

**SNOWSHOE HARE ABUNDANCE AND FORAGING BEHAVIOUR IN RECENTLY  
BURNED FORESTS**

by

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## Abstract

A combination of climate change and decades of fire suppression has led to an increase in the size of wildfires in North American conifer forests. Large wildfires are more heterogeneous than smaller fires because of their landscape context and fire-weather that ignites them. Larger fires are patchier, and have more opportunities for good habitat, but they also produce large patches of open area where prey species are exposed to predation. For many mammal species, such as snowshoe hares (*Lepus americanus*) this patchiness means having to navigate quite different habitat patches while trying to locate adequate cover and food. The density of animals in burns of different sizes, and how individuals behave while foraging in those within-burn patches, is unknown for many species. This study addresses these knowledge gaps (fire size and within-burn patchiness) with two studies. First, I assessed densities of snowshoe hare in 9 wildfires that burned 13 years ago (3 each of small (~100 ha), medium (1000-5000 ha), and large (>10,000 ha)) and in mature forests in southern British Columbia to determine if fire size impacts hare density. I found that hares were highly variable in large burns but when they were present the densities were the highest of any sites. Hares were absent from small burns and most medium burns. Hares were commonly present in mature forests but at much lower densities than in large burns.

Second, I assessed snowshoe hare foraging behaviour by measuring tortuosity, speed of movement, and amount of browse along winter foraging pathways in open and regenerating patches of the Okanagan Mountain Park fire (>25,000 ha) and surrounding mature forest. I found that hares moved the fastest and browsed the least in open patches, and moved slower and ate more in sapling patches. Hares did not change tortuosity. The data from these two studies show that fire size is an important predictor of snowshoe hare

density and that hares change foraging behaviour to some degree based on the type of habitat they are in.

## **Preface**

This research was conducted at the University of British Columbia Okanagan under the supervision of Dr Karen Hodges. For all work presented in this document I was entirely responsible for identifying and selecting field sites; conducting all field work; writing statistical code in R; developing statistical models; displaying, interpreting and analyzing data; and writing and editing this thesis with feedback provided by Dr Hodges. The initial research concept was created by Dr Hodges, with field design, data collection methods, and statistical analysis decided upon jointly. Funding was provided by NSERC.

A version of chapter 2 will be submitted to a peer-reviewed journal (Hutchen, J., and Hodges, K.E. Impact of wildfire size on snowshoe hare populations in Southern British Columbia). Dr Michael Russello, Dr Robert Lalonde, and Dr Karen Hodges assisted with selecting the number and location of wildfires to be studied. I was responsible for collecting and analyzing data and writing the manuscript. Dr Karen Hodges designed the field techniques used to survey hare populations in previous work, assisted with data interpretation and reviewed drafts of the manuscript.

A version of chapter 3 will be submitted to a peer-reviewed journal (Hutchen, J., and Hodges, K.E. Snowshoe hare foraging behaviour in post-fire conifer forests). I was responsible for selecting field locations, collecting and analyzing data, and writing the manuscript. Dr Karen Hodges provided feedback and assisted with appropriate analysis and reviewed drafts of the manuscript.

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## **Chapter 1 Introduction**

### **1.1 The impact of climate change on wildfire regimes**

Wildfires are the dominant terrestrial disturbance in North American coniferous forests (Agee 2000). These large disturbances have historically created a patchwork of seral stages that support various faunal communities (Agee 2000, Hodson et al. 2011, Miller et al. 2012, Perera and Buse 2014). As climate change leads to warmer and drier conditions across the globe, the frequency, size and severity of wildfires is predicted to increase (Westerling et al. 2006, Miller et al. 2009). A shift in the fire regime of these forests to more frequent, larger fires will result in succession being skewed to younger forests (Hessburg et al. 2005), disrupting the current state of forest succession, and thus changing the habitat suitability for local species.

Forests are characterized by their fire regimes (Agee 1993). Northern boreal forests normally see large, infrequent crown fires on a time interval of 150-300 years with fire sizes commonly greater than 10,000 ha (Fahnestock and Agee 1983, Agee 2000). While these large fires are typical of the northern taiga (Keane et al. 2008), southern boreal and sub-boreal montane forests are more commonly modified by less severe, smaller surface fires that occur more frequently (20-50-year return intervals) along with other forms of disturbance (Henry 2002). Climate change is causing the large, severe fires characteristics of the boreal fire regimes to burn in southern ranges, where the forests have evolved under a less severe regime (Westerling et al. 2006, Nitschke and Innes 2008).

## **1.2 Wildfire characteristics – size and severity**

Two of the major wildfire characteristics are size and severity. These characteristics are two of the physical aspects of a fire that are most affected by climate change (larger fires burning hotter, Westerling et al. 2006).

Fire severity describes the net effect of the interaction between fire intensity (peak temperatures and residence time) and vegetation (Keeley 2009, Perera and Buse 2014). The simplest way to categorize fire severity is into classes (low, medium, and high) based on the formation of wildfire residuals, or the resultant forest structure of both living and dead trees post-fire (Perera and Buse 2014). Most definitions rank these severities based on the level of mortality the dominant tree species experiences (Kennedy and Fontaine 2009), though considerable debate remains as to what percentage of mortality is required for each class (Odion et al. 2004, Covert-Bratland et al. 2006, Bowman 2007). While the effects of within-burn fire severity patches have been reported for some taxa (avifauna, Kotlair et al. 2002, 2007; ungulates, Wan et al. 2014), the impact of severity on many mammal taxa remains poorly understood.

Fire size is a measure of the absolute area burned. Estimates for what constitutes a large wildfire are based on forest type, with the minimum average estimate of “large” fire in North America being 400 ha (Westerling et al. 2006), and northern forests seeing the highest threshold value for a large fire (>10,000 ha, Keane et al. 2008). Larger fires produce more heterogeneous burn scars, with abundant fire skips and residual patches, and tend to be more severe than smaller fires (Turner et al. 1994, Lutz et al. 2009, Miller et al. 2012).

Heterogeneity in the burn scar – in the form of fire skips and residual patches – is of critical importance for mammal movement post-fire. For example, Vanbianchi et al. (2015) showed

that Canada Lynx (*Lynx canadensis*) were more likely to use residual patches to cross a recent burn if those patches were of sufficient size and quality to provide adequate habitat.

### **1.3 The impact of fire regime changes on wildlife**

Small mammals are abundant, can be easy to count, and populate a diverse range of habitats, making this taxon a popular group to study after forest disturbances (Fisher and Wilkinson 2005). Most studies of the effects of fire on small mammals have been population counts of species present (Hutchen et al. 2017). Very few species have received individual attention for small mammal response to fire and fewer still have been studied more than once in North America (5 species, Hutchen et al. 2017). The most commonly studied species in single-species fire research has been the snowshoe hare (*Lepus americanus*).

Species experiencing changes in their ecosystem's historical fire regimes may experience population fluctuations and demographic changes that would not be expected based on classical theory. Little is known about the ecological impacts of frequent, large wildfires on contemporary landscapes that were historically characterized by less severe, small surface burns (Keane et al. 2008). Drier conditions resulting from climate change may also cause a fundamental shift in secondary succession of trees and shrubs post-fire by increasing the environmental stress on young trees (Littell et al. 2010).

To understand how changing fire regimes impact wildlife, it is ideal to study a species whose entire range spans multiple historical fire regimes so that comparisons may be drawn between populations that have evolved with large wildfires and ones that have only recently been exposed to them. However, such studies are challenging to implement. It is more practical to focus initially on ecologically important species in areas experiencing changes in

fire regime. One such species is the snowshoe hare, whose northern populations span the Canadian boreal and are subjected to infrequent stand-replacing wildfires and whose southern populations in Canada and the contiguous U.S. experience more frequent, but less severe, surface fires (Mori and Johnson 2013, Ireland and Petropoulos 2015).

#### **1.4 Snowshoe hares**

Snowshoe hares are keystone herbivores and the primary prey species for a host of boreal carnivores including lynx, marten (*Martes americana*), and great horned owls (*Bubo virginianus*; Hodges 2000a, b, Hodges and Sinclair 2003, Krebs et al. 2001a). Snowshoe hares primarily favour early seral forests during the shrub-sapling phase and mature forests with canopy gaps that provide sufficient openings for understory growth of a high density of shrubs and saplings for foraging and cover (Paragi et al. 1997, Aubry et al. 2000, Buskirk et al. 2000, Hodges 2000a, b, Koehler et al. 2008, Hodges et al. 2009, Hodson et al. 2011). This habitat preference is conserved across disturbance regimes. In Quebec, Hodson et al. (2011) also found that hare abundance was positively related to the availability of early-successional shade-intolerant deciduous trees, which are the preferred winter browse of snowshoe hares in eastern mixed hardwood forests (Telfer 1972, Newbury and Simon 2005).

While the habitat requirements for snowshoe hares are well known, there remain large knowledge gaps as to how changing wildfire regimes will impact forest succession (Littell et al. 2010), thus changing the distribution of preferred snowshoe hare habitat. Despite being a keystone species in boreal, fire-disturbed ecosystems, knowledge of snowshoe hare response to wildfire is restricted, with only eight studies conducted since 1970 (Keith and Surrendi 1971, Fox 1978, Paragi et al. 1997, Hodges et al. 2009, Hodson et al.

