlight, and to better integrate them into the environment. Photo taken by Alvaro Garcia-Olaechea.

2.4 Data Analysis

2.4.1 Small mammal density estimates

I used spatially explicit capture-recapture (SECR) in the secr package in RStudio (Efford, 2020; RStudio 2020, Version 3.7) to estimate densities of deer mice and southern red-backed vole populations, the two species with sufficient captures to support SECR models. SECR is an approach to estimate population density using detection histories (captures and re-captures) of marked individuals, while considering spatial locations of traps (Efford, 2020; Efford & Fewster, 2012). Each site had five capture occasions, for which capture histories were constructed for all captured individuals (excluding those that escaped before marking or died in the trap). I estimated density for each species in the five treatment types and during each month of sampling. This process created 20 data sets: one data set represents sampling of one harvesting treatment in one of the two months. I ran null SECR models (i.e., no covariates) on each data set to obtain density estimates, since I did not hypothesize that variable other than harvest treatment would have a significant effect on small mammal densities.

2.4.2 Habitat use

For red squirrel and common shrew, there were insufficient captures to estimate densities using secr, and we did not ear tag these two species. Common shrew had a high rate of mortality (discussed in 2.6.4) and we decided to not inflict further stress on the individuals that survived the stress of trapping. Red squirrels were expected to not be captured frequently enough to warrant the additional stress and handling necessary to ear tag the few individuals. To assess variation across treatments, I therefore analyzed capture rates as an index of habitat use, recognizing that without individual identity, this measure confounds abundance and movement (e.g., can double-count the same individuals or not account for detectability; Hopkins & Kennedy, 2004). I used generalized linear models (GLM, function glm() in R) to compare habitat

use across treatments for red squirrels and common shrews. I modeled the total number of captures in each month and replicate as a Poisson random variable with harvest treatment as a categorical independent (predictor) variable with five levels, with clearcut as the reference level (intercept).

2.4.3 Small mammal diversity

I used the vegan package in R (Oksanen, 2019) to calculate the Shannon diversity index for small mammals. Shannon diversity is a mathematical measure that uses the species richness and relative abundance of each species sampled. It assumes that all species have an equal chance of being captured and does not weight species by dominance (Krebs, 1999). I calculated Shannon diversity in each of the 15 treatment plots, using raw capture totals for all species summed across both sampling months for each replicate. I then calculated the mean and standard error of diversity estimates across replicates within each treatment, and compared treatments using a oneway analysis of variance (ANOVA). Additionally, I ran a generalized linear mixed model with Shannon diversity as the response variable, harvesting treatment and volume of coarse woody debris as fixed effects, and replicate as a random effect. The replicate was treated as a random effect because treatments within replicates are non-independent. This model was exploratory, to examine if an additional habitat feature was also influencing small mammal community diversity. Coarse woody debris is known to be an important habitat feature for small mammals (Sullivan & Sullivan, 2019) and was observed in the field to vary across treatments and replicates. Volume of coarse woody debris was measured using systematic transects with calipers as part of MTP sampling.

2.5 Results

2.5.1 Summary of trapping efforts and small mammal detections

Seven small mammal species were captured a total of 826 times over 4140 trap nights in June and August of 2019 (Table 2.2). The only two species that could be consistently uniquely tagged during field work were *P. maniculatus* (deer mouse) and *M. gapperi* (southern red-backed vole). There was a total of 449 captures and recaptures of deer mice, and 283 captures and recaptures of southern red-backed voles over the course of the June and August 2019 trapping sessions in all three replicates of the forest harvesting treatments. Excluding individuals that could not be tagged and mortalities, the number of captures and recaptures for density estimates decreased to 350 and 241 for deer mice and southern red-backed voles, respectively.

Table 2.2: Summary table of small mammal captures. Number of captures (includes
captures, recaptures, escapees and mortalities), each species' percentage of total captures, and for
deer mice and southern red-backed voles the number of unique individuals based on ear tags. All
data was collected during 2019 June and August live trapping on 15 plots in JPRF.

Species	Number of Unique Individuals	Number of Captures	Percentage of Captures
North American Deer mouse (<i>P. maniculatus</i>)	188	449	54.36
Southern Red-backed Vole (<i>M. gapperi</i>)	137	283	34.26
Red Squirrel (<i>Tamiasciurus</i> hudsonicus)	-	29	3.51
Common Shrew (Sorex cinereus Kerr)	-	58	7.02
Meadow Vole (<i>Microtus</i>	-	4	0.48
Short-tailed Weasel (Mustela	-	2	0.24
Least Weasel (Mustela nivalis) Total	-	1 826	0.12

Treatment	Clearcut	Sood Trop	60%	30%	Control
Species	Clearcut	Seeu mee	Retention	Retention	Control
North American					
Deer mouse (P.	131	104	67	75	72
maniculatus)					
Southern Red-					
backed Vole	26	57	100	57	43
(M. gapperi)					
Common Shrew					
(Sorex cinereus	19	11	8	11	9
Kerr)					
Red Squirrel					
(Tamiasciurus	4	-	9	7	9
hudsonicus)					
Meadow Vole					
(Microtus	3	-	-	1	-
pennsylvanicus)					
Short-tailed					
Weasel (Mustela	1	1	-	-	-
erminea)					
Least Weasel					1
(Mustela nivalis)	-	-	-	-	I
Total					826

Table 2.3: Summary table of small mammal captures by treatment. Number of captures (includes captures, recaptures, escapees and mortalities). There were three replicates of each harvesting treatment and two months of sampling (June and August).

2.5.2 Density estimates

Density estimates across treatments ranged from one (SE = 0.5) to 26 (SE = 12.4) mice per hectare (Fig. 2.4) and one (SE = 0.9) to six (SE = 1.8) voles per hectare (Fig. 2.5). Density estimates of deer mice ranged from one mouse/hectare (60% treatment, SE = 0.48) to six mice/hectare (clearcut, SE = 1.31) in June, and from five (30% treatment, SE= 1.47) to 26 individuals (control, SE= 12.91) per hectare in August (Fig 2.4). I considered differences between density estimates to be statistically significant when the 95% confidence intervals did not overlap . In June, there was a significantly higher density of deer mice in the clearcut than in the 60% partial harvest, consistent with our hypothesis that deer mice are generalist, meadowdependent species that would appear more in the clearcut than any other treatments (deer mouse density was higher in clearcut than any other treatment, but other differences were not statistically significant). By contrast, in August there was a significantly higher density of deer mice in the control plot than in the 30% partial harvest, and deer mouse density was similar in all treatments except for control (Fig. 2.4). The upper confidence interval for the control density estimate is more than two times the estimate itself (density = 26, UCI = 63). The control treatment had 24 captures of 20 unique animals, and thus the low number of recaptures resulted in high uncertainty in the estimate.



Figure 2.4 Spatially explicit capture-recapture density estimates of deer mice across forest harvesting treatments in June (left) and August (right), with 95% confidence intervals. The order of the harvesting treatments in this figure is: clearcut, seed tree, 60% retention, 30% retention and control. The 30% retentions are placed next to controls because they have an understorey that has not been disturbed (in the patches) by logging machinery. Additionally, as the 60% retentions were by basal area rather than % of area, they do not necessarily have more canopy cover than the 30% retentions.

For southern red-backed vole, the highest density in both June and August was in the 30% partial harvesting treatment (June density = six voles/hectare, SE = 1.79; August density = five voles/hectare, SE = 2.52; Fig 2.5). However, there were no statistically significant differences in density estimates between harvesting treatments. In June, density estimates for the partial harvesting treatments were similar (5, 5 and 6 voles per hectare, for seed tree, 60% and 30%, respectively), and all higher than for the control, which is consistent with our hypothesis that southern red-backed voles would appear most in the partial harvesting treatments. However, the confidence intervals of these estimates overlap, and therefore there were no statistically significant differences between them. There were not enough vole captures (and no recaptures)

in the clearcut in June and the control in August to allow density estimation with a secr model. The upper confidence interval for vole density in the 30% treatment in August is more than two times the estimate itself (density = 4 voles/ hectare, UCI = 13).



Figure 2.5 SECR density estimates of Southern red-backed voles across forest harvesting treatments in June (left) and August (right), with 95% confidence intervals. The order of the harvesting treatments in this figure is: clearcut, seed tree, 60% retention, 30% retention and control. The 30% retentions are placed next to controls because they have an understorey that has not been disturbed (in the patches) by logging machinery. Additionally, as the 60% retentions were by basal area rather than % of area, they do not necessarily have more canopy cover than the 30% retentions. The two dots without error bars represent the 'minimum number of southern red-backed voles alive' – the number of individuals that were live trapped that could not be used to calculate a density estimate. For control treatments in August, this was four individuals, and for clearcuts in June, this was six individuals.

2.5.3 Habitat usage by common shrews and red squirrels

Common shrews were captured 58 times over the two trapping months, with more captures in clearcut than other treatments. Parameter estimates from the Poisson count GLM indicated that shrews were captured significantly less frequently in the 60% partial retention than

the clearcut (Table 2.4).

Table 2.4. Poisson generalized linear model results for common shrew captures across the gradient of forest harvesting treatments. Raw capture count is the number of captures of shrews, not unique individuals. The significant p-value for the 60% partial retention treatment is bolded.

	Raw Capture Count	Estimate	Std Error	z-value	p-value
Clearcut (Intercept)	19	1.15	0.23	5.02	5.05*10^-7
Control	9	-0.75	0.40	-1.85	0.06
30%	11	-0.55	0.38	-1.44	0.15
60%	8	-0.87	0.42	-2.05	0.04
Seed	11	-0.55	0.38	-1.44	0.15

Red squirrels were the least captured of the four main species, with 27 live captures and two mortalities across all replicates and both months (Table 2.2). There were insufficient captures to statistically model differences across treatments, but the majority of red squirrel captures (25 of 29 = 86%) were in treatments with greater canopy cover (i.e., 60% retention, 30% retention and control; Table 2.3).

2.5.4 Small mammal community diversity

Across all small mammals captured (summed over both months of sampling), the Shannon diversity index tended to be greater in the control and two partial harvesting methods than the clearcut or seed tree treatments (Fig. 2.6). This diversity measure included the four focal species analyzed above, as well as meadow vole, short-tailed weasel, and least weasel (Table 2.3). Diversity was highest in control forest (mean Shannon Index = 1.007, estimate = 1.01, SE = 0.14), closely followed by the partial harvesting treatments (30% mean SI = 0.999, 30% SE = 0.17, 60% mean SI = 0.976, 60% SE = 0.17). Mean diversity values for seed tree and clearcut were considerably lower, at 0.63 and 0.75, respectively (significantly lower for seed tree: estimate = -0.38, SE = 0.17, p-value = 0.02). In spite of this trend toward lower diversity in the more open treatments, the differences for clearcut were not statistically significant due to the small sample size and variation among replicates within treatments (Fig. 2.6; estimate = -0.26, SE = 0.17, p = 0.12).

Table 2.5: Generalized linear mixed model results for small mammal diversity with treatment and coarse woody debris as predictor variables. Significant p-values are bolded.

	Estimate	Std. Error	Z value	p-value
Intercept (Control)	1.01	0.14	7.23	4.9*10^-13*
30% Retention	-0.01	0.17	-0.05	0.96
60% Retention	-0.03	0.17	-0.18	0.86
Seed Tree	-0.38	0.17	-2.26	0.02*
Clearcut	-0.26	0.17	-1.55	0.12



Figure 2.6: Mean and replicate-specific Shannon diversity index value for each treatment. Each dot represents a replicate diversity value for that treatment, and the black lines represent the mean for that treatment (n=3).

Clearcut and seed tree treatments in replicate two had much lower diversity values, compared to the other treatments and replicates (Figure 2.6). Our expectation was that the lower diversity in replicate two could potentially be explained by an environmental variable – the amount of coarse woody debris in the clearcut and seed tree treatments. Coarse woody debris ranged from $41.7 - 538.2 m^3$ across sampling units (mean =215.6 m³, standard error = 33.6 m³), and coarse woody debris volumes in clearcut and seed tree treatments in replicate two were 166 and 290.7 m³, respectively. We tested a post-hoc hypothesis that this difference in diversity could be related to variation in coarse woody debris by adding this variable to a model at the sampling unit level (n = 15). The significant effect of coarse woody debris in the model results suggest that it has a negative effect on the community diversity index, which is contrary to our expectations. However, by controlling for coarse woody debris, Shannon's diversity in the seed tree and clearcut treatments are significantly lower (p-value = 0.002, 0.015, respectively) than in the control forest.

 Table 2.6: Generalized linear mixed model results for small mammal diversity with

 treatment and coarse woody debris as predictor variables. Significant p-values are bolded.

	Estimate	Std. Error	Z value	p-value
Intercept (Control)	1.232	0.162	7.617	2.6*10^-14*
30% Retention	-0.056	0.137	-0.409	0.682
60% Retention	-0.034	0.135	-0.248	0.804
Seed Tree	-0.423	0.137	-3.095	0.002*
Clearcut	-0.338	0.139	-2.425	0.015*
Coarse Woody Debris	-0.001	0.0003	-2.415	0.016*

2.6 Discussion

2.6.1 Species' densities across the harvesting gradient

Density of deer mice was highest in the clearcut treatment and lowest in the partial retention treatments. Other studies generally demonstrate that this species is a habitat generalist that favours low coniferous cover, with population increases 5-10 years following clearcutting (Zwolak, 2009). Deer mice forage on seeds and insects found in clearcuts, but there is a large volume of conflicting literature about their response to cover. Our results contrast with Fuller et al. (2004), where deer mice were most abundant in partially harvested stands (and mature deciduous forest, not part of our experimental design) and absent from most clearcuts. We suggest that deer mice were more abundant in clearcuts in our study, likely because of their ability to proliferate and succeed in an early-successional stage ecosystem as a generalist species.

The 30% and 60% partial harvesting treatments were best at supporting populations of southern red-backed voles and red squirrels. Southern red-backed voles had marginally higher estimated densities in the partial retention treatments than the clearcut or control, supporting our hypothesis that the voles would prefer the mix of open and closed canopy cover in close proximity. Sullivan and Sullivan (2001) found that southern red-backed vole was most abundant in group seed-tree, patch-cut and uncut forests, which is similar to our findings, even in a completely different climatic region of BC. Vole preference for partial retention could be explained by the fact that harvest machinery moves through the cutblock, disturbing the undergrowth and coarse woody debris (CWD), exposing roots and debris and thereby creating conditions that are ideal for one of southern red-backed vole's favourite foods: hypogeous ectomycorrhizal fungi (Sullivan & Sullivan, 2001). Sullivan & Sullivan (2001) also found that vole numbers decreased significantly in seed tree and clearcut treatments relative to uncut

controls. Declines similarly occurred in clearcuts in our study, but we also found that voles used the seed tree treatment at similar levels as the partial retention treatments.