2011, Strong and Jung 2012, Allard-Duchene et al. 2014, Cheng et al. 2015). Most of these studies used relative abundances (Strong and Jung 2012, Cheng et al. 2015) or live-trapping (Hodges et al. 2009) of hares to determine whether hares undergo a population increase, decline, or remain the same following a wildfire. In all cases, snowshoe hares had very low densities in the early years following fire. When fires of multiple ages were compared, older burns had more snowshoe hares present than younger burns (Paragi et al. 1997, Hodges et al. 2009), which is attributed to increased time for vegetation regrowth. Allard-Duchene et al. (2014) and Hodson et al. (2011) also compared the population-level responses of snowshoe hares to wildfire and forestry practices. Both found that hare populations followed similar patterns of immediate decline followed by a period of growth after both fires and forestry. Paragi et al. (1997) used snowtrack surveys of hares and lynx to assess the presence/absence of these species in burned forests, and found that hare tracks occurred less frequently in more recent burns.

Three studies (Paragi et al. 1997, Hodges et al. 2009, Cheng et al. 2015) clearly reported the size of the fires being studied. Hodges et al. (2009) worked on the 1988 wildfires in Yellowstone National Park (> 250,000 ha total for the 7 fires) and a more recent fire in 2003 (7305 ha) while Paragi et al. (1997) worked in two fires in Alaska: a 1966 fire of 13,300 ha and a 1985 fire of 19,700. Other papers either failed to report fire sizes at all (Strong and Jung 2012) or reported the total size of the fire systems for the years studied but were unclear about the size of individual fires studied.

The time-frames of study ranged from 0-4 years post-fire (Hodges et al. 2009, though they studied mostly in 13+ year old forest) to 200 years post-fire (Allard-Duchene et al. 2014). The average time-since-fire when a study began was 13.1 years from the youngest fire



in the study. 70.3 years was the average time-since-fire of “older” fires studied (these areas were commonly used as pseudo-controls).

All studies employed fecal pellet surveys to index hare abundance, except for Hodges et al. (2009) and Paragi et al. (1997). Hodges et al. (2009) used a combination of fecal pellet surveys and live-trapping. Paragi et al. (1997) used snow track surveys to count how many tracks occurred along a transect. The movement patterns described by Paragi et al. (1997) are not true indicators of hare behaviour, because there is no formulaic relation between the frequency of hare snow tracks and abundance.

These studies have all asked essentially the same question: do snowshoe hare populations change after fire? All studies that conducted population counts (Hodges et al. 2009, Strong and Jung 2012, Allard-Duchene et al. 2014, Hodson et al. 2011, Cheng et al. 2015) found that, in general, hare populations were less abundant after a wildfire. However, a few papers identified patches in a burn that had very high densities of hare (Hodges et al. 2009, Cheng et al. 2015). Paragi et al. (1997) concluded that snowshoe hare response to fire may be positive in their system, but because of how robust the different methodologies are (e.g. tracks counts as an index for abundance do not provide accurate numbers) these conclusions are hard to compare against other studies.

One of the most glaring omissions in this field to date are behavioural surveys. In large mammal-fire studies, assessments of anti-predator behaviour and foraging behaviour make up most of studies (Volkman, Hutchen, and Hodges, manuscript in preparation). No behavioural studies have been done for snowshoe hares with regards to wildfire. In the small mammal-fire literature the only studied “behaviour” is changed home range size following fire (Hutchen et al. 2017). With the diversity of behavioural studies available for mammals,

understanding how small mammals behave in burned forests will be very informative. For example, an increase in the number of deer mice (*Peromyscus maniculatus*) following a fire may not mean better habitat for mice. The populations inside the burned area may be population sinks and studies of demography and anti-predator behaviour to determine how well mice within the burn are surviving could address this possibility.

### **1.5 Goals for this thesis**

One of the most obvious gaps in current fire studies of small mammals is an understanding of the effect of fire size on population response. Previous papers treated all fires as the same level of disturbance, regardless of size (e.g. Hodges et al. 2009 treated the 1988 Yellowstone fires as a single disturbance, and separately considered a more recent 7305 ha fire). The physical size of a wildfire is the product of multiple factors: fire behaviour, weather, terrain, and season (Bessie and Johnson 1995, Turner et al. 1997, Perera and Buse 2014). Fires of vastly different sizes represent significantly different disturbances at a landscape scale (Agee 1998, Keane et al. 2008). Large fires physically affect more land and tend to be more severe (Agee 1998), and produce much more heterogeneous burn scars than small fires (Agee 1998, Keane et al. 2008). These differences are well known by fire ecologists but mammal ecologists who study fire have been slower to adopt the mentality that the physical structure (or scale) of a disturbance impacts mammal response.

In Chapter 2, I address the issue of fire size with regards to snowshoe hare populations. Given the robustness of known index methods (Krebs et al 2001b, Mills et al. 2005, Hodges et al. 2009, 2014), I can safely use surveys of fecal pellets to assess the relative abundance of snowshoe hare populations in wildfires that vary in size. With these population

counts, I could then determine if the impact of a given fire on hare abundance is positive, negative, or neutral and then compare the populations between fires. For example, if small fires always saw an increase in hares after a fire and large fires always saw a decline, then I could conclude that small fires positively impact hares and large fires negatively impact hares.

Chapter 3 will address the lack of behavioural data in small mammal-fire studies. Snowshoe hares have been studied in depth in regards to their foraging habits and diet (Hodges 2000a, b, Hodges et al. 2014, Hodges and Sinclair 2003, 2005, Ellsworth et al. 2013, 2016). Hares flee from predators in significantly straighter pathways than they make while foraging due to the trade-off between speed and making angular movements (Caro et al. 2004, Hodges et al. 2014). While snowshoe hares display plasticity in the tortuosity of movement pathways, it is currently not known whether hares change those movements based on habitat. Whether movement pattern changes are the result of an individual hare making conscious decisions about how to move or the result of a more basic biology is not known. In this thesis, I only considered whether snowshoe hares change tortuosity in different forest patches, but I do not attempt to discover the cause.

## **Chapter 2 Impact of wildfire size on snowshoe hare populations in Southern British Columbia**

### **2.1 Background**

Wildfires are growing in size, severity, and frequency as a result of climate change and fire suppression (Westerling et al 2006, Keane et al. 2008, Miller et al. 2009, Harvey 2016). Fire is the leading disturbance in North American conifer forests (Keane et al. 2008) and is a natural part of the regrowth cycle (Turner et al. 1994). However, large fires are increasingly common outside their historic fire ranges (Keane et al. 2008). Fire regimes are associated with certain forest types and can range from small, frequent, low-severity fires in southern pine forests (Keane et al. 2008) to severe, large, infrequent fires in northern boreal forests (Turner et al. 1998, Kennedy and Fontaine 2009). The size and severity of a wildfire are hugely important in understanding the effect the fire will have on vegetation (Perera and Buse 2014). Studies of large-scale disturbances such as hurricanes (Bellingham 1991, Basnet et al. 1992) and volcanos (Franklin et al. 1985, Adams et al. 1987) consistently show that the intensity and size of these disturbances has a strong impact on the landscape (Turner et al. 1997).

The larger a disturbance, the more heterogenous the resulting landscape (Turner et al. 1997, 1998, Kashian et al. 2004). Fires are no different, with larger fires being more heterogeneous in burn severity (Turner et al. 1994, 1997, Kashian et al. 2004, Keeley 2009, Perera and Buse 2014). The size and shape of a burn determines the spatial structure of post-fire habitat (Schoennagel et al. 2008, Perera and Buse 2014, Harvey et al. 2016). Severely burned patches tend to be more spatially concentrated towards the center of large fires as well (Turner et al. 1994, Harper et al. 2004). Larger fires also have a reduced edge:area ratio,

with density of living trees commonly decreasing as distance into the burn increases (Turner et al. 1994, Turner et al. 1997, Haeussler and Bergeron, 2004, Harper et al. 2004). This edge:area ratio is important because it highlights a difference in the regrowth patterns following large and small fires: regeneration after a large fire is less reliant on seed dispersal from the surrounding unburnt forest because of the sheer distance between the edge and center (Turner et al. 1997, Harvey et al. 2016), whereas smaller burns are greatly affected by the available seedbanks of edge forest because dispersal is less limited (Perera and Buse 2014).

Understanding the internal patchiness of burn severity is helpful in determining the post-fire availability of wildfire habitat because burn severity and patch size have a strong impact on vegetation regrowth, which in turn affects how wildlife use burned areas. For example, after the 1988 fires in Yellowstone National Park, lodgepole pine (*Pinus contorta*) grew more densely in large patches that experienced moderate or severe burns (Turner et al. 1997, Anderson et al. 2004, Kashian et al. 2004). Most small fires are smaller than a few hundred hectares (Westerling et al. 2006, Keane et al. 2008), meaning these small fires may be smaller than a “large” internal patch in Yellowstone (Turner et al. 1997). Small fires are less patchy than large fires mainly because they are not on the same physical scale as larger fires and cannot contain the same variety of severities (Bessie and Johnson 1995, Cui and Perera 2008, Perera and Buse 2014). Wildfire size, and the patchiness of burn severities therein, clearly has a strong impact on post-fire vegetation (Anderson et al. 2004, Perera and Buse 2014), and given that vegetative structure is largely what wildlife respond to after disturbance (Lindemayer et al. 2008, Hodson et al. 2011), it is likely that the size of a wildfire determines wildlife response.

When studying how animal populations respond to burned forests it is beneficial to work with a taxon that is easily constrained to a specific spatial scale that corresponds to the size of the fire. This is why most population-level studies of animals focus on small mammals (Hutchen et al. 2017). However, very few studies of small mammal response to fire compare multiple fires in a single study (Hutchen et al. in 2017) and those that do tend to focus on multiple prescribed burns of the same size (Kennedy and Fontaine 2009, Fontaine and Kennedy 2012). I am not aware of any studies that have attempted to determine whether the size of a wildfire has an impact on the post-fire population responses of wildlife. Given that animals move across landscapes and use habitat on multiple spatial scales (Boyce et al. 2003) it is very likely that they respond differently to wildfires of different sizes because of associated differences in quantity and quality of available habitat.

### **2.1.1 Snowshoe hare biology and known impacts of wildfire**

Snowshoe hares (*Lepus americanus*) are an abundant keystone prey species and are found across Canada and the northern United States in a range of fire-disturbed ecosystems (Hodges 2000a, b, Hodges and Sinclair 2003, Krebs et al. 2001a). Although they are one of the most well-studied small mammals in fire systems (Hutchen et al. 2017), our knowledge of snowshoe hare response to wildfire is limited. Of the eight studies of snowshoe hare response to fire published in North America, the majority used either relative abundances (Strong and Jung 2012, Cheng et al. 2015) or live-trapping (Hodges et al. 2009) to determine that hares experienced very low densities in the early years after a fire. Other studies considered the different degrees of snowshoe hare population response to wildfire and forestry practices (Hodson et al. 2011, Allard-Duchene et al. 2014). In general, younger

burns have fewer snowshoe hares present than older burns (Paragi et al. 1997, Hodges et al. 2009), which is attributed to increased time for vegetation regrowth. Interestingly, they have been excluded from most other meta-analyses of North American faunal responses post-fire (Zwolak 2009, Fontaine and Kennedy 2012, Griffiths and Brook 2014, but see Fisher and Wilkinson 2005). Snowshoe hares display an immediate population decline post-fire (Hodges et al. 2009), but recolonization of individual animals has been noted as early as 1 year post fire (Keith and Surrindi 1971).

While the habitat preferences of snowshoe hares are well-described (Hodges 2000a, b), there remain large knowledge gaps as to how the heterogeneity of post-fire vegetation will impact the distribution of preferred snowshoe hare habitat. Snowshoe hares favour early seral, regenerating stands but also use closed-canopy mature stands (Paragi et al. 1997, Hodson et al. 2011, Hodges et al. 2009) where canopy gaps provide a high density of shrubs and saplings for foraging and cover (Hodges 2000a, b, Hodson et al. 2010a, b, Holbrook et al. 2017). In Quebec, Hodson et al. (2011) found that hare abundance was positively related to the availability of early-successional shade-intolerant deciduous trees, which are the preferred winter browse of snowshoe hares in eastern mixed hardwood forests (Telfer 1972, Newbury and Simon 2005). In western forests, dense lodgepole pine stands < 30 years old support higher numbers of snowshoe hares than mature forests (Mowat and Slough 2003, Hodges 2000b, Hodges et al. 2009, Cheng et al. 2015).

The relationship between fire size and vegetative regrowth is being explored, but in general large fires tend to have more internal vegetation patchiness than small fires do, so there are more diverse habitats available for species. Given that snowshoe hare habitat

preferences are well known, it is possible to predict how snowshoe hare populations will respond to wildfire size. Specifically, I have 2 main hypotheses:

- 1) Snowshoe hares will have higher population densities in large burns than small burns, because large burns support patches of dense sapling regrowth, and
- 2) Snowshoe hare populations will be more variable in density in large burns relative to small burns, due to increased landscape heterogeneity.

## 2.2 Methods

I used geographic information system data layers obtained from IMAPBC (<http://maps.gov.bc.ca/ess/sv/imapbc/>) to locate all wildfires that burned in the southern interior ecoprovince of British Columbia, Canada in 2003 or 2004. This ecoprovince contains the Thompson-Okanagan ecozone as well as proximate similar montane forested regions (Scudder and Smith 2011). This date range corresponds to the “establishment stage” of forest succession, where snowshoe hare abundance is thought to be highest post fire (Fisher and Wilkinson 2005). This approximately thirteen-year post-fire sample time is also consistent with the time-frame of previous snowshoe hare studies that noted hare recolonization after fire (Hodges et al. 2009, Cheng et al. 2015). In keeping the age of burns consistent, I could consider fire size as an independent variable and avoid the inherent variability in differing regrowth stages. Dominant canopy species in the Thompson-Okanagan are Ponderosa pine (*Pinus ponderosa*) and Lodgepole pine at low elevations, transitioning into Douglas-fir (*Pseudotsuga menziesii*), Red cedar (*Thuja plicata*), and Western Hemlock (*Tsuga heterophylla*) at higher elevation, with subalpine fir (*Abies lasiocarpa*) at high elevations.

I divided wildfires into three classes based on size: (1) “small”, 80-200 ha, (2) “medium”, 1,000-5,000 ha, and (3) “large”, 10,000-26,000 ha. Small fires are < 200 ha



because fires of this size and smaller are the most common (Cumming 2001, Cui and Perera 2008, Baker 2009). Medium fires were selected to span the range of fire sizes between the small, common fires, and large, infrequent fires. There is no clear definition for what constitutes a “large” wildfire in the literature. “Large” wildfires have in the past been categorized as any fire over 400 ha (Westerling et al. 2006) or over 10,000 ha (Daniel et al. 2007; Keane et al. 2008). I chose large fires to be > 10,000 ha because these fires pose the most significant risk to human infrastructure as well as ecosystems (Daniel et al. 2007).

I chose 3 fires from each size class (Table 2.1; see Appendix A for fire maps). To limit confounding factors such as forest type, elevation, and other microhabitat features, I chose fires that were as like each other in physical context as possible while still being accessible from a road or trail. Only two accessible fires burned more than 10,000 ha of forest in the 2003 fire year (Okanagan Mountain Park Fire (>25,000 ha) and McClure Fire (> 27,000 ha). However, the McClure fire jumped the North Thompson river, so I have treated the two sides of the McClure fire as independent fires (hereafter referred to as McClure East and McClure West; Table 1) because for snowshoe hares, migration across the North Thompson from one burn to the other is essentially impossible.

### **2.2.1 Measuring relative abundance of snowshoe hares**

To calculate relative abundance of snowshoe hares, I used fecal pellet surveys (Krebs et al. 1987, 2001b). While population counts are most accurate with direct methods such as live-capture, my goal was to sample as many fires as possible across a large spatial scale, which made index methods much more feasible. Fecal pellet surveys provide accurate

patterns of low versus high hare densities when compared to live-trapping data (Mills et al. 2005, Hodges and Mills 2008)

I conducted field work between May and August 2016. Prior to sampling, I used GIS software to create a series of 20 ha plots in each burn. The number of field sites varied from 1 to 7 because small fires could not accommodate the same number of sites as large fires (Table 2.2). Fires were matched with a 20 ha plot in mature forest near to the edge of the burn. Each 20 ha plot was then populated with 80 random points for the pellet transects (Krebs et al. 1987, Krebs et al. 2001b, Mills et al. 2005, Hodges and Mills 2008). A rectangular transect (0.155 m<sup>2</sup>, 5.08 cm × 305 cm) was laid due north at each survey point. Pellets were counted only if they were intact and at least one half was within the transect area. To calculate the mean number of hare pellets in each burn, I first found the averages within each 20 ha plot independently and then averaged across all plots in each fire. A separate average was also calculated for only the plots that had pellets present. Using the formula provided by Krebs et al. (2001b) I then translated the average number of pellets in each 20 ha plot into an estimate of hares/ha.

### **2.2.2 Vegetation surveys**

Within each site I sampled vegetation at 15 randomly selected points. At each location, I used a densitometer to measure canopy cover and a 2 m coverboard read from 10 m due south of the pellet plot to measure understory cover (Hodges et al. 2009). Shrub cover was recorded as the percent cover per species along a 10 m x 0.5 m belt transect. Total shrub cover could be greater than 100% because individual species cover could overlap other species' cover. The number of downed logs (>5 cm diameter) was recorded in the transect.

Within a 1 m radius circle at the north end of the pellet plot, I recorded the species, relative height, and diameter at breast height (DBH) of all sapling trees (DBH <7.5 cm). I used variable distance sampling with a relascope and a metric basal area factor of 4 (Husch et al. 2003, Hodges et al. 2009) to identify canopy trees and snags, which were then measured with a DBH tape to determine DBH.

### **2.2.3 Regression analyses and AIC modelling**

I used one-way ANOVAs to test whether the relative abundance of snowshoe hares differed in large, medium, or small fires, and mature forest. Linear regression was used to relate hare pellet density to the vegetation variables.

To determine what variable or set of variables best explains snowshoe hare abundance, I used Akaike's information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). A set of *a priori* models were chosen prior to field surveys based on previously identified relationships between hare abundance and post-fire vegetation (Hodges et al. 2014, Cheng et al. 2015). Models with  $\Delta$ AIC values <2.00 were considered to have stronger support than the other *a priori* models. Models were also compared based on AICc weights. All statistics were done in R 3.3.2 (R Core Team 2016) using R Studio 1.0.136 (RStudio Team 2016) with the package AICcmodavg (Mazerolle 2016) used to evaluate candidate AIC models.