2.6.2 Habitat usage of untagged species

While density estimates were only feasible for deer mice and southern red-backed voles, spatial variation in captures indicated that habitat use of shrews and red squirrels also varied with harvest treatments.

In agreement with my hypothesis, we found greater numbers of shrews in clearcuts than any of the other harvesting treatments or control plots. Recently harvested blocks have ripped up CWD, which insects and invertebrates break down, providing a food source for shrews (Fisher & Wilkinson, 2005). In the long term, Sullivan & Lautenschlager (1999) found shrew species to appear in relatively similar numbers across forested and clearcut sites, which further highlights the need for longer term studies at JPRF into the changes in community composition and species density in the years and decades following harvesting.

Red squirrels were captured most frequently in the unharvested control plots, followed by partial retention, then clearcut and seed tree retention treatments. Trapping was conducted roughly one and a half years after harvesting, and we observed a decline in number of captures from the full canopy cover in the control to none in the clearcut. This was expected as red squirrels are conifer seed specialists, with fewer recorded observations in clearcuts, though they have been found to use cut blocks as an occasional summer forage area (Fisher & Wilkinson, 2005). In contrast to our results, Herbers & Klenner (2007) found little difference in red squirrel density between harvesting treatments one year after logging. After two to four years, however, they found that density declined with increased tree removal, congruent with our results.

We captured more squirrels (17) in August than in June (10). At the end of summer and early fall, young red squirrels are dispersing from the maternal territory they originated from, to

new territories where they may breed for the first time; this is called natal dispersal (Haughland & Larsen, 2004). For red squirrels, this dispersion may be based on resource competition, and has been understudied in heterogeneous habitats like the varied harvesting treatments in this project (Haughland & Larsen, 2004). Haughland and Larsen (2004) found that over a third of their radio-collared squirrels explored contrasting habitat to the type from which they originated, but that settlement occurred in philopatric habitat types (same type/similar to what their mother raised them in). In the August trapping session at JPRF, we could have been trapping those exploratory dispersers before settlement period, resulting in the higher number of total captures.

2.6.3 Diversity

At JPRF, the greatest diversity of small mammals occurred in the control plots and partial harvesting treatments, and lowest was in the seed tree (significant) and clearcut treatments, though this trend was mostly driven by one replicate (replicate two). When coarse woody debris was included as a predictor variable in the models, the clearcut harvesting treatment, as well as the volume of coarse woody debris, had previously unseen significantly negative effects on the diversity indices. These clearcut result is consistent with the hypothesis that a heterogeneous canopy created by partial harvesting will support both forest- and meadow-dependent species in the small mammal community (trend seen especially with southern-red backed voles and red squirrels; Table 2.3). However, this clearcut result was elicited only when coarse woody debris was included in the model, indicating the overstory retention levels were not the only factor at play causing the low diversity values in replicate two. Coarse woody debris functions as habitat for small mammals, as well as for their mustelid predators (Sullivan & Sullivan, 2019). In fact, coarse woody debris can be more abundant in recently harvested areas, providing a vast amount of habitat for small mammals in the decade following logging (Sullivan & Sullivan, 2019). The post-hoc model showing negative association of coarse woody debris with diversity was

unexpected, and based on the literature, indicate that there may be another variable driving the lower diversity in the open-canopy treatments.

There were three species that we captured less than five times each: meadow voles, shorttailed weasel and least weasel. We captured meadow voles three times in the clearcuts and once in a 30% partial retention, which followed the expectation that this species would have a positive response to forest harvesting (Kirkland, 1990; Fisher & Wilkinson, 2005). Overall, data on weasels and mustelids is thin, though weasels are expected to frequent harvested areas, potentially for the abundant small mammal prey (Sullivan et al., 1999). We captured short-tailed weasels once in clearcut and once in seed tree retention treatments, which is consistent with the expectation that they are following an abundant food source in clearcuts, though we cannot make any inferences based on just two captures. The least weasel was captured only once, in a control forest. In searching for information about least weasel diet and habitat, it became clear that this is an understudied species generally, but especially in Canada and British Columbia. A review paper by Proulx (2012) highlights that American and European research on least weasels cannot be applied to the specific conditions in the diverse biomes of Canada nor to the different forest harvesting methods we examined. Overall, little can be inferred about this single capture of a least weasel in the control forest plot, other than least weasels are understudied. To combat the broader issues of low detection numbers and undetected species in future analyses for small mammal diversity, species accumulation curves or other related methods could be used to estimate the probability of undetected species and thereby better incorporate uncertainty into species richness estimates (Colwell et al., 2004).

2.6.4 Limitations and considerations

One major limitation of this small mammal analysis was the small sample sizes for many species and accordingly low statistical power to detect differences among harvest treatments.

This could be due to the period of trapping being too short (only one summer), or a function of the area sampled (just a small portion of the research forest). This also limited the complexity of the small mammal models and the number of variables that could be examined (see A.4 for an unsuccessful foray into sex-specific deer mouse SECR models) Future studies should sample more plots for longer, across years if possible. Longer-term research is needed to determine if these harvesting treatments have a lasting effect on the populations of small mammals. Over 44 years of trapping in the boreal forest of Kluane, Yukon, Krebs et al. (2018) noted 3-4-year cycles in southern red-backed voles, with continually growing peak population sizes. They also noted irregular fluctuations of deer mice, showing no cyclic trend. Krebs et al (2018) also posited that social behaviour is intensely related to vole population cycles but this hypothesis remains unexamined. Therefore, the regular and irregular fluctuations of small mammal populations could have a drastic effect on the generality of results from short-term studies like ours. Essentially, we cannot infer if the harvesting treatments had direct effects on small mammal diversity or densities, as we did not sample the area before harvesting was undertaken. However, we have provided a snapshot of immediate post-harvesting patterns, and a baseline for follow-up comparisons.

Our inferences on the effects of forest harvest treatment on small-scale patterns of diversity were based on the small mammal community of seven species detected in JPRF. However, there were some notable species that were not live trapped over the course of the project. Dusky shrew (*Sorex monticolus*), long-tailed vole (*Microtus longicaudus*), northwestern chipmunk (*Tamias amoenus*), jumping mouse (*Zapus* spp.), and northern bog lemming (*Synaptomys borealis*) are all species that were captured in another small mammal study in the sub-boreal spruce zone of BC that we did not capture over the course of this project (Sullivan et

al., 1998). This could be a function of the small area sampled in our study (i.e., a small portion of the research forest), or of not sampling for long enough. Measures of community dynamics can be influenced by rare species, and future work should consider additional sampling and modelling methods that aim to address imperfect detection (Colwell et al., 2004; Gotelli & Colwell, 2001; Iknayan et al., 2014).

Mortality is a significant issue in small mammal trapping studies and can disproportionately affect species like the common shrew (Shonfield et al., 2013). The summer of 2019 at JPRF was a particularly active bear season. We determined it prudent to not put any particularly odorous foods in the traps, like krill/shrimp. This meant that even though we were aware of shrews' insectivorous diets, for the safety of the field crew and the animals in the traps, did not want to draw further attention of predators to them, and to prevent repeated visits from investigative animals. Peanut butter was also eliminated from food to be put in the traps through this line of logic. To attempt to prevent mortality of shrews, we used cut-up earthworms in the traps. These issues with food source and inability to fully support shrew metabolism may have impacted our shrew capture rate, as well as mortality rate. Common shrews had a mortality rate of 72.4% (42 individuals of 58 captures), followed by Southern red-backed vole (8.5%, 24 of 283 captures), red squirrels (6.9%, 2 individuals of 29 captures) and deer mice (4.7%, 21 of 449 captures). We found that very few published papers include their rates of mortality, with the exception of cases where attempts to mitigate mortality were part of the experimental design (i.e., inclusion/exclusion of trap covers, Stephens & Anderson, 2014).

Live trapping is an invasive method that is also labour- and field-intensive. With the increasing prevalence of camera traps (discussed in Chapter 3) there is potential to examine other methods to determine small mammal community diversity and species densities. Villette et al.,

(2016) demonstrated that camera trapping can be a non-invasive method that produces robust density estimates for small mammals. Throughout the 2019 trapping season, we simultaneously ran a camera trapping grid (under the supervision of field assistant Katie Tjaden-McClement). The results of our co-occurring camera trapping investigation revealed that we did not have the statistical power to infer small mammal species' densities, but that the cameras were a better indicator of community diversity, capturing video of species that are rarer in the ecosystem and those that are 'trap shy' (neophobic species; Stryjek et al., 2019; Tjaden-McClement, 2020). The species captured exclusively on camera trap in the study were: Northern flying squirrel (*Glaucomys sabrinus*), yellow-pine chipmunk (*Neotamias amoenus*) and jumping mouse (*Zapus spp*). I suggest that more studies in the future test the validity of small mammal camera trapping to eventually phase out more invasive methods for density estimates.

2.7 Management Implications & Conclusions

Small mammals are an integral part of forest ecosystems, and there is a deficit of small mammal studies of this type in the Sub-Boreal Spruce biogeoclimatic zone of British Columbia. While future studies should focus on increasing samples sizes for greater statistical power, our results suggest that some species benefit from the retention of a partial canopy cover in forest harvesting blocks. Clearcut harvesting with maintenance of small patches of trees grew in popularity around 2004 in BC, and this system makes up approximately 85% of current harvests (Environmental Reporting BC, 2018). The results of this study suggest that retention patches covering 30-60% of the harvested area may lead to similar diversity values as intact forest.

In terms of local and direct benefits, we hope that these results will encourage operators to re-evaluate their best practices for wildlife reserves in clearcuts, or to more frequently practise harvesting methods that have been demonstrated to support a diverse mammal community such as the two partial harvesting methods we tested here. Actions taken by operators and

policymakers to use science to inform best harvesting practices for wildlife will increase the biodiversity and resilience of BC's forests. As well, continued monitoring of small mammals through live trapping or camera trapping over longer time periods, larger spatial scales, and preand post-harvesting, will illuminate the longer-term effects of harvesting on population cycles. By avoiding the negative effects of complete canopy removal, higher diversity and healthier populations of a wider variety of small mammal species can be supported, which will in turn support mesocarnivores, raptors and ultimately a more biodiverse ecosystem.

Chapter 3: Responses of large mammals to forest harvesting treatments across a latitudinal gradient

3.1 Introduction

3.1.1 The need to balance forest harvest and wildlife habitat

The international importance and economic value of extractive natural resource industries must be reconciled with the ecological and socio-cultural importance of wildlife and the spaces they inhabit. Conversion of complex ecosystems to more homogeneous, human-dominated landscapes has contributed to global declines of biodiversity (Flynn et al., 2009). In Australia, the recent destructive wildfires may have been exacerbated by policy and logging practices rather than solely climate change (Lindenmayer et al., 2020). In the tropics, Sodhi et al. (2004) brought to light the fact that fires, logging practices, bushmeat hunting, wildlife trade and global chemical cycles are playing a role in biodiversity changes, bringing southeast Asia to the cusp of a disaster unless concrete, multinational conservation agreements are made. Thorn et al. (2020) demonstrated that approximately 75% of a naturally disturbed forest must remain intact (free of logging post-fire or beetle disturbance) to preserve 90% of the biodiversity present in an ecosystem. It is imperative in the face of increasing scale of abiotic and biotic disturbances, fueled further by climate change, that the effects of natural resource extraction on mammals be evaluated (Noss, 2001). This is needed to determine best practices for industry and conservation of wildlife communities, as well as for the people who depend upon them (Turner & Clifton, 2009).

Forest harvesting is part of the economic backbone of BC and Canada (BC Chamber of Commerce, 2016). Particularly since the creation of the *Forest and Range Practices Act* (FRPA) in 2002, logging in BC has undergone policy changes intended to improve forest stewardship and balance economic and environmental values, including values pertaining to wildlife

management (Province of British Columbia, 2002). However, the success of these changes from the perspective of biodiversity conservation and environmental protection is debated (Hoberg & Malkinson, 2013; West Coast Environmental Law, 2004). In particular, the widespread use of clearcutting and the resulting homogenized landscape can be problematic for mammal species that depend on forest cover and structural diversity (Potvin et al., 2005; Potvin, et al., 1999).

Since FRPA's implementation, forest harvest practices have shifted from large-scale industrial clearcutting methods towards a "natural disturbance emulation paradigm", which aims to use harvesting to create a similar set of conditions as would be present after a natural disturbance, like fire (Long, 2009). In forest management, partial harvesting methods that retain live residual trees help mimic natural fire or beetle refugia by conserving structural and species diversity, and thus may be useful in maintaining wildlife habitat (Simard et al., 2020).

Partial harvesting methods have been suggested and used to mitigate the effects of clearcut harvesting on biodiversity, to combine ecological and economic goals in managed landscapes, and to permit timber extraction while maintaining forest structural and functional diversity (Fuller et al., 2004; McComb et al., 1993). Partial cutting and leaving seed trees are more expensive methods than clearcutting (Wilson & Wilson, 2001), but they have the potential to provide more wildlife habitat and structural diversity in comparison to clearcutting. However, empirical evidence that partial harvest methods benefit the mammal community remains rare.

In BC, partial cutting, or variable retention harvesting, is not applied frequently; in fact, 92% of harvesting is clearcutting or clearcutting with small patches of trees left for wildlife and seedling regeneration (Beese et al., 2019). Moreover, the proportion of a harvested area with any level of retention is usually well below 20% (Beese et al., 2019). The interior region of BC (which broadly includes the Okanagan, Kootenays, Cariboo, Bulkley-Nechako, Omineca and

Peace regions) also has a larger maximum clearcut size than coastal regions and less public pressure to stop clearcutting (Beese et al., 2019). Clearcuts can be larger in the interior, with many clearcuts up to one thousand hectares in size, as the guidelines for cut size are dependent on the natural disturbance types typical for the region (i.e., stand-replacing fires occur on 100-200-year cycles in the interior, rather than 250+ years on the coast; Daniels & Gray, 2006). A study undertaken in the Cariboo region of BC examined the quality and size of wildlife tree patches (WTPs) to determine if retained areas of forest were providing useable and high-quality habitat for forest-dependent species (Price, 2007). They found the following across a random sample of 20 harvested areas: 1) WTPs tended towards the smallest sizes, especially for ones that were internal to the harvesting area boundaries, 2) WTPs were not representative of the forest pre-harvest ("immature or stagnant stands") and 3) long pieces of coarse woody debris were lacking in the harvested areas compared to WTPs (Price, 2007). These trends suggest that wildlife habitat is left only in the most convenient configurations from the perspective of the harvester and in the least amounts possible, rather than with an emphasis on creating high quality habitat. There is thus a need to evaluate the local value of partial retention in these interior forests, to determine how improvements can be made to the protection or creation of wildlife habitat in landscapes managed for forest harvest.

3.1.2 Expected responses of mammals to forest harvesting and project locations

Homogeneous, open clearcuts, have been found to be detrimental for some mammal species that depend on the forest cover and structural diversity of old or uneven-aged stands (Potvin et al., 2005; Potvin et al., 1999). Generally, small mammals and some ungulates (e.g., elk and white-tailed deer) make use of cleared areas immediately following disturbance, and their presence tapers off as the stand grows. In contrast, mustelids such as weasel species and martens, have the opposite trend, avoiding young cut blocks in spite of abundant prey, and

instead inhabiting older forests and using retained older forest patches in disturbed areas (Fisher & Wilkinson, 2005). Some species, like lynx, red foxes, and snowshoe hares use regenerating forest types more than recently cut or uncut forests (Fisher & Wilkinson, 2005). However, there is a data gap regarding carnivores with large home ranges, like bears and large cats. As well, there is a lack of information on wildlife responses to reserve areas in harvested stands and to partially harvested forests, particularly at the community level as most studies focus on one or a small number of species (Fisher & Wilkinson, 2005).

Clearcuts allow more sunlight to reach the previously shaded forest floor, enabling many vascular plants to flourish without the presence of trees overhead. In some studies, plant species richness is up to 35% greater five to eight years after clearcutting than in old forests (Hauessler et al., 2002). While this forage is beneficial to some large mammals, predominantly ungulates like moose and elk (Apps et al., 2013), the animals are also more visible in large-scale clearcuts. Animals depend on their habitat for concealment and protection from predators (Camp et al., 2012). Increased visibility in clearcuts is a risk for prey species, as they can be more easily spotted by predators and (Camp et al., 2012).

Based on a detailed review of existing literature (Table 3.1), I hypothesized that responses to forest harvesting treatments will be highly variable across larger mammal species, even within some taxonomic groups (Table 3.1). I hypothesized that martens, cougars and wolverines would respond negatively to forest harvesting, based on their preference for dense cover (Lavoie et al., 2019; Wainright et al., 2010; Weir, 2004). Overall, I predicted that the four main ungulate species in my study areas (white-tailed deer: *Odocoileus virginianus*, mule deer: *Odocoileus hemionus*, moose: *Alces alces* and elk: *Cervus canadensis*) would show preference for the partial harvesting treatments, allowing them to feed on vascular plants in recently

harvested areas while staying in close proximity to covered areas where they are more secure from predators (Koot et al., 2015; Fisher & Wilkinson, 2005). In the literature, weasel species, wolves and coyotes are noted to take advantage of changes in their environments and utilize recently harvested areas (Hatler et al., 2003b; Sullivan & Sullivan 1999; Fisher & Wilkinson, 2005). Other species, like black and grizzly bears, have extremely varied habitat requirements that include denning in old growth forests, preference for berries (typically growing in open fields) and hunting for juvenile ungulate prey; thus, I hypothesized that partial harvesting could provide this varied canopy that would be utilized more by bears (Brodeur et al., 2008; McClelland et al., 2020).

Based on the literature review and available data on the distributions of focal species in BC (Klinkenberg, 2020) the expected size of the mammal communities was not significantly different between the three project locations (Table 3.1 and A6). I did not anticipate that the locations would be the main factor affecting relative abundance or use of treatments by each species. The scale of the harvesting treatments is small relative to the home range or territory sizes of many of the medium- and large-bodied mammals. The disturbances and habitat quality around the MTP sites could thus have significant effect on their usage of the area. At John Prince and Alex Fraser, the surrounding area is research forest lands, logged at a slower and lesser rate than typical economically driven forest tenures. Jaffray is in the middle of one of these more typical logging tenures. Overall, I was not expecting major differences in the diversity of species present at each site based on the literature, but there are a few species that do have higher densities in particular parts of the province. Moose were expected to increase with increasing latitude (i.e., more at Alex Fraser and John Prince) and cougars were expected to be at higher densities in the lower latitudes of the province (more at Jaffray; Table A6).

3.1.3 What other factors affect an animal's presence in a particular area?

The effects of forest disturbance on wildlife are influenced by other aspects of the individual animal's habitat. For example, water, forage, and roads are important factors that influence the habitat quality perceived by a given wildlife species.

Proximity to water in wetlands, lakes and streams is crucial for understanding habitat usage by wildlife for many reasons, and regardless of the scale of examination, sources of water and the forage in and around them can influence species' presence in an area. The vegetation associated with riparian areas is often exclusive to those wetter soil conditions (Gregory et al., 1991). For some wildlife, like moose or bears, wetlands and aquatic areas contain important sources of nutrition in the form of sodium-rich aquatic vegetation (Fraser et al., 1984; Hilderbrand et al., 2004).

The availability of high-quality vegetative forage is critical for many wildlife, particularly browsing ungulate species., Moose, for example, select habitat for forage rather than based on predation risk except during calving and rutting (Francis et al., 2020). Furthermore, the benefit of early seral vegetation outweighed predation risk even in highly disturbed landscapes (Francis et al., 2020). Forage availability can be monitored by remote sensing indicators of vegetation productivity, such as the normalized difference vegetation index (NDVI), which has been shown to be useful in predicting suitable habitat for many species, but especially herbivore species distributions and populations over time (Pettorelli et al., 2011).

Finally, roads can have significant negative impacts on some wildlife species; they can cause direct harm through vehicle strikes and can be barriers to movement (Proctor et al., 2020). Roads also cause indirect harm through increased access for hunters and recreators into remote places, and/or changes to wildlife behaviour (Boston, 2016).

3.1.4 Emphasis on ungulate species

Ungulates are a main focus of government protection, important considerations in forest management, are valued by First Nations, and are game species targeted by hunters. They are a group of species that have the same diet type (herbivory), are taxonomically related (Order: *Artiodactyla*, Family: *Cervidae* and *Bovidae*) and in many ecosystems, fill functional roles that overlap, through their influence on the plant community, as prey for large carnivores and with similar life history traits (Hobbs, 1996; Bergerud & Elliot, 1998; DeMarchi & Bunnell, 1993).

The four main forest ungulate species in the BC interior (moose, elk, white-tailed deer and mule deer) are of importance to First Nations, hunters in general, and as forest ecosystem herbivores (Blood, 2000; Weisberg & Bugmann, 2003). The BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development has a specific mule deer winter range plan (Koot et al., 2015) and an overarching ungulate winter range plan to preserve habitat that supports ungulate species with enough nutritionally sufficient forage for the most energetically stressful season (Ministry of Forests, Lands, Natural Resource Operations and Rural Development, 2020). Moose are a culturally significant species for First Nations across Canada, and T'exelcemc makes particular note of moose being a species they are intrinsically tied to, and a traditional food (William, 2020). In community meetings, members of the T'exelcemc also asked many questions about white-tailed deer, as they are curious about the range expansion of this species and the interactions or potential effects on mule deer, another culturally important species.

3.2 Objectives and hypotheses

My overall objective in this study was to use wildlife camera traps to determine how large mammal species respond to a gradient of forest harvesting intensity, from clear-cutting, through different levels of tree retention, to intact unharvested forest. In this chapter I determine if: 1) patterns of large mammal community diversity (i.e., multispecies habitat use) vary across a gradient of forest harvesting treatments; 2) these responses vary between locations along the latitudinal gradient; 2) responses to treatments by individual species are consistent or variable; and 3) responses include variation in behaviours across treatments. Examining the effects of logging on the working landscapes of interior BC is critical to learning how to balance development with conservation of wildlife habitat.

Table 3.1 List of hypotheses for each species' response to forest harvesting. The table also includes the provincial status of the species (yellow, blue or red) as well as the potential expected sites to capture the species. I examined the literature available for each species, with a focus on Canadian or British Columbia studies to compare to conditions as similar to this project as possible.

Common Name	Scientific Name	Status	Expected Site for Possible Captures	Expected Response to Harvesting
Moose	Alces alces	Yellow	AFRF, JPRF	Positive response to clearcutting for forage but require nearby forest for cover (partial harvest). (Summary by Fisher & Wilkinson, 2005)
Elk	Cervus canadensis	Yellow	Jaffray	Preference for partial harvesting (access to forage and dense cover), however elk do not seem to alter movement or home range due to harvesting (Summary by Fisher & Wilkinson, 2005)
White-tailed Deer	Odocoileus virginianus	Yellow	Jaffray, AFRF	Preference for partial harvesting (selection for some cutblocks, high edge-to-area ratios, negative response to slash) (Summary by Fisher & Wilkinson, 2005)
Mule Deer	Odocoileus hemionus	Yellow	Jaffray, AFRF, JPRF	Preference for clumpy seed tree retention – snow interception by large trees to lower energy output and access to lichens (Koot, Day, Ewen & Skea, 2015)
Coyote	Canis latrans	Yellow	Jaffray, AFRF, JPRF	Use of fragmented landscapes, some preference for regenerating cutblocks (partial harvest preference) (Summary by Fisher & Wilkinson, 2005)
Grey Wolf	Canis lupus	Yellow	AFRF, JPRF	Large data gaps – seasonal usage of post-clearcut or burnt stands following prey, abundance of studies showing use of open and diverse areas (Summary by Fisher & Wilkinson, 2005) – potentially partial harvest or clearcuts as prey species increase?
Red Fox	Vulpes vulpes	Yellow	AFRF, JPRF	Tracks found in regenerating stands (30+ years), more than cut or uncut forest – preference for partial harvest. (Summary by Fisher & Wilkinson, 2005)
Lynx	Lynx canadensis	Yellow	JPRF, AFRF, possibly Jaffray	Lynx abundance follows snowshoe hares, found in regenerating stands, rare in recently cut or old growth (partial harvesting.) (Summary by Fisher & Wilkinson, 2005)
Bobcat	Lynx rufus	Yellow	Jaffray, possibly AFRF	Affected by snow depths – clearcuts in northern parts of range would be detrimental due to thick snow, partial retention and smaller cutblocks preferable (Gooliaff, 2018; Hatler, Poole & Beal, 2003a)

Cougar	Puma concolor	Yellow	Jaffray, AFRF, possibly JPRF	Some habitat preference for dense vegetation, some use of clearcuts, varied use of different habitat types dependent on life phase (Wainwright, Darimont & Paquet, 2010) – partial harvest.
Striped skunk	Mephitis mephitis	Yellow	Jaffray, low likelihood AFRF and JPRF	Uses forest clearings and edges, wetlands and urban areas – partial harvest.
Wolverine	Gulo gulo	Blue	Jaffray, AFRF, JPRF	Wide range of food sources, but generally depending on mature forest & have landscape level habitat requirements – negative response to harvesting (Weir, 2004)
American marten, Pacific marten	Martes americana, Martes caurina	Yellow	Jaffray, AFRF, JPRF	Preference for full canopy cover (prey abundance), clearcuts as marginal habitat, importance of residuals for survival and recruitment – negative response to harvesting (Lavoie et al., 2019)
Ermine/Short-tailed Weasel	Mustela erminea	Yellow	Jaffray, AFRF, JPRF	Preference for cutblocks – slash piles as rest sites (Summary by Fisher & Wilkinson, 2005), preference for clearcut (Sullivan et al. 1999) – though scant information – clearcut preference
Long-tailed Weasel	Mustela frenata	Yellow	Jaffray	No data about response to harvest, but positive relationship with exploiting open/human-influenced areas – clearcuts? (Summary by Fisher & Wilkinson, 2005)
Least Weasel	Mustela nivalis	Yellow	AFRF, JPRF	Able to use clearcuts, forests and most habitat types at any elevation – no preference (Hatler, Mowat & Beal, 2003b)
American Black Bear	Ursus americanus cinnamomum	Yellow	Jaffray, AFRF, JPRF	Preference for full canopy cover and mature forest for denning, deciduous or regenerating forests for forage – partial harvesting? (Brodeur et al., 2008; Summary by Fisher & Wilkinson, 2005)
Grizzly Bear	Ursus arctos	Blue	Jaffray, AFRF, JPRF	New cutblocks increased food sources, but significant data gaps (Summary by Fisher & Wilkinson, 2005)
3.3 Methods

3.3.1 Study Areas

The study area for this part of my thesis includes the three previously described locations across BC's interior: Jaffray (north of Cranbrook), Alex Fraser Research Forest (northeast of Williams Lake) and John Prince Research Forest (northwest of Fort Saint James) (see Figure 1.1 in the Introduction). All three sites are part of Dr. Suzanne Simard's MTP (The University of British Columbia, 2018).

These three sites occur in mixed Douglas-fir conifer forests, at elevations between 880-1075m, share the same soil order (Luvisol), are mostly south-facing, gently sloped and range in stand age from 82-129 years (Simard et al., 2020). The three locations represent the largest latitudinal gradient in the MTP, spanning a 900km latitudinal gradient (Figure 1.1; Simard et al., 2020).

3.3.2 Wildlife Sampling Design

In recent years, camera trapping has been rapidly increasing in popularity as a way to remotely acquire data on medium- and large-bodied terrestrial animals and to evaluate distribution, abundance and behavior of wildlife (O'Connell, Nichols & Ullas Karanth, 2011; Burton et al., 2015). Between December 2018 and March 2019, I set up 45 wildlife camera traps across the study sites, with one camera at the centre of each of the Mother Tree sampling plots (one camera per harvesting treatment and five cameras per replicate = 15 cameras at each of the three locations). I set up 15 Reconyx PC900 cameras (Reconyx, Holman, WI) at Jaffray, 12 Hyperfire HP2X cameras and three PC900 cameras at Alex Fraser Research Forest, and 15 Bushnell Prime Low Glow cameras (Bushnell, Overland Park, Kansas) cameras at JPRF. I set up each camera at approximately a one-metre height and facing north as well as a clearing or game

trail when possible. I set all cameras to take five images at a motion trigger (with no quiet periods or delay) to better evaluate the behaviour being demonstrated by the individual(s). Other variables, like sensitivity, were kept at the default factory settings. The cameras were also set to take one time lapse photo each day at 12:00pm (to ensure the dates that cameras were operational). Cameras were active between December 2018 – May 2020 for Jaffray, February 2019 – May 2020 for AFRF, and March 2019 – April 2020 for JPRF.