## 2.3 Results

### 2.3.1 Relative abundance of snowshoe hares in burns

Snowshoe hares were found at 14 of 33 total sites (42%). There were significant differences in the number of hare pellets found in large ( $10.4 \pm 13.1$ ), medium ( $0.3 \pm 0.7$ ) or small burns ( $0 \pm 0$ ), and mature sites ( $0.8 \pm 1.0$ ) (Figure 2.1). These numbers translate to densities of 3.8, 0.2, 0.0, and 0.4 snowshoe hares per hectare in large, medium, and small burns, and mature forest, respectively (Krebs et al. 2001b). Snowshoe hare pellets were found at more than half of the sites in all three large burns (Okanagan Mountain Park: 67% (4 of 6 sites), McClure East: 67% (2 of 3 sites) and McClure West: 60% (3 of 5 sites), Table 2.2). In large fire sites, density ranged from 0.0 pellets to 45.2 pellets. McClure East had the highest average number of hare pellets across all 20 ha sites with  $18.6 \pm 23.6$  (density of 5.9 hares/hectare). McClure West had  $9.3 \pm 12.9$  pellets (3.1 hares/ha) and Okanagan Mountain Park had the lowest number of hare pellets with  $7.1 \pm 8.4$  (2.5 hares/ha). When only sites that had hares were considered, the number of pellets were  $28.0 \pm 24.4$  (8.9 hares/ha),  $15.5 \pm 13.8$  (5.2 hares/ha), and  $10.7 \pm 8.1$  (3.8 hares/ha) for McClure East, McClure West, and Okanagan Mountain Park, respectively. When all sites were considered together, the average number of hare pellets found in large burns was  $10.4 \pm 13.6$  pellets (3.8 hares/ha). When only sites that had hare pellets were considered the average was  $16.1 \pm 14.0$  pellets (5.6 hares/ha) (Table 2.2).

Hare pellets were found at only one of the medium burns (Falkland: 1 of 2 sites). The Falkland Fire averaged  $0.9 \pm 1.3$  pellets (0.4 hares/hectare). The average pellets at medium fire sites which had hares was  $1.9 \pm 0$  (0.8 hares/ha). When all medium fire sites were combined there was an average of  $0.3 \pm 0.7$  pellets (0.3 hares/ha). No hare pellets were found in small

fire sites. Mature forest sites had hare pellets in 57% of sites (4 of 7 sites). Pellet density ranged from 0 to 2.7, with an average of  $0.8 \pm 1.0$  pellets (0.4 hares/ha). In the sites that had hares the average was  $1.4 \pm 0.9$  pellets (0.6 hares/ha).

### **2.3.2 Pellet and vegetation regressions**

The density of sapling trees was significantly and positively correlated to number of hare pellets in all sites ( $F_{1,31}=99.75$ ,  $p < 0.01$ ; Figure 2.2). When sapling trees were divided into species, lodgepole pine saplings remained significantly correlated to pellet number on their own ( $F_{1,31}=90.24$ ,  $p < 0.001$ ; Figure 2.3). No other vegetation variable was correlated to the number of hare pellets (Appendix A, Table A.1).

### **2.3.3 Vegetation and fire size correlations**

The numbers of living canopy trees and canopy cover were strongly positively correlated with fire size ( $R^2=0.66$ ,  $p < 0.01$ ;  $R^2=0.78$ ,  $p < 0.01$ , respectively). Sapling number, understory cover, shrub cover, coarse woody debris, snags, and living canopy trees were not significantly correlated to fire size (sapling trees in Figure 2.4, all others in Appendix A, Table A.2). Large wildfires had a wider range in the number of sapling trees present (small:  $7.2 \pm 10.6$ ; medium:  $18.9 \pm 27.5$ ; large:  $50.1 \pm 51.5$ ).

### **2.3.4 AIC model output**

Multivariate analyses determined that only the number of sapling trees was substantially supported in predicting pellet densities in burned forests (Table 2.3). The next three strongest models all had sapling number as a variable and either shrub cover ( $\Delta AIC = 2.31$ ), fire size

class (large, medium, small, or mature forest) ( $\Delta AIC = 2.58$ ), or the number of total canopy trees ( $\Delta AIC = 2.58$ ). Model 1 (sapling trees only) was 3.12 times more likely than the next highest model based on AICc weights.

## 2.4 Discussion

Snowshoe hare density is highly variable after wildfire. I found that wildfire size has a large impact on hare populations, with large burns having the widest range of hare densities and the highest densities overall (Table 2.2). Hypothesis one was therefore supported because I found that hares were indeed found at higher density in large burns than small burns and there was a trend towards sapling trees being more abundant after large fires. Hypothesis two was also supported: snowshoe hare abundance was much more varied in large burns. In large burns, snowshoe hares were either not present at the sampling sites or present in very high density. In small burns, medium burns, or mature forest, hares were either absent or at low density.

Of all the vegetation variables in this study, only the density of sapling trees was correlated with the hare pellet index. AIC models also found shrub cover and the number of canopy trees to have moderate explanatory power when considered with sapling trees. These results support previous studies that found that regenerating lodgepole pine stands offer particularly good habitat for snowshoe hares (Hodges 2000b, Mowat and Slough 2003, Cheng et al. 2015). Lodgepole pine is a serotinous conifer species whose cones open most readily following severe crown fires (Turner et al. 1997, Turner and Dale 1998, Nyland 1998, Anderson et al 2004). It is a favourite food of snowshoe hares in the region of this study due to its nutritional value (Hodges 2000a, b, Ellsworth et al. 2013,2016). I found that hares

were present more frequently and in higher abundances within large fires than any other forest type studied. The plots that had the highest abundances of hares were also those that had the highest density of lodgepole pine saplings, a finding supported by Hodges et al. (2009) and Cheng et al. (2015). I found that there was no difference in understory cover between wildfire sizes or mature forest. Foraging hares ate the most in lodgepole pine stands in winter, which may suggest more available food (Chapter 3).

The positive relationship between snowshoe hare density and dense lodgepole pine sapling stands is also found in forest thinning (Ivan et al. 2014) or regeneration studies (Berg et al. 2012). Animals respond to vegetation and habitat, not the exact disturbance (Monamy and Fox 2000, Boyce et al. 2003, Lindenmayer et al. 2008), so it is unsurprising that the associations between vegetation and hares are similar in post-fire and post-harvest habitats.

The large fire sites in this study were heterogenous and variable in the vegetative cover measured. This variability is likely the reason I did not find significant difference in overall vegetation between the different sizes of burns. Heterogeneity is expected in large burns (Turner et al. 1994, 1997, 1998, Turner and Dale 1998) and may contribute to higher populations of animals. Related hare species (*Lepus timidus*) have shown highest abundance in heterogenous habitats when compared with more uniform habitats (Rehnus et al. 2016). Snowshoe hares use a variety of habitats for breeding and foraging (Hodges 2000a, b, Hodson et al. 2011) so heterogeneity within the landscape is an important factor when considering populations.

The high densities of snowshoe hares in large burns may also be influenced by the spatial distribution of regenerating stands. The spatial variation in available patch size and structure following wildfire is predicted to impact the movement of animals across a

landscape (McKenzie et al. 2004) as is the scale of the fire itself (Boyce et al. 2003). Turner et al. (1994) found that severely burned patches tended to be more aggregated and that lodgepole pine saplings regenerated more densely in larger severely burned patches (Turner et al. 1997). While regenerating lodgepole pine stands are good habitat for snowshoe hares in southern British Columbia (Chapter 3), patch dynamics may also play a role in hare abundance. The risk of predation for hares increases as cover decreases (Griffin et al. 2005, Hodges et al. 2014). Snags fall most often in the first 3-15 years post fire (Perera et al. 2011) in areas that experienced less severe burns (Angers et al. 2011, Boulanger et al. 2011) and can result in more open patches than severely burnt areas in this time frame (Perera et al. 2009, 2011). In cases where early lodgepole stands are large enough to support hare populations, but are separated from other less suitable forest types, it is possible that hares will not travel from patch to patch. Indeed, Vanbianchi et al. (2017) found that Canada lynx (*Lynx canadensis*) navigate 10-year-old burned forests in Washington by selecting fire-skips and regenerating stands. The openness of much burned forest may be enough to deter snowshoe hares from making the trek between distant patches because they are more likely to be spotted by predators (Griffin et al. 2005) and such long movements without foraging can be energetically costly, both for movement and stress effects (Creel and Christianson 2008, Creel et al. 2009).

Large, severe wildfires are becoming more common because of climate change. These large-scale disturbances create a distinctly heterogenous landscape of open, regenerating, and unburned patches. We still know very little about how small mammals respond to fire-altered forests in North America (Hutchen et al. 2017). This study builds on the growing body of evidence that shows mammal response to fire is just as dynamic as the



fires themselves (Griffiths and Brook 2014, Zwolak 2009). At the fires in this study, hare population response was not as simple as the increase or decrease described for most small mammals (Hutchen et al. 2017).