3.3.3 Camera trap image processing

I used a custom database developed by the Wildlife Coexistence Lab to process camera trap photos. In each image sequence (defined as the five images taken at each camera trigger), I identified species, group size (number of individual animals across the sequence), age (adult/juvenile/adult + juvenile), behaviour (travelling/foraging/inspecting camera/other), and sex (unknown/male/female/mixed). For behaviour, travelling was classified as directional movement across the camera field of view (not stopping to forage or inspect camera), while foraging constituted an individual's head remaining down at the ground for multiple images and/or clear chewing and ripping up forage images. Staring directly at the camera, approaching it and/or rubbing against the camera was classified as inspecting. Sitting and laying in front of the camera was tagged as 'other' with a comment for 'bedded down'. Over the course of the project, I worked closely with volunteers for their first few sessions, tagging images to oversee species identification, checking all images that volunteers flagged as "unclear/needs examination", and checking through their identifications periodically. When a species could not be identified (too blurry to confirm or not enough of the individual in the camera field of view), it was left as "unknown species" and excluded from analysis. For white-tailed deer and mule deer (which could not, in some few cases be distinguished by tail, antlers or face) we assumed that the captures were of the more common species for the location. The cameras also provided date,

time, moon phase and temperature data. I grouped camera trap images into independent detections, which I defined using a minimum threshold of five minutes between consecutive captures of the same species at the same camera. There is a significant amount of variation on choices for independent detection time thresholds, from no threshold at all up to 24 hours (Burton et al., 2015). The five-minute gap was chosen to reflect the fine scale of behaviours being demonstrated by individual animals. The size of the MTP treatments (~4-5 hectares) and their adjacency is a distance that most of the mammals could travel across within seconds or minutes. The choice of five-minute gaps was intended to be a reflection of the usage of the specific habitat around the camera (within five minutes, an animal could be in another treatment).

3.3.4 Do forest retention practises alter mammal diversity at the community level?

At the small scale of the harvesting units (4-5 ha) of the MTP, it is not possible to determine the effects of harvest intensity on large mammal communities, as all of the 15-harvest units at a single location are home to the same community of species and individuals. Therefore, at the scale of the harvesting units, I am expecting that treatments will have similar diversity values. However, differences in diversity may exist at the broader location level due to the different types of sites and mammal communities present. To determine if forest harvesting intensity, and the interaction between harvesting intensity and location affects diversity, I compared diversity values across the latitudinal locations. I looked for patterns that differentiate use of plots within the community (rather than there being different communities in each plot).

I used the vegan package in R (Oksanen, 2019) to calculate the Shannon diversity index for each of the 45 treatment units, using camera trap detection rates for each species (independent detections from the entire trapping period per 100 active camera days). The Shannon Diversity index is a measure of community diversity (Mazurek & Zielinski, 2004).

Shannon diversity includes both species richness and evenness in its measure of heterogeneity (Hollenbeck & Ripple, 2007). I was interested in whether the latitudinal gradient or harvesting treatment had a greater effect on the diversity of the community. I modelled both variables as fixed effects in a linear model to explicitly test their effects on diversity and selected the best model (lowest AIC) to determine the main factors influencing diversity. While it is not possible to have perfect detection in ecosystems, for these diversity models, I assumed that all available species in the community were detected, and that my index of relative abundance was unbiased across species and space (O'Connor et al., 2017).

For the purposes of diversity and behavioural analyses, I excluded all non-wild and nonmammal species from datasets used in those models. The species excluded were cattle (*Bos taurus*), humans (*Homo sapiens*), domestic cats (*Felis catus*), bird species (Bird spp.) and unknown species.

3.3.5 Species and species group selection

I first considered how responses might differ among taxonomic groupings, but also between species that occupy wider or narrower ecological niches. In the species group analysis, I chose to also examine generalist species. The generalist species are characterized by their expanding ranges, ability to inhabit disturbed areas, and general diets (coyotes: Thornton & Murrray, 2014; black bears: Bastille-Rosseau et al., 2013 and 2016; Sun et al., 2017; white-tailed deer: Dawe & Boutin, 2016; Waller & Alverson, 1997). I expected that generalist species would use open areas (clearcuts and seed tree treatments) more than specialist forest-dependent species.

Research on elusive species, particularly elusive predators, has increased with the widespread use of wildlife camera traps (Kelly, 2008; Head et al., 2013). Some rare and elusive species were detected too infrequently for robust statistical analysis of their patterns, and the

patterns in the species may also be important to consider. For these species, we discuss the general patterns in capture rates.

3.3.6 Are the responses to forest retention practises mammal species/group specific?

In order to determine if forest harvesting or location had mammal species- or groupspecific effects, I first calculated the monthly capture rates of each species or group in each treatment unit (i.e., number of independent detections of a species at each camera in each month; see Table 3.2 for a sample of the modelling data frame). There is non-independence in the sampling units, as the months are repeated over time at the same stations. I used generalized linear mixed models (GLMMs) with a Generalized Poisson distribution in the package glmmTMB (Brooks et al., 2017) to examine variation in monthly detections at each camera as a function of harvesting treatment and relevant environmental covariates (described below, Tables 3.2, 3.3). I included location (JPRF, Alex Fraser and Jaffray) as a random effect, with the individual treatment units (i.e., individual camera trap stations) nested within location. I compared Aikake Information Criterion (AIC; Burnham & Anderson, 2004) values to determine the best model (lowest AIC) for a given species or group of species.

For all models, I used clearcut harvesting as the reference level (intercept) for the categorical variable of harvest treatment, as this is the experimental treatment that is closest to the current status quo (also known as standard operating practice) in the interior of BC. I compared all other treatments to this standard method to determine if they were improvements on the current situation or if they elicited similar responses.

3.3.7 Predictor variables and candidate models

I was interested in determining if the mammal species had a response to a particular harvesting treatment and climatic region (not previously visible in the total community diversity models), and if there were other environmental or anthropogenic variables influencing their usage of a certain treatment. The candidate models (Table 3.4) represent different hypotheses about the most important effects on monthly detections (i.e., habitat use) for each species or group, specifically : 1) forest harvest only , 2) location only (if the climatic gradient has more of an effect, 3) the experimental design (the treatments and camera locations), and 4) the environmental variables (treatments, distance to closest stream and NDVI).

I used the experimental design (location and harvesting treatment), as well as distance to streams and monthly NDVI as covariates in the candidate models to investigate environmental and anthropogenic covariates that could be influencing species' relative abundance (the count of detections as a measure of habitat use) in a given treatment (Table 3.2). The environmental variables I examined reflected the factors described above (section 3.1.4) and included distance to nearest stream (in metres) derived from GIS layers provided by the site managers, and NDVI at a 16-day frequency, measured at 250-metre resolution. Distance to streams and monthly NDVI were scaled by subtracting the mean and dividing by one standard deviation across sites (range from -2 to 2). Stream shapefiles were shared with me via staff at each site, and I derived distances from cameras to the nearest stream using the "sf" package in R (Pebesma, 2018). I extracted NDVI data for each site using "modis" and "modistools" (Tuck et al., 2014) at 16-day intervals. To derive monthly values, for a month that had two 16-day values fall within it, I averaged those two values for a monthly NDVI. For months where only one 16-day value fell within the operational dates of the camera, I averaged that value with one preceding and one following NDVI value.

I also considered distance to roads, wetlands and lakes as variables in the candidate models, but did not include them as they varied strictly with the climatic location (i.e., JPRF, Alex Fraser or Jaffray), not the treatment units themselves (included in A.7). Due to the small

size of the harvesting treatments, most cameras within a location had the same value for these

distance variables. The sampling sites were small relative to these infrequent features on the

landscape (all distances measured to the same road/wetland/lake within a site).

Table 3.2: A small sample from the data frame used for species and species group models.
Deployment.Location.ID is the individual camera/treatment unit, CR is the number of
independent detections in the month, and year_month describes that sampling period. Utm_code,
utm_y and utm_x are the coordinates of the camera, and nDays is the number of days used to
determine the NDVI value.

Deployment. Location.ID	Species	CR	utm_code	utm_y	utm_x	nDays	year_ month
AF_ICH_30P	Alces alces	4	10	5810969	589130	31	Jul-19
AF_ICH_30P	Odocoileus hemionus	1	10	5810969	589130	31	Aug-19
AF_ICH_30P	Odocoileus hemionus	12	10	5810969	589130	32	Oct-19
AF_ICH_30P	Odocoileus hemionus	2	10	5810969	589130	30	Jun-19
AF_ICH_30P	Alces alces	4	10	5810969	589130	32	May-19
AF_ICH_30P	Alces alces	3	10	5810969	589130	30	Jun-19
AF_ICH_30P	Odocoileus hemionus	1	10	5810969	589130	32	May-19
AF_ICH_30P	Ursus americanus	1	10	5810969	589130	31	Jul-19
AF_ICH_30P	Tamiasciurus hudsonicus	1	10	5810969	589130	32	Oct-19
AF_ICH_30P	Alces alces	1	10	5810969	589130	32	Oct-19
AF_ICH_30P	Alces alces	3	10	5810969	589130	30	Sep-19
AF_ICH_30P	Odocoileus hemionus	1	10	5810969	589130	31	Jul-19
AF_ICH_30P	Ursus americanus	1	10	5810969	589130	30	Jun-19
AF_ICH_30P	Puma concolor	1	10	5810969	589130	30	Apr-19

Table 3.3: Description of covariates included in GLMMs for large mammal analysis. This includes only the environmental variables that were not autocorrelated or dependent on climatic location rather than harvesting intensity treatment.

Variable	Description
Treatment	Forest harvesting intensity treatments (CC = clearcut, SEED = seed tree retention, 30% or 30P = 30% partial retention, 60% or 60P = 60% patch retention, CON = control unharvested forest) – fixed effect
Streams	Distance to the nearest stream from the camera point – fixed effect
NDVI	Monthly NDVI value for each treatment unit – fixed effect
Location	Latitudinal location (3: JPRF, Alex Fraser, Jaffray) – random effect except in candidate model LO (fixed effect)
Deployment.Location.ID	Camera ID (i.e., each treatment unit) – 45

Table 3.4: Candidate GLMMs for individual species and species groupings across the three project sites in interior BC with capture rate as the response term.

Model	Variables included	Fixed/Random
Null (N)	Camera ID	Random
Harvest Only (HO)	Forest Harvest Treatment (TRT)	TRT = Fixed
Location Only (LO)	Location (L)	L = Fixed
Experimental Design (ED)	TRT + Camera ID	Camera = Random
Environmental Variables	TRT + Streams + NDVI + Camera ID	Streams, NDVI =
(ENVR)		Fixed
NDVI	NDVI + Camera ID	
All Variables (TOTAL)	TRT + Streams + NDVI + Camera ID	

3.3.8 Does variation in forest harvesting intensity influence mammal behaviour?

Burton et al. (2015) defined relative abundance as a metric used in camera trap surveys to compare detections across some factor of interest (sites, species, surveys, etc.). They noted that relative abundance often depends on an assumption of equal detectability across the factor(s) being assessed, and that many studies do not test this assumption or consider underlying mechanism that may affect detectability. Camera traps are being used to determine site occupancy and usage, and occasionally, behaviour of different species in human-affected environments (Stewart et al., 2016), though elucidating and applying behavioural data from camera traps is a relatively novel concept and has begun to grow with the proliferation of camera traps (Caravaggi et al., 2017). As well, measures of behaviour are not immune to issues of detectability in camera trapping (Burton et al., 2015). While VHF or GPS collars and direct observations in the field have been used for longer to examine focal species behaviour, they have some significant disadvantages, including the impacts of human handling during collaring, technological failures, and the limitations of single-species data collection (Caravaggi et al., 2017). Camera trap surveys can be used to look at behaviour for many species and are noninvasive. By also analyzing behaviour, I am able to also explain some of this underlying biological reasoning.

I am using behaviour to ask whether harvesting intensity treatment affects whether animals linger within or move quickly through habitat. To determine if species behaviour was influenced by forest harvesting intensity, I examined the likelihood of a species demonstrating a 'travelling' or 'non-travelling' behaviour in a given treatment, using binomial generalized linear models. 'Travelling' behaviour was defined as travelling in a directional movement through the camera field of view, with no other behaviours demonstrated. When animals did not move directionally through the field of view, I classified detections as demonstrating one of the

following behaviours: foraging (animal eating), inspecting the camera, bedding down, or interactions between individuals (e.g., suckling, rutting). For example, if an individual was crossing the camera field of view, but then began to forage or inspect the camera, the behaviour is defined by the non-travelling one being demonstrated. For the purposes of the behavioural analysis, I assume that non-traveling behaviours are more associated with 'security' or a lower perception of 'risk' (as the animals are spending more time in front of the camera to demonstrate these activities), while traveling (less time in front of camera) could be indicative of 'risk'.

For the purpose of analysis, I simplified the "non-travelling" behaviours into a single category and used binomial generalized linear models in the *glm()* function in R to determine if there was a statistically significant difference in the prevalence of a behavioural category by forest harvest treatment. I ran a binomial model for the four focal ungulate species to evaluate the importance of treatments with canopy cover for behaviour. All independent detections of an ungulate species were used in the model for that species. The glm was built with the behaviour type as the response variable (binomial model because there is only a 0 or 1 response of 'travelling'). The sampling unit was the detection event (using the 5-minute threshold described above), and the event was classified as 0 or 1 based on the model input of type of behaviour. Treatment type (canopy cover) is the predictor variable. There were 129 moose events, 577 elk events, 3834 white-tailed deer events and 551 mule deer events.

3.4 Results

<u>3.4.1 Detection summary</u>

We detected a total of 24 wild mammal species across the 45 camera traps at Jaffray, Alex Fraser and JPRF sites between December 2018 and July 2020 (Table 3; Figure 3), as well as cattle, domestic cats, humans, and a wide variety of bird species. Our total sampling effort was 16 746 camera-days, with a mean of 390.9 camera-days between the locations (minimum = 55 days; maximum = 530 days). At Jaffray, the average camera effort was 482 days, followed by 406 days at Alex Fraser, and 229 days at JPRF.

The species pool I recorded at Jaffray included nine wild mammal species: coyote, wolf, elk, marten, bobcat, mule deer, white-tailed deer, cougar, and red squirrel. White-tailed deer was the most captured species (Table 3.4).

I recorded 13 large wild mammal species at Alex Fraser: moose, coyote, wolf, snowshoe hare, lynx, marten, striped skunk, mule deer, white-tailed deer, cougar, black bear, grizzly bear and red fox. Mule deer was the most captured species (Table 3.4).

I recorded 13 wild species at JPRF: moose, coyote, wolf, elk, wolverine, snowshoe hare, marten, short-tailed weasel, least weasel, mule deer, white-tailed deer, black bear and grizzly bear. Black bears were the most captured large-bodied mammal (though red squirrels were captured most overall, Table 3.4).

Across all sites, four wild large ungulate species had the highest capture rates of any species over the entire sampling period and all sites: white-tailed deer, mule deer, elk and moose.

Table 3.5: Total independent detections of each of 24 terrestrial mammal species at the three project sites in British Columbia. *Dakelh* names are from the Carrier Linguistic Society. These names are only listed for species that were captured at JPRF, as that is the site upon the territories of *Dakelh*-speaking peoples. The bottom row of the table is the total species count at each site (total number of species detected).