Snowshoe hares are found at highest densities in dense, regenerating lodgepole pine stands following large wildfires in southern British Columbia. But large burns also had patches where no hares were found. Hares were also absent from all the small burns I surveyed, and from most of the medium fires. In mature forests, hares were found at just over half of the sites but at very low numbers. The huge variation from highest hare density to no hares at all seen in large burns is the product of habitat heterogeneity. Large wildfires can burn in more severe patches and physically reach more diverse landscapes than smaller fires (Keane et al. 2008). This variation leads to a diverse landscape of open stands, densely regenerating sapling stands, and intermediary stands. This patchwork of highly variable habitat is not found in smaller wildfires because they lack the physical size or intensity to create such patches. In turn, this landscape heterogeneity provides snowshoe hares with a diverse range of habitats to interact with, some good (e.g., areas dense in food) and some poor (e.g., open areas with no food).

## **2.5 Directions for future research**

This study shows that snowshoe hare abundance following a wildfire is highly correlated to the density of regenerating lodgepole pine saplings. Further, previous research has shown that lodgepole pine saplings grow most densely in severely burned forest patches. A fruitful next step in this research would be to conduct a detailed population assessment of snowshoe hares using capture-recapture surveys in multiple burns based on burn patch

severity. By using more than one fire, it will be possible to see if the predicted trend that severely burned areas have more snowshoe hares holds across multiple fires.

**Table 2.1** Site descriptions based on data from iMAPBC and the British Columbia Land Classification system with the Vegetation Resources Inventory data set.

Site Name	Fire Number	Size Class	Size (ha)	Ignition date	Ignition source	Elevation (m)	Leading species <sup>1</sup>
Okanagan Mountain Park	K50628	Large	25635	8/16/2003	Lightning	360-1600 <sup>3</sup>	Lodgepole Pine (var. <i>latifolia</i> ), Douglas Fir, Ponderosa Pine
McClure West	K20272	Large	17954 <sup>2</sup>	7/30/2003	Person	380-1400	Interior Douglas-Fire (var. <i>glauca</i> ), Lodgepole Pine (var. <i>latifolia</i> ), Aspen, Spruce hybrid
McClure East	K20272	Large	9183 <sup>2</sup>	7/30/2003	Person	380-1300	Interior Douglas Fir (var. <i>glauca</i> ), Lodgepole Pine (var. <i>latifolia</i> ), Paper Birch
Vaseux Lake	K50661	Medium	4313	8/22/2003	Person	340-1420	Ponderosa Pine, Interior Douglas Fir (var. <i>glauca</i> ), Western Larch
Falkland (Cedar Hills)	K40300	Medium	1223.1	8/1/2003	Person	500-1160	Interior Douglas Fir, Ponderosa Pine, Lodgepole Pine (var. <i>latifolia</i> )
Vermellion Creek	K20436	Medium	1223.1	8/7/2003	Lightning	660-1600 <sup>4</sup>	Interior Douglas Fir (var. <i>glauca</i> ), Spruce hybrid, Engelmann Spruce
Queest Mountain	K30551	Small	169.8	8/20/2003	Lightning	1420-1900	Subalpine fir, Spruce hybrid
Chase	K30400	Small	109.5	8/28/2002	Person	400-900	Douglas-Fir, Ponderosa Pine

<b>Site Name</b>	<b>Fire Number</b>	<b>Size Class</b>	<b>Size (ha)</b>	<b>Ignition date</b>	<b>Ignition source</b>	<b>Elevation (m)</b>	<b>Leading species<sup>1</sup></b>
Owlhead	K30236	Small	84.3	7/24/2003	Person	360-780	Interior Douglas Fir (var. <i>glauca</i> ), Aspen

<sup>1</sup>Based on Stand Age classes. Names represent the exact description on the Land Classification system. e.g. “Spruce hybrid” and “Spruce” were different names, and since the considered polygons were named “Spruce hybrid” that is the name used here.

<sup>2</sup>Total fire size was 27137 ha. Division was done by measuring the perimeter of the fire using the North Thompson River as a barrier in iMAPBC.

<sup>3</sup>We did not go to the highest point on Okanagan Mountain

<sup>4</sup>Only the lower portion of the burn was accessible. Total elevation was 1820-2020

**Table 2.2.** Snowshoe hare pellet counts and hares per hectare at field sites. Hares/ha were calculated using the equations provided by Krebs et al. (2001) that relate hare pellets to abundances of snowshoe hares.

	<b>Pellets <math>\pm</math> SD</b>	<b>Hares/ha</b>
<b>Okanagan Mountain park</b>		
Crawford	4.3 $\pm$ 8.1	1.7
Forest Service Road	21.0 $\pm$ 15.3	7.1
Myra Valentine	4.1 $\pm$ 4.8	1.6
FSR - Logs	13.3 $\pm$ 18.4	4.7
Kupier	0.0 $\pm$ 0.0	0.0
Okanagan Lookout	0.0 $\pm$ 0.0	0.0
Average	7.1 $\pm$ 8.4	2.5 $\pm$ 2.8
<b>McClure East</b>		
Cow Pond	10.7 $\pm$ 14.8	3.9
Highway	0.0 $\pm$ 0.0	0.0
Badger Lake	45.2 $\pm$ 31.9	13.9
Average	18.6 $\pm$ 23.6	5.9 $\pm$ 7.2
<b>McClure West</b>		
Km 10	0.0 $\pm$ 0.0	0.0
Fishtrap	0.0 $\pm$ 0.0	.0.0
Gorman Scotte	29.0 $\pm$ 26.3	9.4
Wolsey Road	1.3 $\pm$ 3.0	0.6
Snake Lake	16.2 $\pm$ 23.0	5.6

	<b>Pellets ± SD</b>	<b>Hares/ha</b>
Average	9.3±12.9	3.1±4.2
<b>Falkland</b>		
Cow Kill	1.8±0	0.8
Rest Stop	0.0±0.0	0.0
Average		0.4±0.6
<b>Vaseux</b>		
Fence	0.0±0.0	0.0
Logging Road	0.0±0.0	0.0
Dutton Creek	0.0±0.0	0.0
Average	0.0±0.0	0.0±0.0
<b>Vermellion</b>		
Middle	0.0±0	0.0
South	0.0±0	0.0
Average	0.0±0	0.0±0.0
<b>Chase</b>		
Middle	0.0±0	0.0
Edge	0.0±0	0.0
Average	0.0±0	0.0±0.0
<b>Owlhead</b>		
Owlhead	0.0±0	0.0
Average	0.0±0	0.0±0.0

	<b>Pellets <math>\pm</math> SD</b>	<b>Hares/ha</b>
Low	0.0 $\pm$ 0	0.0
High	0.0 $\pm$ 0	0.0
Average	0.0 $\pm$ 0	0.0 $\pm$ 0.0
<b>Mature Forest</b>		
Falkland	0.6 $\pm$ 1.2	0.3
Gillard - Okanagan	0.0 $\pm$ 0	0.0
Angel Springs - Okanagan	2.7 $\pm$ 5.3	1.1
McClure	1.5 $\pm$ 2.7	0.7
Owlhead	0.0 $\pm$ 0	0.0
Vaseux	0.0 $\pm$ 0	0.0
Vermillion	0.9 $\pm$ 1.6	0.4
Average	0.8 $\pm$ 1.0	0.4 $\pm$ 0.4

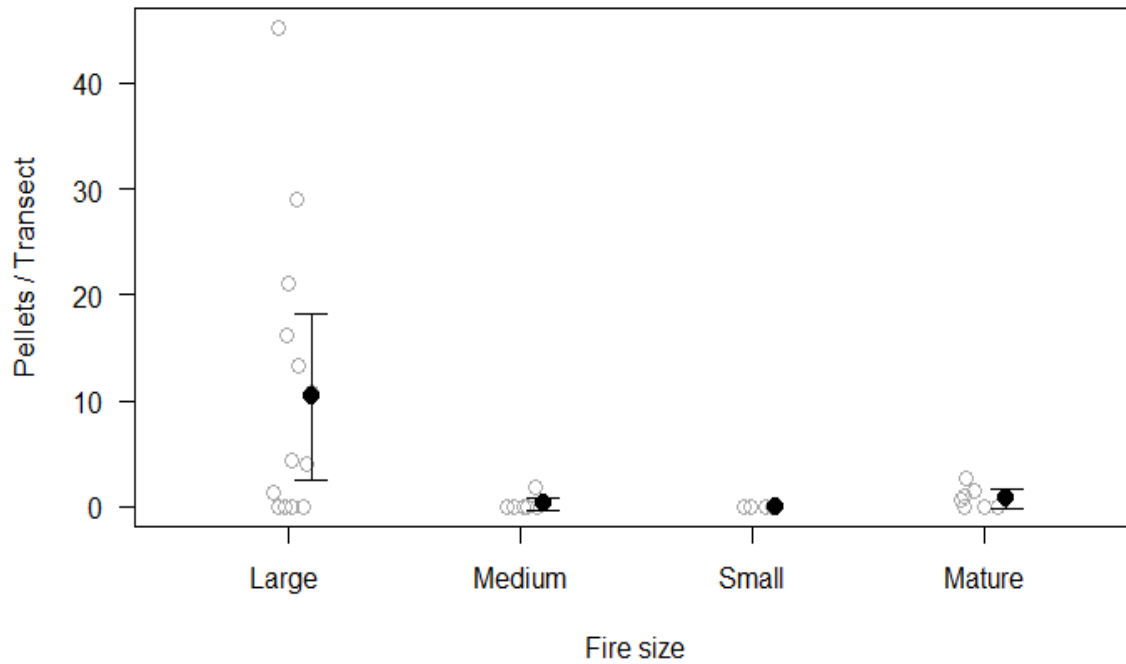
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**Table 2.3.** AIC models relating vegetation to snowshoe hare pellet abundance in all sites (burned and mature).