Latin Name	Common Name	Dakelh name	Jaffray	AFRF	JPRF
			Count	Count	Count
Odocoileus	White-tailed deer		3537	293	4
virginianus					
Odocoileus	Mule deer	yests'e	2	545	4
hemionus					
Cervus canadensis	Elk	yazi	561	-	16
Canis latrans	Coyote		53	2	7
Canis lupus	Wolf	yus	6	9	6
Puma concolor	Cougar		8	2	-
Lynx rufus	Bobcat		1	-	-
Martes americana	Marten	chunih	1	7	2
Alces alces	Moose	duni	-	90	39
Ursus americanus	Black bear	sus	-	21	47
Vulpes vulpes	Fox		-	12	-
Lepus americanus	Snowshoe hare		-	4	6
Ursus arctos	Grizzly bear	shas	-	2	3
Lynx canadensis	Lynx		-	1	-
Mephitis mephitis	Striped skunk		-	1	-
Gulo gulo	Wolverine		-	-	1
Mustela erminea	Short-tailed	nohbai	-	-	1
	weasel				
Mustela nivalis	Least weasel	nohbai	-	-	2
TOTAL SPECIES I	DETECTED (SPECIE	ES RICHNESS)	8	13	13



Figure 3.1: Example camera trap photographs of wildlife across the treatment gradient at all sites in interior British Columbia, Canada. a) Grizzly bear (shas) – clearcut (John Prince); b) elk (yazi) – seed tree treatment (Jaffray); c) white-tailed deer (yests'e) – 60% thinning treatment (Jaffray); d) moose mother and twins ('uma & tsiye) – 30% patch (Alex Fraser); e) black bear (sus) – control forest (John Prince); f) wolverine (noostel) – 30% patch (John Prince). Dakelh names (those in brackets) learned through the Carrier Linguistic Society workbook *Dakelh Animal, Bird, Fish and Insect Terms.* Photos from the camera traps.





Figure 3.2: Example camera trap photographs of the behavioural categories demonstrated by elk (yazi) across the treatment gradient at Jaffray, British Columbia, Canada. a) Foraging, b) Travelling, c) Bedded down, d) fighting (and/or ballroom dancing), e) inspecting camera. Photos from the camera traps.

3.4.2 How does forest retention interact with location to alter mammal diversity at the community-level?

There was no statistical difference in community-level diversity between the different forest harvesting treatments, but latitudinal location had a significant effect on the diversity values (Table 3.6). Diversity at Alex Fraser Research Forest was significantly greater than at Jaffray, with John Prince in between (estimate = -0.62, SE = 0.14, p < 0.0001). For Alex Fraser, the lowest and highest values occurred in the clearcut and seed tree treatments, respectively. For Jaffray, diversity values spanned from 0.25 to 0.77 with no trends among harvesting treatments, and number of species detected ranged from six to nine. And finally, for John Prince, the highest values were in the seed tree treatment, and the lowest in the partial retention treatments. Across all three locations, the highest Shannon diversity values in the seed tree and 30% retention treatments (Fig. 3.2). There was no significant difference in average diversity among harvesting treatments – average diversity indices are nearly all identical, between 0.6 - 0.85.

Table 3.6: Summary of linear models run to examine the effects of treatment and location on Shannon diversity index values. Model = the variables examined. df = degrees of freedom. Δ AIC (Aikake Information Criterion) is the difference in AIC from the lowest model. wt is the AIC weight attributed to the model. Normally, only AIC within two points of the best model would be included, but it is important to note that the location has a significant effect on diversity while treatment does not.

Model	Predictor Variables	df	AIC	∆AIC	wt
Location Only	Location	4	47.89	0	0.93
Experimental Design	Treatment + Location	8	53.11	5.22	0.068
Null	None	2	61.13	13.24	0.001
Harvesting and Location	Treatment x Location interaction	16	63.64	15.75	0
Harvesting Gradient Only	Treatment	6	67.25	19.36	0



Figure 3.3: Average Shannon diversity values across all sites in interior BC. Diversity values span from 0 to 1.6. Sites are distinguished by colour of dots, and average value, regardless of location is the black line.

3.4.3 Are the responses to forest retention practises species/group specific?

This analysis is based on the GLMMs with candidate models built on the project experimental design, with NDVI and streams as environmental covariates. For none of the individual large mammal species (moose, elk, white-tailed deer or mule deer) was harvesting treatment in the 'best' model (i.e., lowest AIC). NDVI (fixed effect) with location and camera (as nested random variables) was the selected model for elk and white-tailed deer (p-value 0.003 and effectively zero, respectively; Tables 3.7). The "total ungulates" and "generalist" models, which included the four above species, had NDVI alone as the top model, likely driven by whitetailed deer and elk. To examine the effects of the variables, I built a full model with all variables and plotted their coefficients (Fig. 3.3). The importance of random effects in each top model varied across the ungulate species: for white-tailed deer, random camera effect was 0.22 and location was 0.31 and for elk, random camera effect was 0.11 and location was 8.2×10^{-10} . For moose and mule deer, the top models were null. For the total ungulate group, random camera effect was 0.06 and location was 0.13. For generalists, random camera effect was 0.1 and location was 0.26.



Figure 3.4: Estimated effects of forest harvesting treatments and environmental factors (NDVI and distance to nearest stream) on independent detections of four focal ungulate species in interior BC. Estimates are from generalized linear mixed models for each species, using detections from December 2018 – July 2020 at 45 camera traps. Estimates are presented as mean and standard error.

Table 3.7: **Top three candidate model results for target large mammal species and species groups**. The top model is bolded in each species/group category. The top model indicates which set of tested covariates influenced the monthly capture rate of each species/species group. Candidate model details for each species/species group. Candidate models are described in Table 3.4, Df = the number degrees of freedom.

Candidate Model	Df	AIC	Candidate Model	Ki	AIC
Generalist Species			Moose		
NDVI	5	2464.15	Null	4	220.31
NDVI + Streams	6	2466.13	Location	4	220.31
NDVI + Streams + Treatment	10	2466.51	Treatment	6	221.9
Total Ungulates			White-tailed Deer		
NDVI	5	3770.92	NDVI	5	1946.16
NDVI + Streams	6	3771.01	NDVI + Streams	6	1948.16
NDVI + Streams + Treatment	10	3778.78	NDVI + Streams + Treatment	10	1953.75
Elk			Mule Deer		
NDVI	5	708.94	Null	4	587.45
NDVI + Streams	6	710.91	Location	4	587.45
Treatment	6	715.14	Treatment	6	589.19

I also captured images of twelve elusive mesocarnivore and apex carnivore species, at all harvesting treatments and across the entire climatic range. In these cases, a species was not captured frequently enough by the camera traps to have a robust dataset for an individual species model, and therefore I have included the types of treatments the species was captured in (Table 3.8). These rare or elusive species are incorporated into the diversity analysis (Fig. 3.3), but not GLMMs (Tables 3.7, 3.8). Alex Fraser and JPRF each had seven of the elusive species, while Jaffray had four (Table 3.8). The number of captures in each of the treatments was nearly identical (five captures in 30%, CC, SEED, CON and four in 60%).

Table 3.8: Details of independent captures of elusive mammal species. Includes the locations where and treatments in which they were captured. Names in brackets are *Dakelh* animal names from the Carrier Linguistic Society. These names are only listed for species that were captured at JPRF, as that is the site upon the territories of *Dakelh*-speaking peoples.

Elusive Species	Number of	Treatment(s)	Location(s)
	Captures		
Gulo gulo (noostel)	1	30%	JPRF
Mephitis mephitis	1	SEED	AFRF
Lynx canadensis (wasi)	1	SEED	AFRF
Lynx rufus	1	CC	JAFF
Mustela erminea (nohbai)	1	30%	JPRF
Mustela frenata (nohbai)	1	CON	JPRF
Mustela nivalis (nohbai)	1	30%	JPRF
Ursus arctos (shas)	5	CC, 60%, CON	AFRF, JPRF
Puma concolor	10	30%, 60%, CON	JAFF, AFRF
Martes americana (chunih)	10	All	JAFF, AFRF, JPRF
Vulpes vulpes (nanguz)	12	CC, SEED	AFRF
<i>Canis lupus</i> (yus)	21	CC, SEED, 60%, CON	JAFF, AFRF, JPRF

3.4.4 Does variation in forest retention practises influence ungulate behaviour?

To further parse if there was a difference in response of ungulates to harvesting treatments, I looked at the behaviours of the focal species, as most of these models were not indicating preference of a particular treatment simply by usage. Moose demonstrated significantly fewer non-travelling behaviours in open canopy treatments (p = 0.0068). Out of 27 behavioural events classified in clearcuts and 19 in the seed tree treatment, only three were of non-travelling behaviours, whereas there were 10 in the control treatment alone. The majority of moose non-travelling behaviours were in covered treatments. White-tailed deer demonstrated significantly more non-travelling behaviours in the partial retention treatments than control forest (p < 0.001). Elk and mule deer did not demonstrate any significant differences in the travelling or non-travelling behaviours under different amounts of canopy cover.

Table 3.9. Binomial generalized linear model results for ungulate demonstration of travelling or non-travelling behaviours. Treatments are merged into partial canopy, open canopy or full control forest (reference level for this model). Travelling was 0 and non-travelling was 1 in the binomial model. Negative coefficients mean more traveling relative to control forest.

Treatment Type	Estimate	Std. Error	P-Value
Moose			
Open Canopy	-1.92	0.71	0.0068 **
Partial Canopy	0.35	0.48	0.46
Elk			
Open Canopy	0.15	0.27	0.55
Partial Canopy	-0.05	0.29	0.85
White-tailed deer			
Open Canopy	0.08	0.09	0.36
Partial Canopy	0.29	0.09	0.0008**
Mule deer			
Open Canopy	0.16	0.25	0.51
Partial Canopy	-0.13	0.27	0.65



Figure 3.5: Bar charts showing the different activities demonstrated by four focal ungulate species (moose, elk, white-tailed deer and mule deer) in each forest harvesting treatment, including data from all three project sites. The "other" category includes any non-travelling behaviour that could not be categorized as foraging or inspecting the camera (i.e., interactions between individuals, like mating pursuit, or bedding down).

3.5 Discussion

Location significantly affected large mammal community diversity, which I assume to be related in part to variation in climate conditions. Forest harvesting intensity had no effect on diversity or habitat use at the scale of this study. Moose demonstrated behaviours that were significantly different between open and closed canopy cover.

3.5.1 Forest harvest intensity a weak predictor of mammal community diversity

The latitudinal gradient had more of an effect on the diversity of the large mammal community than the harvesting treatments. This is likely due to inherent differences in the large mammal communities among climatic locations. Moreover, the 4-5 ha spatial extent of the harvesting treatments were likely too small to detect differences in community-level diversity – this limitation is explored further below in section 3.5.5.

Though some large mammal species (e.g., cougar) demonstrated trends of more use of the closed-canopy than open-canopy treatments, this difference was not statistically detectable at the fine scale of these treatments for the whole community. What was illuminated in this analysis was the strong effect of climatic region on species diversity. Here, Jaffray, the most southern and arid site, had significantly lower large mammal diversity values than Alex Fraser Research Forest. Jaffray also had a much lower diversity of tree species in the forest than Alex Fraser (Simard et al., 2020). Another major difference between these two sites is the type of tenure they are under – Alex Fraser is a research forest, which is not logged commercially or to make more money than is needed to sustain the research and educational activities at the site, whereas the Jaffray site is in the Cranbrook Timber Supply Area under Canfor license.

3.5.2 Are the responses to forest retention practises species/group specific?

Forest harvesting intensity (treatment) was not the top AIC-selected model of habitat use for any individual ungulate species or species groups. Rather, NDVI was the predictor variable that could explain more of the independent detections of elk and white-tailed deer than any other single variable. The vast majority of independent detections in the ungulate and generalist groups are of white-tailed deer, by an order of magnitude (Table 3.5). NDVI and harvesting treatment are different measurements of the living forest but are certainly interrelated. NDVI is a measure of 'greenness' or the density of green on the landscape (Weier & Herring, 2011), but it cannot be used to distinguish between tree canopy greenness and shrub-layer greenness. Treatment was an experimental variable that directly manipulated the forest canopy, and therefore, the amount of sunlight reaching the forest floor. These two variables are unique; however, they are related. The treatment variable is coarser (it is categorical, with five levels) and NDVI is much finer-scale (as a continuous variable). NDVI, through this finer scale, may capture more variation than is reflected in the treatments.

Our models suggest that the detection of elk and white-tailed deer are both driven by the availability of forage (seen through NDVI as an index of vegetation productivity), but these two species demonstrated usage of opposite treatments (Fig. 3.3). Elk showed significantly higher usage of the clearcuts, while white-tailed deer showed highest usage of control forests. Both of these species were captured mostly at Jaffray (92% and 97% of detections of white-tailed deer and elk, respectively; Table 3.5). This opposite usage of treatments could be related to the interspecies interactions and their preferred forage types.

Elk forage predominantly upon low-growing sedges, grasses and ferns, which are difficult to access in winter months under snow (Wilmshurst et al., 1995). Elk are recognized as an opportunistic species, their migrating and foraging influenced by a variety of factors, but it is consistently noted that elk select habitat with "forage, escape, and cover resources" (Ministry of Environment, British Columbia). Elk are generally herd species, and there are noted instances of

elk demonstrating aggression towards, and even killing, deer species that are a perceived threat to their young or forage (Stephens et al., 2003). In winter, white-tailed deer have been shown to select sites where there is evergreen shrub ingrowth, even when they are sites that have little to no canopy interception of snow (Pauley et al., 1993). When snow is a 'manageable' depth (< 30cm), there seems to be no hindrance to white-tailed deer movement or foraging, however at peak winter, white-tailed deer select sites for cover instead of abundant forage (Pauley et al., 1993). It is possible that at Jaffray, where there is little precipitation, elk and white-tailed deer have slightly segregated in their use of the different treatments, based on different forage types (elk preferring grassy species, and deer preferring evergreen species) as well as elk aggression/herd activity.

For both mule deer and moose, the AIC-selected model was null (only random effects included). Hodder et al. (2013) found that there was very little overlap in the diets of mule deer, moose and elk in northern forests, similar to those in this project. Mule deer at the northern end of their range at JPRF, and to a lesser extent at AFRF, may be consuming the best available forage given the conditions, particularly in winter (Hodder et al., 2013). For mule deer, it is also worth noting that the Tl'azt'en Nation (those who co-manage JPRF) requested that there be no harvesting of Douglas fir in their territory, on the grounds that their territory is the most northern range of Douglas fir and that it provides key wintering grounds for deer (Nicholls, 2017). The Tl'azt'en Nation noted that where Douglas fir has been harvested, they had seen resident deer populations migrate away or disappear (Nicholls, 2017). However, MFLNRORD deemed that limiting the harvesting of mature Douglas fir on the territory of the Tl'azt'en people would have severe socio-economic impacts on the timber supply area and the research forest (Nicholls, 2017).

Moose have been shown to avoid new cutblocks and older forests, and instead select for regenerating blocks, where their preferred forage is growing (Mumma et al., 2021). Furthermore, Mumma et al. showed that the selection of regenerating cutblocks by moose was stronger in the Prince George area (between our JPRF and AFRF study sites) than further south in the province. This same trend has been shown in other areas as well: in northern Ontario, it was shown that moose prefer deciduous forage (often found in newly disturbed areas), yet they may strongly avoid very recent disturbances (Street et al., 2015). At the scale of this study, we were examining if moose would use or demonstrate particular behaviours in canopy-covered treatments more. It is likely that at this stage (only one year post-harvest) that moose are exclusively travelling through clearcuts because their preferred forage has not yet flourished (these stands are still in the new cutblock successional stage). There has been growing concern that clearcutting is negatively affecting moose populations in British Columbia, especially in the central interior (Gorley, 2016). However, we do not have any evidence that moose used any particular treatment significantly more than another in this study, or that NDVI drove their detections.

3.5.3 Elusive species

Over the course of data collection, twelve elusive species were captured by the camera traps. Overall, there was no distinctive trend in use of a particular harvesting treatment for elusive carnivores. There are a few species that did appear exclusively in the control and partial harvesting treatments and a few species that appeared mostly in the open-canopy treatments. Cougars and foxes tended to use the opposite spectrum of the harvesting treatments, recording some of the highest capture rates of the elusive group. Cougars were exclusively captured in covered treatments (control, 30% and 60%). This series of captures was consistent with the literature: cougars have varied responses to logging, depending on their life phase, the region of BC and how their main prey in the area are responding to forest harvesting (Wainwright et al.,

2010). In west-central Alberta, cougars avoided novel anthropogenic disturbances (particularly during the day) and became more tolerant of the disturbances as they became more common across the landscape (Knopff, Knopff, Boyce & St. Clair, 2014). In the Alberta study, cougars responded either positively or neutrally to edges, and avoided core forest and all anthropogenic features. Edge habitat is more plentiful in the patch harvesting and partial retention treatments in our study. Particularly at the Jaffray site in the Kootenays where there is less dense understory, there are more natural openings as well in the control forest.

Foxes were captured on camera traps only in the clearcut and seed tree treatments at Alex Fraser Research Forest. They are a generalist canid predator, mostly feeding on small mammals and some small mesocarnivores and forest birds, like grouse (Dell'Arte et al., 2007). Foxes appear to have diets that diverge from other mesocarnivores, to target different small mammal species for prey when logging intensity is increased (foxes and martens have similar diets without logging; Sidorovich et al., 2010). Additionally, red foxes have been greatly expanding their range into Canada's arctic, and it is suggested that they have been benefitting from habitat changes (Berteaux et al., 2015).

Wolves and coyotes were both frequent users of the open canopy harvesting treatments. For wolves, the behaviour documented in the captures in open-canopy treatments was exclusively travelling, and the longest wolf sequence captured was in a partial retention treatment, with eight individuals (potentially tussling to establish dominance). The literature and my hypotheses for wolves supported these findings (for example, ample studies show wolves using linear features and clearcuts: Dickie et al, 2016).

3.5.4 Behaviour influenced by forest harvesting treatments

When we consider the amount of cover present in an individual animal's microenvironment and bioenergetics of a given species (the energy balance and budget of an

individual when the temperature, radiation, food consumption, locomotion and life phase are considered), it often becomes clear that canopy cover is physically and energetically necessary for some life processes. The demonstrated behaviour by a species in front of a camera can indicate the individual's perceived risk, and further, spatial variation in these demonstrated behaviours could indicate the individual's perceived suitability of the habitat (Stewart et al., 2016). Over large scales, these changes to perceived suitability can influence distribution (Stewart et al., 2016).

With widespread logging over vast areas of ungulate habitat in the interior of BC, the necessary shelter from predators, hunters, the elements and for calf protection has diminished (Timmermann & McNicol, 1988). However, the use of cover for the purposes of security (rather than for temperature and condition amelioration) is not well understood. Of the four focal ungulate species, elk and mule deer showed no differences in types of behaviour demonstrated regardless of amount of canopy cover. Moose had the starkest behavioural response to canopy cover – with no non-travelling behaviours shown in the clearcut (no canopy) treatment. White-tailed deer demonstrated non-travelling behaviours significantly more in partial harvesting treatments than control forest. White-tailed deer have been noted, in the context of clearcut forest harvesting, to prefer the edge areas of cutblocks, and that use of clearcuts decreased significantly past 100 metres from the edge of the forest (Tomm et al., 1981). This demonstration of more non-travelling behaviours in the partial harvesting treatments aligns with our hypothesis for white-tailed deer taking advantage of a mixture of open and closed canopy areas, and preference for smaller harvested areas.

The moose response may be a reflection of preferred forage rather than perceived risk. Courtois et al. (2002) note in their study that moose selected habitat with mixed and/or

coniferous stands for most of the year and avoided clearcuts except for early winter, particularly at the fine scale, but with an important distinction: this preference was noted 7-11 years after harvest. Immediately after forest harvesting, the ingrowth of species are typically small herbaceous plants and grass – the preferred diet of elk, but not moose. This study provides some insight into some of the biological reasoning for habitat usage, based on the behaviours that the individual ungulates are demonstrating.

3.5.5 Considerations and improvements

The main limitation of these analyses is the stark difference between the size of the harvesting treatments and the size of large mammal home ranges. For example, the average treatment size was four hectares, but the average home range size of a moose can be up to 800 square kilometres for a migratory male adult (DeMarchi, 2003). This disparity between the scale of the project and the scale of a mammal's movements also made using certain variables in the modelling process unrealistic. Though there is a wealth of literature describing the significant effects of roads on ungulates and carnivores (Proctor et al., 2020; Parsons et al., 2020), at each location, the same singular or same two road(s) were the only features to which distance could be measured, with minor differences between them, rendering the variable ineffective. The same situation applied to wetlands and lakes. At such a small scale, choosing appropriate environmental variables was critical to not overreaching conclusions. For future research into the responses of the large mammal community to forest harvesting, the treatment unit sizes will need to reflect the amount of ground any of these species can cover over days, weeks, months. This research presents a valuable fine-scale perspective on site usage but cannot be used to make inferences on preference or avoidance of any habitat type. Future research must link fine-scale habitat and behaviours to individual fitness and larger population demographic responses.

3.5.6 Recommendations for management and future research

This chapter is relevant for forest managers and local communities to understand site usage of large fauna in a working natural resource landscape. Regulators and forest managers must be aware of wildlife inhabiting the areas where operations occur for many reasons, including the safety of workers and animals, mandates to maintain wildlife patches in harvesting landscapes, for endangered or vulnerable species, and for regionally important species. The following recommendations are those I would make when considering the data presented here, as well as the literature:

- Patch or partial retention harvest provided habitat for some species (moose and whitetailed deer) to demonstrate non-travelling behaviours. This study could be scaled up to, for example, the size of a moose home range to determine if the effect on behaviour and time spent in the covered treatments is the same.
- Additionally, further hypotheses linking mammal diversity to forest diversity indices could be tested, (like tree species richness, understorey plant diversity, heterogeneity of surrounding habitat), including hypotheses based on functional linkages (e.g., herbivory, seed predation or dispersal). Testing how wildlife are in turn, affecting the plant associations and vegetation in their habitat is also an important aspect to examine in future work. In the context of forestry, research into the diet types and browsing habits of herbivores would be important to determine the success of planting efforts and how ungulates interact with management.
- GIS and LANDSAT research has been growing exponentially in recent years, including that which focuses on land-use change and natural disturbances in British Columbia and northern forests (Pickell et al., 2015; Arnett et al., 2014; Erickson, 2017). However, the Forest Practices Board report that identifies biodiversity targets being sub-par, given the

context of mountain pine beetle and salvage logging, brings to light the necessity of stronger minimum retention targets and biodiversity requirements (Forest Practices Board, 2020). I believe that larger scale, remote sensing analyses of the quality of harvesting targets from the perspective of wildlife habitat are needed and must be linked to larger-scale assessments of the wildlife themselves.

- Additionally, when considering the other abiotic, biotic and anthropogenic effects
 occurring in interior BC forests, and the landscape homogenization through logging and
 fire, my results suggest the importance of leaving patches of forest for animals seeking
 refuge. The positive associations with canopy cover for moose and elusive species can
 inform forest management decisions to better maintain habitat that supports specialist
 species.
- Managers and biologists working within the framework of forestry should not exclusively be managing for species that can broadly use many types of habitat and have generalist diets. Forest management should also consider species who could become energetically stressed or have decreased fitness based on negative alterations to their habitat.

3.6 Conclusions

Understanding responses of the larger mammal community, and of species groups and individual species, to forest harvesting disturbances empowers more informed decision-making regarding forest retention on logging landscapes. In this chapter, I showed that at the largest scale, the gradient of forest harvesting treatments did not have significant effects on the mammal community, but that the locations did have a strong effect on the richness and diversity of the community. I also showed that NDVI was more strongly linked to habitat use by elk and whitetailed deer than was harvest treatment. Finally, I showed that at the finest scale, forest harvest treatments may influence the behaviour of some species. The results of this study highlight the importance of fine-scale research in assessing the effects of forest harvest on habitat use and behaviour of a range of mammal species, including forest specialists. The conclusions of this chapter suggest that increased retention (at least a partial canopy cover) will support a variety of species, including specialist species and their range of behaviours.

Chapter 4: Preservation of wildlife habitat on a logging landscape

4.1 Synthesis and Conclusions

Human resource-extraction industries are impacting biodiversity and species habitat globally (Katzner et al., 2020). While some species show positive responses to these widespread changes to the environment, like range-expanding generalists and predators that take advantage of human tracks and linear features (roads, seismic lines, cutblock edges; Dickie et al., 2016), there are many other species that have unknown or documented negative responses to clearcuts. In BC, clearcut logging is one of the most widespread and prolific anthropogenic effects on forest environments and the wildlife that live within them (Shackelford et al., 2018). Vast clearcut logging alters wildlife habitat and biodiversity, habitat selection and inter-species dynamics of the entire mammal community (Thorn et al., 2017; Schleuning et al., 2011). Mitigation of logging impacts on habitat are crucial in the face of changes occurring to forests, as fires, pest outbreaks and climate change cause further disruptions to safe habitat, plant associations and temporal relationships between vegetation and animals (Daniels et al., 2011; Mills et al., 2013 – e.g., snowshoe hare fur colour change out of sync with their environment). There is more literature describing the responses of both small and large mammals to fires or clearcut logging, but significantly less demonstrating the response of the whole community of mammals to the potential logging mitigation tools we have available – specifically, partial harvesting. In BC, partial harvesting is not applied frequently (clearcutting and variations of clearcutting make up 92% of harvesting; Beese et al., 2019), but these methods can be used to mitigate negative implications to biodiversity, and they combine ecological and economic goals in managed landscapes (Fuller et al., 2004; McComb et al., 1993).

My thesis used a combination of live trapping mark-recapture and camera trap data to determine if the mammal community would respond positively to partial harvesting methods in

comparison to control forests and full canopy removal. Across both data sets I was able to examine diversity metrics of the small and large mammal communities and investigate density and habitat usage (small mammals) as well as species'/species' group responses to the harvesting gradient and behaviour (large mammals). This work provides insight into whether partial harvesting methods provide enough canopy cover to support more diverse small mammal populations, and/or facilitate non-travelling behaviours by large mammals on a fine scale. I assessed the local value of partial retention across BC's interior forests, to determine how improvements could be made to the preservation of wildlife habitat on a logging-heavy landscape.

In Chapter 2, I examined the effects of a gradient of forest harvesting methods on the small mammal community in an understudied area: northern BC. John Prince Research Forest (JPRF) (in the sub-boreal spruce zone of northern BC) is an area where no small mammal trapping data had been collected previously. In the field, I used live trapping and mark-recapture, and analytically I used spatially explicit capture re-capture, metrics of habitat usage and diversity indices to determine individual species and community responses to different forest harvest methods. I found that generally, partial harvesting was providing habitat that supported a small mammal community just as diverse as the intact forest (and more so than clearcut harvesting). Declines in small mammal diversity with increased levels of forest harvesting can inform better forest management for wildlife conservation and habitat preservation by maintaining variable retention or patches. For some species, like red squirrels and southern red-backed vole, there was notable benefit to maintaining at least partial cover in forest harvesting blocks. These results provide retention targets that have been tested and will encourage operators to re-evaluate their best practices for wildlife reserves in clearcuts, or to more frequently practise harvesting methods.

that have been demonstrated to support a robust and diverse mammal community. Actions taken by operators and policymakers to use science to inform best harvesting practices for wildlife will increase the resilience of BC's forests. By mitigating the negative effects of complete canopy removal, higher diversity and healthy populations of a wider variety of small mammal species can be supported, which will in turn support mesocarnivores, raptors and the vegetative community (Sullivan et al., 2017; Cheveau et al., 2004; Moorhead et al., 2017).

In Chapter 3, I increased my scope by expanding my study to a 900-kilometre latitudinal gradient, as well as the forest harvesting treatment gradient (Simard et al., 2020). Across these factors, I examined large mammal responses using camera trapping, to examine community diversity in the different sites and treatments as well as species' habitat usage, and behaviours. I found that that climatic region was an important determinant of diversity. In contrast, forest harvesting did not have a significant effect on treatment usage, but some species such as moose preferred treatments with greater canopy cover.

The latitudinal gradient between my sites, from the east Kootenays to the Nechako, had more of an effect on large mammal community diversity than forest harvesting treatment. However, when I delved into individual species' responses, more interesting nuance was uncovered. For example, moose displayed more non-travelling behaviours and some elusive species (e.g., cougar) were captured only in treatments with full or partial canopy cover. The positive associations between moose and elusive species with canopy cover can inform forest management decisions to better maintain habitat that allows for a more diverse community of large mammals. Understanding the community, species group, and individual animal responses to logging disturbances in their environment empowers more informed decision-making regarding forest retention on logging landscapes. The results of this study highlight the

importance of fine-scale research, as well as the impacts of forest harvesting on specialist mammals. I suggest that maintenance of adequate canopy cover is necessary to maintain balance between wildlife habitat and forest harvest on this working landscape.

4.2 Research strengths and limitations

This study can be the base of a long-term study to determine how the mammal community responds to these partial harvesting methods. We discussed earlier how partial harvesting is a less frequently implemented forest management strategy – frequency of use has been slowly increasing since its inception. As it is a true replicated experimental design, the study can be expanded to include other sites of the MTP in different BEC zones and a site on the coast, to have small scale cross-province sites that can be compared. This project also further informs the possibilities and importance of using behavioural data from camera trap detections (Caravaggi et al., 2017; Beirne et al. in prep).