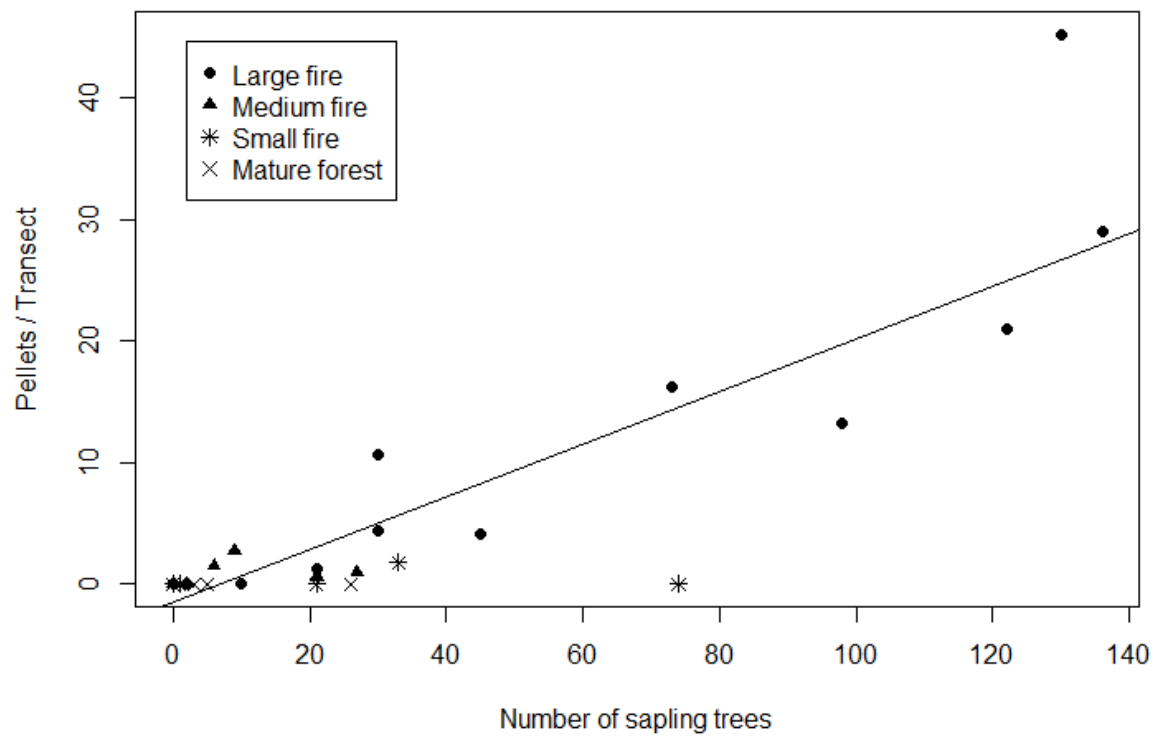
<i>Model variables</i>	<i>K</i>	<i>AICc</i>	<i>ΔAICc</i>	<i>Model Likelihood</i>	<i>AICcWt</i>	<i>LL</i>	<i>Cum.Wt</i>
Saplings	3	167.68	0	1	0.53	-80.29	0.53
Saplings + Shrub cover	4	169.99	2.31	0.31	0.17	-80.04	0.70
Saplings + Canopy Trees	4	170.25	2.58	0.28	0.15	-80.17	0.85
Saplings + Fire class <sup>1</sup>	4	170.26	2.58	0.27	0.15	-80.18	0.99
Saplings + Snags + Fire class	6	176.71	9.04	0.011	0.01	-80.15	1.00
Canopy cover	3	202.48	34.80	0.00	0.00	-97.69	1.00
Fire class	3	202.98	35.30	0.00	0.00	-97.94	1.00
Canopy trees	3	204.67	37.00	0.00	0.00	-98.79	1.00
Canopy cover + Understory cover	4	205.15	37.47	0.00	0.00	-97.62	1.00
Snags + Understory cover	4	206.13	38.45	0.00	0.00	-98.11	1.00
Canopy cover + Understory cover + Shrub cover	5	206.45	38.77	0.00	0.00	-96.72	1.00
Canopy cover + Understory cover + Fire class	5	206.72	39.04	0.00	0.00	-96.86	1.00
Canopy trees + Understory cover	4	206.96	39.28	0.00	0.00	-98.53	1.00

<sup>1</sup>Fire class is divided into 4 categories: small, medium, or large fires that burned in 2003-2004, and mature forest that had not burned in the previous several decades.

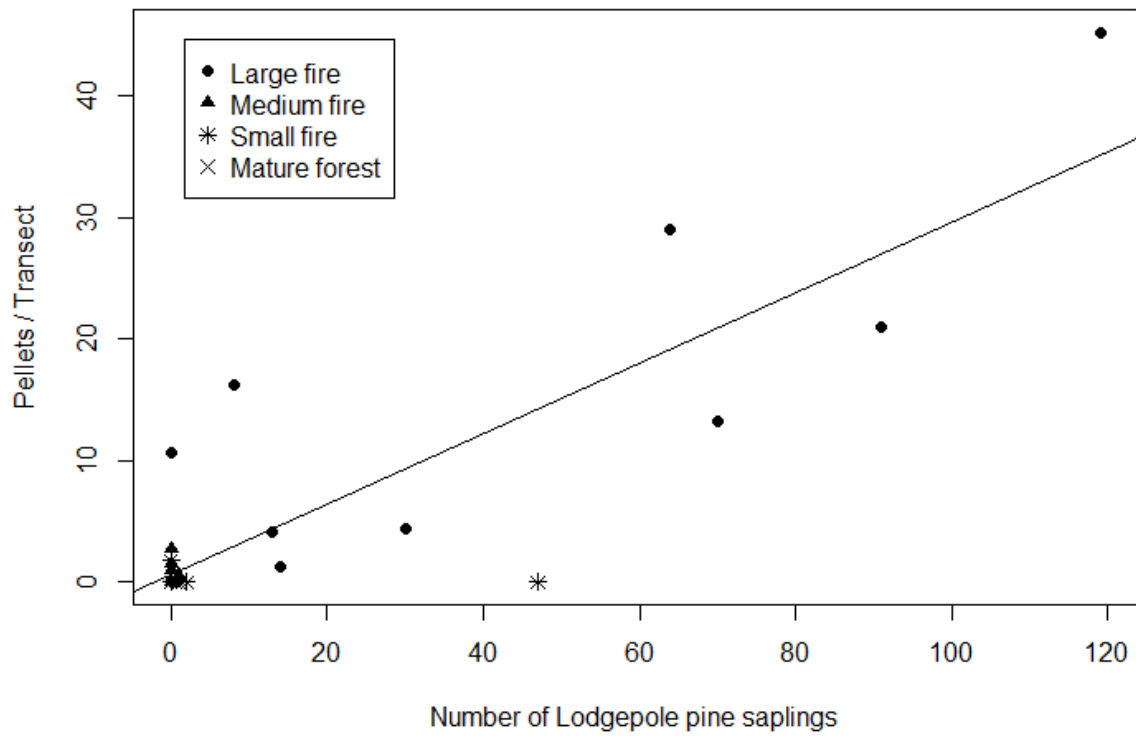




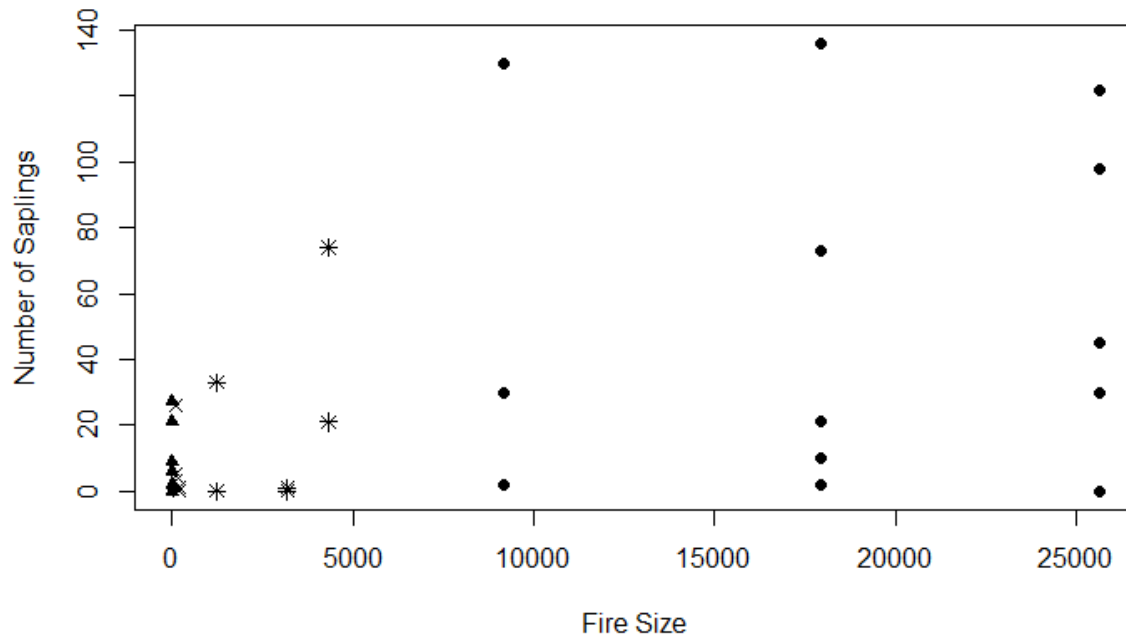
**Figure 2 1.** Snowshoe hare pellet counts across large, medium, and small fires, and mature forest sites. One-way ANOVA found significant difference in the number of hare pellets ( $F_{3,27}=3.21, p=0.038$ ). Open dots are individual averages from 20 ha sites. Filled dots are the average pellets counts from all plots sampled for a given fire size. Error bars are 95% confidence intervals.