This study also included the first small mammal trapping session undertaken at JPRF (a great first step in more long-term monitoring of this important part of the food web), but the dataset that we did sample was too sparse to support SECR estimates at the treatment-unit level. This limited amount of data did lead towards merging the replicates to have robust datasets – which requires more assumptions regarding small mammal distances traveled and the independence of the treatment units.

The main limitation this project that affected inferences about large mammal responses was the fine scale of the harvesting blocks – they cannot be scaled up to large scale size of common commercial forest harvesting, and we cannot reasonably examine species habitat selection at higher orders of selection (e.g., home range). There is a stark difference between the size of the harvesting treatments and the size of large mammal home ranges. For future research into the responses of the large mammal community to forest harvesting, the treatment unit sizes will need

to reflect the amount of ground any of these species can cover over days, weeks, or months. This doesn't mean that this research was not valuable, as small scales are important, but we cannot indicate any avoidance or preference of a treatment as selected habitat, based on their size. Future work at one climatic location could treat the entire series of replicates as partial harvesting (as the overall canopy is a mixture of harvested and intact) and compare it to the surrounding larger scale clearcuts and intact forests. Jaffray would be a particularly interesting location to re-examine the experimental design and mammal responses, as it is part of the Cranbrook Timber Supply Area, not a research forest. The objectives of these two types of sites differ significantly – timber supply areas are intended to do exactly that, while research forest have combined experimental, harvesting, educational, habitat and community values. Harvesting follows the status quo commercial harvesting of the province.

4.3 Applications and Future Work

This thesis helped to identify the fine-scale responses of wildlife to forest harvesting methods other than the clearcut status quo, but there are three further directions that this research could be taken: 1) large scale analysis of the intended versus implemented retention in logging areas, 2) interdisciplinary research across habitat and wildlife fields to examine the threats to habitat quality and quantity through multiple expert lenses, and 3) further expansion of the themes presented in this thesis with specific objectives outlined by the First Nations upon whose territories the project is undertaken.

The first important area of further investigation would be to conduct a large-scale geographic information systems (GIS) study to examine if the provincial retention targets in harvesting areas are being met, how frequently they are being implemented, and if they are in forest that is representative of the habitat being used by the mammal community (not relegated to a steep cliff section that was deemed "wildlife patch" simply because it is more difficult to log).
There is a great deal of remote sensing research that has already been undertaken examining the intensity of disturbance in boreal forests, rapid identification of new disturbances, and simulating natural disturbances and conditions that create suitable habitat for species under significant anthropogenic stressors (Pickell et al., 2015; Arnett et al., 2014; Erickson, 2017), however I have not yet seen peer-reviewed research that examines if at a landscape scale, objectives for quality and quantity of wildlife habitat retention are being met. This type of GIS analysis would be well-complemented by a camera trap sampling design to determine if the areas with more/less adherence to habitat quality measures are successfully capturing more species (either in diversity or density). A power analysis would be crucial before commencing a survey like this to ensure the sampling design would have sufficient statistical power to detect the desired effects. I strongly recommend that further work in the area of forest harvesting impacts on wildlife investigate the true size, frequency and location of wildlife reserve patches.

Additionally, it is important to foster communication and collaboration between researchers working with all aspects of habitat management and disturbance. More anthropogenic influence on wildlife is through indirect interactions (through habitat disturbance – fire, logging, oil/gas, suburban or urban expansion) rather than direct manipulation to a wildlife population (the exceptions being hunting/trapping and culls). For example, the findings in Leclerc et al. (2021) would be a fascinating project to expand with wildlife sampling using camera and/or live trapping to further inform these landscape level habitat schemes. They discuss the complex and interrelated nature of abiotic and biotic disturbances and how they interact with forest management activities to provide suitable mule deer winter range. As well, the authors highlight that failure to acknowledge complexity of ecosystems leads to the failure of management objectives, including forest harvesting.

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Our final recommended area of future research is to further develop specific communitydriven questions around moose and deer with Williams Lake Nation. Members of the community on multiple occasions in the field, during community meetings and on video calls (during COVID-19) have voiced their concern around the influx of white-tailed deer to their territory. This concern is focused on three aspects: 1) potential inter-breeding with mule deer – specifically, the potential decreased fitness and winter hardiness of mule deer if their genetics are "weakened" by hybridization with white-tailed deer; 2) if not breeding, displacement of mule deer by white-tailed deer with continuing range expansion; and 3) human industry and associated impacts altering the environment to increase competition between the species for forage or negatively impacting mule deer habitat (Hewitt, Sandy, Lulua Sandy – personal comm.). During this project, we have documented a few instances of mixed-species deer groups on CTs.

In the introduction, we briefly addressed the methodology, intent and background of Two-Eyed Seeing, focused on Reid's (2020) and Bartletts's (2012) papers. The impact of forest harvesting on wildlife, of any size or area of the province, is on the traditional territories of many First Nations. As collaborators and conservation scientists, we uphold the responsibility to adequately share and proliferate the knowledge gained from projects like this. We believe that there is immense potential for expansion to address these ungulate-specific questions in the framework of Two-Eyed Seeing. Wong et al. (2020) published a paper highlighting the blatant disregard for First Nations' rights and abuse of collaboration from natural scientists, as well as a framework of ten calls to action for natural scientists, to continue to push the status quo in science towards reconciliation. I therefore recommend that future studies heed those calls for action and pursue a more transparent and collaborative approach to wildlife research with First Nations. This thesis has provided the baseline and starting steps to inform further questions in

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many of these future research areas and has contributed as small piece to collective understanding of how humans and wildlife share managed landscapes.

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Appendix



A.1 SECR conducted at the treatment unit level

A.1.1. *P. maniculatus* densities in June (6a) and August (6b) across all treatments and replicates. Plots with no density displayed had unreasonable estimates greater than 50, and confidence intervals that did not overlap.



A.1.2. *M. gapperi* densities in June (10a) and August (10b) across all treatments and replicates. Plots with no density displayed had unreasonable estimates greater than 50 and confidence intervals that did not overlap a reasonable estimate, or no captures at all.

Table A.1.1: Table showing the number of detections, number of unique animals, densities (mice per hectare), standard errors and confidence intervals of *P. maniculatus* derived from spatially explicit capture-recapture models. Density estimates range from 0.54 to 1389753637 mice/ha. These models did not have data merged across replicates, which meant that each model was being run with a smaller amount of capture and recapture data.

Session	Model	Detections	# Animals	Density (D)	D_SE	D_lcl	D_ucl
	R1_CC	15	8	3.905	1.744	1.693	9.008
	R1_Seed	13	6	2.183	1.458	0.664	7.178
	R1_Con	3	2	4.062	10.605	0.244	67.504
	R1_30P	9	4	2.371	1.389	0.817	6.877
	R1_60P	12	4	0.54	0.288	0.202	1.439
	R2_CC	18	10	5.345	2.426	2.289	12.482
	R2_Seed	17	10	8.279	3.242	3.949	17.357
	R2_Con	5	4	402.592	378.683	84.569	1916.537
	R2_30P	10	5	0.786	0.382	0.319	1.936
	R2_60P	4	4	799629.134	NA	NA	NA
	R3_CC	24	13	10.393	3.367	5.595	19.304
	R3_Seed	10	8	8.224	7.8	1.711	39.527
	R3_Con	16	11	8.676	4.666	3.231	23.298
	R3_30P	13	10	9.155	5.367	3.155	26.565
June	R3_60P	4	4	5486914.31	9053044.36	580059.095	51902002.6
August	R1_CC	9	7	37.529	121.412	1.758	801.357
	R1_SEED	2	2	36323875.3	23668683.7	11319597.5	116561028
	R1_CON	6	5	31.307	8020.657	0.046	21405.37
	R1_30P	1	1	1389753637	1779007498	201599686	9580447315
	R1_60P	6	5	54.963	161.604	2.875	1050.821
	R2_CC	10	7	60.924	66.061	10.822	342.989
	R2_SEED	17	10	8.279	3.242	3.949	17.357
	R2_CON	5	4	402.592	378.683	84.569	1916.537
	R2_30P	14	11	5.611	2.861	2.187	14.395
	R2_60P	4	4	799629.134	NA	NA	NA
	R3_CC	25	15	12.695	4.267	6.686	24.106
	R3_SEED	25	14	10.251	3.397	5.446	19.297
	R3_CON	13	11	122.376	176.217	15.337	976.46
	R3_30P	18	9	5.488	2.105	2.654	11.346
	R3_60P	14	10	8.636	4.339	3.408	21.884

A.2 Small mammal mortality patterns



A.2.1. Proportion of mortality instances for the four main species trapped (from top left to bottom left, clockwise: *P. maniculatus, M. gapperi, S. cinereus, T. hudsonicus*). This proportion is reflected as a percentage of the total number of interactions with a species (which includes captures, recaptures and escapees). For example, in the control treatment for red squirrels, the mortality rate is 10%, as there were nine successful red squirrel captures and one mortality.



A.3 Small mammal minimum number alive, detection averages and movement

A.3.1: The average detection rates of *M. gapperi*. These values were calculated by dividing the number of detections by the number of animals, at each treatment plot and replicate in June (left) and August (right).



A.3.2: The average number of traps an individual vole was captured at in a plot in June (left) and August (right).



A.3.3: The average detection rates of *P. maniculatus*, calculated by dividing the number of detections by the number of animals, at each treatment plot and replicate in June (left, Fig. 7a) and August (right, Fig. 7b).



A.3.4: The average number of traps an individual mouse was captured at in a plot in June (8a, left) and August (8b, right).

Based on the parsed results with null SECR models that had some gaps in reliable estimates, I put together the data for minimum number of animals alive. This number is the number of unique ear tags trapped at a given treatment and replicate. The minimum number of *P*. *maniculatus* across the treatments in the June and August trapping sessions show a general trend in increasing numbers of unique animals from most crown cover to least, indicating that there are more individuals in clearcut and seed tree treatments than control or partial harvest methods (June: 40 in clearcut, 24 in seed tree, 12 in 60P, 19 in 30P, 17 in control; August: 29 in clearcut, 26 in seed tree, 19 in 60P, 21 in 30P, 20 in control; Fig A.3.5). This trend is more noticeable in June, and in the R3 replicate in August.



A.3.5: The minimum number of *P. maniculatus* alive, determined by the number of unique ear tag identifiers, at each treatment plot and replicate in June (left) and August (right).

As the SECR density estimates were also inconsistent for Southern red-backed voles, I looked into the minimum number alive to determine their responses to the harvesting treatments as well. As stated above, this number is the number of unique ear tags trapped at a given treatment and replicate. In five of the six sessions, 60% retention had the highest number of individuals (June: 6 in clearcuts, 17 in control, 24 in 30% retention, 30 in 60% retention, and 23 in seed tree; August: 6 in clearcut, 8 in control, 11 in 30% retention, 14 in 60% retention, and 6 in seed tree; Figure A.3.6).



A.3.6: The minimum number of *M. gapperi* alive, determined by the number of unique ear tag identifiers, at each treatment plot and replicate in June (left) and August (right).

A.4. Sex-specific SECR models

Using the more parsed data set (separated into month, species, treatment and replicate) I forayed into examining if there were sex-specific differences in sigma, an index of home range size. To determine if the null models were ignoring another factor, I ran sex-specific models, where the sigma ~ g, which makes sigma differ between males and females (Efford, 2020). These models, shown in Figure 9, did not reveal any consistent differences between male and female sigma, which is an indicator of home range sizes for deer mice. I compared the AIC values of the null and sex-specific models (shown below in Table A.4.1). Only five of the plots had sex-specific models as an improvement on the null model.In 7 plots, the male sigma value was larger than female, but in 5 of those plots, the confidence intervals overlapped the female estimate of sigma. Three plots had larger female sigma values than male. Only the replicate two 60% partial harvesting plot had distinctly separate male and female values. Differences between replicates were also as inconsistent as differences between treatments.



Figure A.4.1: Sigma values for sex specific SECR models for *P. maniculatus* in June. Sigma value is associated with home range size.

Model	AIC_NullModel	AIC_SexModel	Delta AIC (sex - null)
R1_CC	133.395	141.431	8.036
R1_CON	33.919	33.904	-0.015
R1_30P	82.916	89.772	6.856
R1_60P	109.528	116.954	7.426
R2_CC	152.454	167.378	14.924
R2_CON	143.441	50.699	-92.742
R2_30P	44.283	103.937	59.654
R2_60P	99.234	48.291	-50.943
R2_SEED	42.443	156.119	113.676
R3_CC	182.407	202.144	19.737
R3_CON	90.999	150.539	59.54
R3_30P	133.622	123.187	-10.435
R3_SEED	107.415	103.074	-4.341

Table 2: AIC values for null SECR and sex specific SECR models for *P. maniculatus*

A.5 Large mammal diversity comparisons



Figure A.1.1: On the left, average diversity values when independent captures are 'rated' per 100 active camera trapping days, versus the chart on the right showing average diversity values without active camera trapping days included. This figure includes all independent detections on the camera at all three project sites.



A.6 Large mammal independent detections events

Figure A.6.1. This figure shows the independent detections of all species at Jaffray, with whitetailed deer (*Odocoileus virginianus*) being the most-detected species (five times more frequently detected than the next highest species).



Figure A.6.2. The number of independent detections of each of the large-bodied terrestrial mammal species at Alex Fraser. Cattle (*Bos taurus*) were left in to show the prevalence of the species at this site.



Figure A.6.3: The number of independent detections of each of the large-bodied terrestrial mammal species at JPRF.

Covariate	Wetlands	Lakes	Streams	Roads
Wetlands	1.00	-0.01	0.29	-0.11
Lakes		1.00	0.58	0.99
Streams			1.00	0.54
Roads				1.00

A7: Correlation between continuous spatial covariates for large mammal analysis

Clearly, roads and lakes were highly correlated (0.99). However, it was worth looking at the spread of the scaled values across sites to determine if each of the covariates was accurately depicted (or if the location was confounding the potential effect of the feature of interest).



Figure A.7.1: The mean and range of scaled distances to wetlands from each camera location, separated by climatic location.



Figure A.7.2: Average and range of scaled values for camera distance to nearest lake. Separated by climatic location.



Figure A.7.3: Average and range of scaled values for camera distance to nearest stream. Separated by climatic location.


Figure A.7.4: Average and range of scaled values for camera distance to nearest road. Separated by climatic location.

	0 0	0			1 3	
Common Name	Scientific Name	Status ◆	Expected Site for Possible Captures*	Expected Response to Harvesting	Expected Response to Climate Gradient	Potential Responses to Climate Change
Caribou (southern mountain population)	Rangifer tarandus	Red	Jaffray, AFRF	Negative response to clearcuts (avoidance) (Festa-Bianchet, Ray, Boutin, Cote & Gunn, 2011)	Negative response to warmer climates (or lower elevation) (Festa-Bianchet, Ray, Boutin, Cote & Gunn, 2011)	Significant population declines, warmer climate & industry creates interactions and competition between caribou & other ungulates (Festa-Bianchet, Ray, Boutin, Cote & Gunn, 2011)
Mountain Goat	Oreamnos americanus	Yellow	Jaffray (low likelihood AFRF)	Negative response to canopy removal (for forage and increased snow depth) (Mountain Goat Management Team, 2010)	Rocky mountain range only includes Jaffray (no north- central BC populations) (Mountain Goat Management Team, 2010)	Negative response to decreasing amount and range of high-elevation alpine habitat (Mountain Goat Management Team, 2010)
Bighorn Sheep	Ovis canadensis	Blue	Jaffray	Habitat requirements include open meadows, clearcut or burned areas (all steep- slope), positive response to harvesting (Demarchi, 2004)	Dependent on steep slopes and range only overlaps Jaffray (Demarchi, 2004)	Negative response to increased invasive grass species and other ungulate foraging competition (Demarchi, 2004)
Moose	Alces alces	Yellow	AFRF, JPRF	Positive response to clearcutting for forage, but require nearby forest for cover (partial harvest?) (Summary by Fisher & Wilkinson, 2005)	Increasing density with increasing latitude (different, smaller subspecies – Shira's – in Kootenays, current population decline around Williams Lake)	Moose density decline at southern edge of range, decreasing lifespan and cranial size with warmer temps (Hoy, Peterson & Vucetich, 2017)

Table A6: Large mammals species' expected responses to forest harvesting, climate gradient and climate change. Species selected through examining range maps and building a potential community pool for all sites of this project.

Elk	Cervus canadensis	Yellow	Jaffray	Preference for partial harvesting (access to forage and dense cover), however elk do not seem to alter movement or home range due to harvesting (Summary by Fisher & Wilkinson, 2005)	Abundant in Kootenays and north central, AFRF typically has not had many – new sightings in recent years (Koot, 2018)	Potential positive response – warmer winters and changing summer precipitation allow for enhanced recruitment and survival (Wang, Hobbs, Singer, Ojima & Lubow, 2002)
White-tailed Deer	Odocoileus virginianus	Yellow	Jaffray, AFRF	Preference for partial harvesting (selection for some cutblocks, high edge- to-area ratios, negative response to slash) (Summary by Fisher & Wilkinson, 2005)	Population expansion into more northern latitudes (Blood, 2000d; MFLNRORD, n.d.; Koot, 2018)	Positive response – colonization of new areas as temperatures become more tolerable
Mule Deer	Odocoileus hemionus	Yellow	Jaffray, AFRF, JPRF	Preference for clumpy seed tree retention – snow interception by large trees to lower energy output and access to lichens (Koot, Day, Ewen & Skea, 2015)	Relatively consistent across range (thus far, almost exclusively white-tailed deer captured in Kootenays)	Increasing precipitation combined with large harvesting openings would cause increased energy outputs in winter (potential negative response to CC)
Coyote	Canis latrans	Yellow	Jaffray, AFRF, JPRF	Use of fragmented landscapes, some preference for regenerating cutblocks (partial harvest preference?) (Summary by Fisher & Wilkinson, 2005)	Expansion into habitats all over Canada – consistent across sites Potentially more in Kootenays where wolves had been extirpated and are re-establishing (Hatler & Beal, 2003)	Generalist diet, significant range expansion over time – likely positive response to warming winters (northern expansion?)
Grey Wolf	Canis lupus	Yellow	AFRF, JPRF	Large data gaps – seasonal usage of post-clearcut or	Range coincides with moose range (wolves more	Negligible effect (MFLNRORD, 2014)

				burnt stands following prey, abundance of studies showing use of open and diverse areas (Summary by Fisher & Wilkinson, 2005) – potentially partial harvest or clearcuts as prey species increase?	abundant in central-north region, have re-established in south Kootenays) (MFLNRORD, 2014)	
Red Fox	Vulpes vulpes	Yellow	AFRF, JPRF	Tracks found in regenerating stands (30+ years), more than cut or uncut forest – preference for partial harvest? (Summary by Fisher & Wilkinson, 2005)	Abundant in north-central regions, very low densities in Kootenays (E-Fauna BC)	North-ward expansion of range with warming temperatures (Hetem, Fuller, Maloney & Mitchell, 2014)
Lynx	Lynx canadensis	Yellow	JPRF, AFRF, possibly Jaffray	Lynx abundance follows snowshoe hares, found in regenerating stands, rare in recently cut or old growth (partial harvesting?) (Summary by Fisher & Wilkinson, 2005)	Consistent between AFRF, JPRF (low density in Kootenays)	In eastern Canada show negative response to & population declines with climate change and contracting range (Carroll, 2007)
Bobcat	Lynx rufus	Yellow	Jaffray, possibly AFRF	Affected by snow depths – clearcuts in northern parts of range would be detrimental due to thick snow, partial retention and smaller cutblocks preferable (Gooliaff, 2018; Hatler, Poole & Beal, 2003a)	Likely no populations above Prince George, morphologically distinct from lynx to hunt in drier places (Gooliaff, 2018)	Generalist diet, potential northward range expansion (Gooliaff, 2018)
Cougar	Puma concolor	Yellow	Jaffray, AFRF, possibly JPRF	Some habitat preference for dense vegetation, some use of clearcuts, varied use of different habitat types dependent on life phase	Higher density at lower latitude, decreases with latitude (E-Fauna BC, 2018)	Very little information – recommended connectivity of habitat with latitude and elevation (Wainwright, Darimont & Paquet, 2010)

				(Wainwright, Darimont & Paquet, 2010) – partial harvest?		
American badger	Taxidea taxus	Red	Jaffray, low likelihood AFRF	Have been documented using cutblocks and regenerating forests, as well as open dry Douglas fir forests. Tolerant of human disturbance, dependent on fire cycles and grasslands – clearcut or partial harvest (Adams & Kinley, 2004)	Typically only in drier parts of Kootenays	Road kill is most significant threat to declining population, climate change has minimal direct impacts other than through potential effects on prey species (Adams & Kinley, 2004)
Striped skunk	Mephitis mephitis	Yellow	Jaffray, low likelihood AFRF and JPRF	Uses forest clearings and edges, wetlands and urban areas – partial harvest?	Vast majority of skunk populations in southern part of BC (E-Fauna)	Low impact, stress or mortality from extreme weather events, concerns around rabies and control programs (Helgen & Reid, 2016)
Wolverine	Gulo gulo	Blue	Jaffray, AFRF, JPRF	Wide range of food sources, but generally depending on mature forest & have landscape level habitat requirements – negative response to harvesting (Weir, 2004)	Low density across province, density dependent on food sources – consistent across study sites (Weir, 2004)	Snow-dependent carnivore (for dispersal), snowpack and populations declining together – strong negative response to climate change (Brodie & Post, 2010)
American marten, Pacific marten	Martes americana, Martes caurina	Yellow	Jaffray, AFRF, JPRF	Preference for full canopy cover (prey abundance), clearcuts as marginal habitat, importance of residuals for survival and recruitment – partial harvesting (Summary by Fisher & Wilkinson, 2005)	Consistent density across sites	In eastern Canada, negative response & population declines with climate change and contracting range (Carroll, 2007)

Ermine/Short- tailed Weasel	Mustela erminea	Yellow	Jaffray, AFRF, JPRF	Preference for cutblocks – slash piles as rest sites (Summary by Fisher & Wilkinson, 2005), preference for clearcut (Sullivan et al. 1999) – though scant information – clearcut preference	Consistent density across sites	Very limited information – as range expands into arctic, potential for contraction into northern parts, changing prey and competitors?
Long-tailed Weasel	Mustela frenata	Yellow	Jaffray	No data about response to harvest, but positive relationship with exploiting open/human-influenced areas – clearcuts? (Summary by Fisher & Wilkinson, 2005)	Distribution mostly in southern half of province (Hatler, Mowat & Beal, 2003b)	Low sensitivity (Price, Lloyd & Daust, 2017)
Least Weasel	Mustela nivalis	Yellow	AFRF, JPRF	Able to use clearcuts, forests and most habitat types at any elevation – no preference (Hatler, Mowat & Beal, 2003b)	Distribution mainly in northern half of province (Hatler, Mowat & Beal, 2003b)	Potential northward migration into arctic and subarctic, exploiting novel prey species (Hof, Jansson & Nilsson, 2012)
American Mink	Neovison vison	Yellow	Jaffray, AFRF, JPRF	Semi-aquatic, prefer riparian areas, use snags/ledges/stumps for denning – requiring structural diversity often maintained with riparian forest harvesting policy (Hatler & Beal, 2003) – negative response to cutting	Denser populations in north-central area – potentially decreasing density with decreasing latitude	Potential northward migration into arctic and subarctic, exploiting novel prey species (Hof, Jansson & Nilsson, 2012)
Fisher	Martes	Blue	**AFRF,	Partial harvest or uncut –	More potential habitat	Likely negative response to
	pennanti		JPRF	importance of residuals and	areas around JP than AF	climate change – species at
				canopy cover, generally	(more fishers at higher	risk, degradation of habitat
				recognized as old-growth	latitude) (Badry, 2004)	(Lewis, Powell & Zielinski,
				dependent (Summary by		2012)

				Fisher & Wilkinson, 2005) – negative response to harvest		
American Black Bear	Ursus americanus cinnamomum	Yellow	Jaffray, AFRF, JPRF	Preference for full canopy cover and mature forest for denning, deciduous or regenerating forests for forage – partial harvesting? (Summary by Fisher & Wilkinson, 2005)	Consistent across sites	Climate change and anthropogenic effects on ability to hibernate, increased use of human food sources, generalist species
Grizzly Bear	Ursus arctos	Blue	Jaffray, AFRF, JPRF	New cutblocks increased food sources, but significant data gaps (Summary by Fisher & Wilkinson, 2005)	Consistent across sites, densest populations in Kootenays	Likelihood of plant forage being available at only higher elevations, low elevation populations at higher risk of conflict, but generally CC is low-level threat (Roberts, Neilson & Stenhouse, 2014)
North American porcupine	Erethizon dorsatum	Yellow	Jaffray, AFRF, JPRF	Require trees for food and suitable denning sites – negative response to clearcut (Summary E-Fauna BC, 2018)	Generally spread throughout province	Threats include parasites and disease, potential expansion with warmer winters?

All status information from BC Conservation Data Centre, 2018. * All expected sites based on E-Fauna BC.

** E-Fauna BC does not have a map for this species currently. Approximate range was obtained via BC Ministry of Water, Land and Air Protection (Weir, 2003).

Common Name	Scientific Name	Status	Closest Expected Site	Expected Response to Harvesting
Snowshoe Hare	Lepus americanus	Yellow	Jaffray, AFRF, JPRF	Rarely appear in cutblocks, need understory cover (summary by Fisher & Wilkinson 2005) – negative response to clearcut
Nearctic brown Lemming	Lemmus trimucronatus	Yellow	JPRF	Frequents grasslands & meadows – positive response to harvesting? (E-Fauna BC, 2018)
Long-tailed vole	Microtus Iongicaudus	Yellow	AFRF, Jaffray	More found at clearcut sites than forest, but strong annual fluctuation (Sullivan et al. 1999) - positive response to clearcutting
Meadow vole	Microtus pennsylvanicus	Yellow	Jaffray, AFRF, JPRF	Kirkland (1990) review and summary by Fisher & Wilkinson (2005) show abundance of meadow voles after harvest – positive response to clearcut
Southern red- backed vole	Myodes gapperi	Yellow	Jaffray, AFRF, JPRF	Significant disparity between study results – Kirkland (1990) review showed initial positive response to harvest, and potential steep drop-off after a few summers. Sullivan (1999) shows forest supported more voles – partial retention?
Bushy-tailed woodrat	Neotoma cinerea	Yellow	Jaffray, AFRF	Preference for open spaces, rocky areas, easily adaptable to human disturbances like mines (E-Fauna BC, 2018) – positive response to clearcuts
North American Deer mouse	Peromyscus maniculatus	Yellow	Jaffray, AFRF, JPRF	Abundant in clearcuts, forage on seeds/insects found in new clearcuts; but more cover is assoc. with higher overwinter survival, some studies show higher abundance with less cover (Summary by Fisher & Wilkinson, 2005) – seed tree or 30% partial harvest? Conflicting reports of clearcut effect on recruitment
Heather vole	Phenacomys intermedius	Yellow	Jaffray, AFRF, JPRF	Occupies mossy meadows, shrubby areas in forests (BC CDC, 1993) – positive response to harvesting?
Meadow jumping mouse	Zapus hudsonius	Yellow	AFRF	Preference for cutblocks (summary by Fisher & Wilkinson, 2005) – positive response to harvesting
Woodchuck	Marmota monax	Yellow	JPRF, AFRF	Woodchucks occupy open meadow areas & woodland edges –positive response to clearcut/partial harvest

Table A7: Small mammal species' expected responses to clearcut harvesting. Potential community pool determined through examining range maps and selecting species with ranges overlapping JPRF.

Yellow-pine chipmunk	Neotamias amoenus	Yellow	Jaffray, AFRF	Occurred more frequently at clearcut sites than forest (Sullivan et al. 1999) – positive response to cut
Red Squirrel	Tamiasciurus hudsonicus	Yellow	Jaffray, AFRF, JPRF	Conifer seed specialist, less tracks in clearcuts, cut blocks as occasional summer forage areas (Summary by Fisher & Wilkinson, 2005)
Columbian Ground Squirrel	Spermophilus columbianus	Yellow	Jaffray, AFRF	Generally, squirrels correlated with canopy heterogeneity and larger trees (Summary by Fisher & Wilkinson, 2005) – negative response to clearcut
Common shrew	Sorex cinereus Kerr	Yellow	Jaffray, AFRF, JPRF	No response (Sullivan et al. 1999), positive response to harvesting (Fisher & Wilkinson, 2005) – overall lit shows positive response to clearcutting in the short term
American pygmy shrew	<i>Sorex hoyi</i> Baird	Yellow	JPRF	No response (Sullivan et al. 1999, positive response to harvesting (Fisher & Wilkinson, 2005) – overall lit shows positive response to clearcutting in the short term
Dusky shrew	Sorex monticolus	Yellow	Jaffray, AFRF, JPRF	No response (Sullivan et al. 1999), positive response to harvesting (Fisher & Wilkinson, 2005) – overall lit shows positive response to clearcutting in the short term
Water shrew	Sorex palustris	Blue	Jaffray, AFRF	No response (Sullivan et al. 1999), positive response to harvesting (Fisher & Wilkinson, 2005) – overall lit shows positive response to clearcutting in the short term

This list of small mammals does not include exotic species, such as Eastern Cottontail (*Sylvilagus floridanus*) and house mouse (*Mus musculus*). Bolded species are those that were live trapped, others are ones that were expected, based on their ranges, to be potentially trapped.