**Figure 2.2.** Snowshoe hare pellets per transect in relation to sapling trees. Pellet number was strongly correlated with the density of sapling trees in each 2 m radius vegetation plot in burns and mature forest ( $R^2=0.76$ ,  $p < 0.01$ ).



**Figure 2.3.** The number of Lodgepole pine sapling trees per plot related to the number of hare pellets. Lodgepole pine sapling density in 2 m radius vegetation plots was significantly correlated to pellet number ( $R^2=0.74$ ,  $p < 0.01$ ).



**Figure 2.4.** Sapling density per 2 m radius vegetation plot in relation to fire size. Saplings were not significantly correlated to fire size ( $R^2=0.14$ ,  $p = 0.06$ ).

## Chapter 3 Snowshoe hare foraging behaviour in post-fire conifer forests

### 3.1 Background

Animals are under strong pressure to adapt their foraging behaviours to maximize the food they consume and minimize their risk of predation (Stephens and Krebs 1986, Lima and Dill 1990). As individuals forage across landscapes, they are constantly forced to answer whether the reward of staying in this patch outweighs the risk (Henderson and Quandt 1971, Stephens and Krebs 1986, Houtman and Dill 1998)? However, the riskiness of any given habitat is hard to quantify and is not a simple measure of if a predator is present and hunting (Bowers and Dooley 1993, Griffin et al. 2005, Verdolin 2006, Cresswell 2008). For many prey animals, the indirect effects of predation, such as lower body conditions and increased stress hormones, can be almost as detrimental to continued survival as being eaten (Lima 1998, Cresswell 2008, Creel and Christianson 2008, Creel et al. 2009). Most studies agree that the riskiness of a given habitat patch is tied to the vegetation within, with more open patches possibly being riskier for most prey due to lack of cover (Barbour and Litvaitis 1993, Tufto et al. 1996, Prugh and Golden 2014, Pereoglou et al. 2016).

One of the leading drivers of forest heterogeneity and patchiness in North America is wildfire (Larsen 1980, Bessie and Johnson 1995, Jenkins et al. 2001, Westerling et al. 2006, Keane et al. 2008, Perera and Buse 2014). The severity at which a fire burns, the size it grows to, and the landscape on which it burns all contribute to a highly complex post-fire burn scar (Anderson et al. 2004, Perera and Buse 2014, Keeley 2009). Severely burned patches have fewer residual trees than moderately or lightly burned patches immediately post-fire (Hely et al. 2003, Perera et al. 2009), but as years pass, regeneration of sapling trees can be highest in patches that burned with moderate severity (Anderson et al. 2004). The

differences in cover and available food following a wildfire create highly patchy landscapes on which animals must find adequate food sources while navigating highly risky patches (Agee 2000, Hodson et al. 2011, Miller et al. 2012, Perera and Buse 2014). Post-fire heterogeneity is a rich area of study for small mammal behaviour, as most studies of small-mammal response to fire only describe post-fire population changes in burned forests compared to unburned forest (Hutchen et al. 2017).

The studies on how snowshoe hares respond to fire have examined changes in abundance (Keith and Surrindi 1971, Fox 1978, Paragi et al. 1997, Hodges et al. 2009, Hodson et al. 2011a, Strong and Jung 2012, Allard-Duchêne et al. 2014, Cheng et al. 2015). Snowshoe hares are keystone herbivores and the primary prey species for a host of boreal and montane carnivores including Canada lynx (*Lynx canadensis*), marten (*Martes americana*), and great horned owls (*Bubo virginianus*; Hodges 2000a, b; Hodges and Sinclair 2003, Krebs et al. 2001a). Snowshoe hares primarily favour early seral, regenerating sapling stands but are also found in closed-canopy mature stands (Paragi et al. 1997, Hodson et al. 2011, Hodges et al. 2009) and avoid open areas in forests such as canopy gaps, recent thinning, or clearcuts (Ferron et al. 1998, Griffin and Mills 2004, Fisher and Wilkinson 2005). These patterns in hare abundance and habitat associations are consistent following wildfire as well (Fisher and Wilkinson 2005).

Hares show population declines immediately following a wildfire (Hodges et al. 2009), and population changes inside the burn are linked to increases in vertical canopy cover and understory cover (Hodson et al. 2011), or the density of lodgepole pine (*Pinus contorta*) saplings in areas where lodgepole pine is native (Cheng et al. 2015, Chapter 2). Despite the focus on abundance in studies on snowshoe hare response to fire, foraging

behaviour of hares has been studied in detail in other contexts (Hodges and Sinclair 2003, 2005, Hodges et al 2014, Hodson et al. 2011), with many studies demonstrating risk-induced changes in dietary consumption of nutrients (Rogowitz 1988, Hodges and Sinclair 2003, 2005) or changes in home range size (Hodges 1999, Beaudoin et al. 2004). To date, no study has looked at the movement decisions of snowshoe hares while foraging in altered vegetative conditions after a wildfire.

Snowshoe hare behaviour while foraging can be broken down into three components: tortuosity, speed, and browse (Hodges and Sinclair 2003, 2005, Hodges et al. 2014).

Tortuosity refers to the number of angles made by an individual along a movement pathway, as animals often make more zig-zags in habitats with abundant resources (Fuller and Harrison 2010, Hodges et al. 2014). Hodges et al. (2014) showed that foraging hares moved much more tortuously than hares fleeing the direct threat of a predator. Straight lines are less energetically costly for a fleeing animal and are therefore the best option to out-run a predator when there is the option to do so (Ydenberg and Dill 1986). Speed is how fast an animal moves on a foraging pathway, an estimate of the time spent in each area (Lima and Zoliner 1996, McAdam and Kramer 1998, Tufto et al. 1996). Browse is the amount and type of food consumed along a pathway, with a predicted trade-off between speed of movement and time spent eating (Hodges 1999, Godvik et al. 2009, Bartumeus et al. 2016).

The patches left after a wildfire do not produce uniform habitats. Vegetation after many fires is patchy, clustered, and variable (Perera and Buse 2014). At two extreme ends of this variation in Western forests are open stands and regenerating sapling stands. Open stands have not experienced significant sapling tree regrowth, but have lost overstory tree cover. Sapling stands contain dense post-fire sapling regeneration. The availability of browse in

these stands differs: sapling conifers in western North American forests are some of snowshoe hares' preferred diet (Hodges 2000b), and sapling stands have more available browse and provide more cover for hares than open stands (Rehnus et al. 2016).

For a snowshoe hare seeking to maximize its food intake and minimize its chances of being eaten, the ideal foraging strategy would be to spend more time eating in patches with lots of food and cover from predators and spend less time eating in patches with less food and cover (Stephen and Krebs 1986). In a post-fire landscape, hares should move slower and eat more in sapling stands and move faster and eat less in open stands. Further, since sapling stands can be incredibly dense and provide cover in all directions (Lewis et al. 2011, Ewacha et al. 2014), it would make sense that hares in sapling stands will move more tortuously, given that they do not have to continually seek cover.

In this study, I examine how the foraging behaviour of snowshoe hares (*Lepus americanus*) differs in open and regenerating burned patches, and in mature forests. I use vegetation surveys to describe the microhabitat vegetation along snowshoe hare foraging pathways. I also use measures of hare tortuosity, speed, and browse to assess movement changes made while foraging. With these data, I address the following two predictions:

- 1) Snowshoe hares would browse the least, move the fastest, and have less tortuous pathways in open patches than in either sapling or mature patches
- 2) Hare speed, tortuosity, and browse will be related to the vegetation cover along the pathways.



## 3.2 Methods

### 3.2.1 Study Area

I conducted this field work in the area burned by the Okanagan Mountain Park Fire (Figure 3.1, full map in Appendix B, Figure B.1). The wildfire burned south of Kelowna, British Columbia, encompassing the entirety of Okanagan Mountain Provincial Park (hence the name) and northern sections of Myra Bellevue Provincial Park (Appendix B). The Okanagan Mountain Park Fire began due to a lightning strike on the evening of August 16<sup>th</sup>, 2003 and quickly grew into a Rank 6 crown fire, the most damaging wildfire ranking (BCMFR Wildfire Management Branch 2011). This wildfire burned 25,635 ha of forest. Over 2500 fires burned in the interior of British Columbia in 2003 (referred to as Firestorm 2003, Filmon 2004) with the Okanagan Mountain Park fire being the largest fire in British Columbia's recorded history and one of the most devastating, with over 33,000 Kelowna residents evacuated and 238 homes burned or significantly damaged (Geomans and Ballamingie 2013).

Before the fire, the low elevation forests were primarily ponderosa pine (*Pinus ponderosa*)-Lodgepole pine and Douglas fir (*Pseudotsuga menziesii*)-Lodgepole pine at higher elevations. The adjacent Myra-Bellevue area contained Douglas fir-lodgepole forest, with occasional red cedars (*Thuja plicata*). Regrowth in both systems was dominated by lodgepole pine saplings, with some aspen (*Populus* spp.) and birch (*Betula* spp.). Open sites had primarily willow (*Salix* spp.), birch, and rose (*Rosa* spp.). These three shrubs also comprised the majority of shrub cover at most sites. I chose unburned mature forest sites in mostly Douglas fir-lodgepole pine forests to the east of the Okanagan Mountain Park Fire to best match pre-fire conditions for most of the burned sites. Okanagan Mountain Park and

southern sections of the burn were not chosen as field sites due to winter road-closures and restricted access.

After sites in “burned” and “unburned mature” forests were selected, the burned sites were further divided in “open” and “sapling” stands. Open stands were visually identified in the field as patches of burn with few to no sapling conifers, but some had deciduous cover and standing snags. Sapling stands were identified in the field as stands that contained dense patches of regenerating lodgepole pine saplings. Anderson et al. (2004) found that lodgepole pine stands in Yellowstone were densest in moderately burned patches, however the exact relationship between patch severity and vegetative regrowth is complex and not easily simplified into open/severe burns or regrowth/moderate burns.

### **3.2.2 Snow tracks of snowshoe hares**

I obtained foraging pathways by searching forest stands for snowshoe hare tracks over two winters (2015-16 and 2016-17), and then backtracking for a minimum of 30 m along the pathway. Snow conditions rarely allowed me to find clear tracks longer than 30 m, especially if hares used a runway that prevented identifying individual pathways. Foraging pathways were distinguished from potential fleeing pathways by the absence of nearby predator tracks or the presence of either fecal pellets (hares defecate while foraging; Hodges, 1999) or browse (twigs with the characteristic 45° angle of browse; Hodges et al. 2014). Pathways were divided into 5 m sections and marked at each section end with a pin flag (Hodges et al. 2014). To calculate turning angles a sighting compass was used to measure the bearings between each flag. The number of tracks in each section was recorded to measure

the average speed of each hare (Hodges et al. 2014). This index determines travel speed and does not consider time spent feeding.

Tortuosity was calculated using a fixed-step random walk model (Bovet and Benhamou 1988). These models use  $\alpha_i$ , the consecutive turning angles, to describe an N-step path with  $\Phi$ , the mean vector, where  $\Phi = \arctan(\sum \sin \alpha_i / \sum \cos \alpha_i)$ . The correlation was calculated as  $r = [(\sum \cos \alpha_i)^2 + (\sum \sin \alpha_i)^2]^{0.5} / (N-1)$ , where  $N$  is the number of turning points along a path. Given that  $r$  lies on a continuum from 0 to 1 (random to perfect correlation), with 1 meaning no tortuosity, then the tortuosity ( $t$ ) can be described as  $1-r$  (Hodges et al. 2014).

### **3.2.3 Vegetation and browse surveys**

I surveyed vegetation at 3 points along each hare pathway (beginning, middle, and end). At each point, I used a 2 m radius sample plot and counted the number of all living and dead saplings and canopy trees (living trees were identified to species). Canopy cover was measured using a densitometer and standing directly over the section pin flag. Understory cover (1 m above snow level) was visually estimated to 5% by backtracking the pathway by 5 m.

Snowshoe hare browse on woody material shows a distinctive 45° angle and is easily distinguished from browse by other herbivores (Hodges et al. 2014). For each 5 m pathway section, I identified fresh browse points along the pathway. Each browse point was identified to species and I used calipers to measure the diameter of the twig. I used these measures to calculate the total number of browse points per pathway and the average diameter of browse per species.

### 3.2.4 Analyses

I used one-way ANOVAs to test whether forest stand type (open, mature, and sapling) affected the tortuosity, average number of steps, and average browse of hare foraging pathways. ANOVAs were also used to determine difference in vegetative cover between patches. I used linear regression to determine whether pathway tortuosity, speed, and browse were significantly correlated.

### 3.3 Results

I sampled 34 snowshoe hare tracks (18 burn and 16 mature) over 2 winters (2015-2016 and 2016-2017). The mature forest tracks were in red cedar, lodgepole pine, or Douglas fir forest and burned tracks were in open birch/willow stands (11 tracks) or regenerating lodgepole pine sapling stands (7 tracks; Appendix B, Figure B.2).

Canopy cover was significantly lower in open stands in the burn ( $12.21 \pm 20.47$  mean  $\pm 1$  SD) than mature stands ( $41.0 \pm 30.8$ ) ( $F_{2,31}=3.59$ ,  $p=0.039$ , Figure 3.2a). Sapling stands in the burn ( $25.0 \pm 30.1$ ) had an intermediate degree of canopy cover. There was no difference in understory cover between open, sapling, or mature forest ( $24.7 \pm 25.7$ ;  $19.8 \pm 12.4$ ;  $12.7 \pm 12.7$ , respectively;  $F_{2,31}=1.50$ ,  $p=0.238$ , Figure 3.2b). No difference was found in the total number of trees, or the number of Douglas-fir, lodgepole pine, or snag trees, found along hare pathways (Appendix B, Figure B.3).

Understory cover and canopy cover were not significantly correlated to hare tortuosity or browse in open, sapling, or mature stands (Table 3.1). Canopy cover was significantly correlated with hare speed in sapling stands, but not open or mature stands

(Table 3.1). Understory cover was not correlated to hare speed in open, sapling, or mature patch comparisons (Table 3.1).

### **3.3.1 Movement comparisons in Open, Sapling, and Mature patches**

Foraging hares moved with similar tortuosity among open ( $n=11$ ,  $0.59\pm 0.17$ ), sapling ( $n=7$ ,  $0.63\pm 0.18$ ), or mature ( $n=16$ ,  $0.54\pm 0.28$ ) stands ( $F_{2,31}=0.77$ ,  $p=0.65$ ) ( $F_{2,32}=0.77$ ,  $p=0.39$ , Figure 3.3). Hares moved at different speeds in open and mature stands but not open/sapling or mature/sapling (Figure 3.4,  $F_{2,32}=0.7$ ,  $p < 0.05$ ). Hares took fewer steps per 5 m segment (i.e. moved the fastest) in open patches ( $7.0\pm 2.4$ ). All patches showed significant differences in the amount of browse (Figure 3.5;  $F_{2,32}=13.6$ ,  $p < 0.01$ ). Snowshoe hares ate the most in sapling stands ( $3.8\pm 3.0$  stems / 5 m of pathway), a moderate amount in mature forest ( $1.1\pm 0.7$  stems / 5 m), and ate very little in open stands ( $0.3\pm 0.4$  stems / 5 m).

Open stands had 5 browsed species with birch and rose being browsed 1.8 times more often than the next most common species; sapling stands had only 3 browsed species with lodgepole pine trees being browsed 38.5 times more often than the next most common species; and mature stands had 13 species browsed with willow 1.6 times more common than the next most common species (Appendix B, Table B.1). Open stands were also the only forest type where no browse was found along 6 of the pathways.

Only lodgepole pine was analyzed for size differences in browse between stand types. There was no difference in the size of lodgepole pine twigs browsed in open, mature or sapling stands ( $F_{2,176}=1.2$ ,  $p=0.3$ ) with average browse sizes of  $0.25\pm 0.00$  cm,  $0.36\pm 0.03$  cm, and  $0.38\pm 0.02$  cm, respectively. In open stands hares browsed on lodgepole pine only 5 times (compared to 152 in sapling and 22 in mature; Appendix B, Table B.1). Tortuosity, browse,

and speed were uncorrelated to each other in the patches, though there was a trend towards positive relationships (Figures 3.6, 3.7, 3.8).

### **3.4 Discussion**

Snowshoe hares browsed far less often and moved the fastest in open stands, but no differences were seen in pathway tortuosity among stand types. Hares browsed on a higher diversity of species in mature forests (Appendix B) but they browsed the most often in sapling patches and ate mostly lodgepole pine saplings. Lodgepole pine saplings are a preferred browse species for snowshoe hares (Hodges 2000a, b). The smaller stems of sapling conifers are more nutritious than larger stems (Boutin 1984, Hodges and Sinclair 2003, Ellsworth et al. 2013) and are better able to support over-winter hare weight due to the higher nutritional content (Pease et al. 1979).

The highest densities of snowshoe hares after wildfire are found in areas with dense sapling regrowth (Chapter 2). Snowshoe hares at high densities consume more bark and larger twigs (Fox and Bryant 1984, Hodges 2000b), which are less nutritious (Ellsworth et al. 2013). The consumption of less nutritious browse is theorized to occur because of higher populations leading to increased intraspecific competition between hares and interspecific competition with other herbivores (Telfer 1972, Hodges 2000b). Given the low frequency of lodgepole pine browse in open patches, and the low hare densities found in open patches, it is unlikely that these stands are commonly used for foraging. Since I found no difference in the browse diameter for sapling and mature stands, it is likely that the higher densities of hares in sapling stands have not yet reached carrying capacity for those patches (Hodges 2000b).

Hares moved the fastest in open stands, taking the fewest steps to travel the same distance relative to mature stands and sapling stands. Hares who took more steps tended to eat more, though this correlation between amount of food eaten and the number of steps was non-significant. Back-tracking measures the number of steps taken over a fixed distance and is not a true measure of speed (Hodges et al. 2014). Hares that took the same number of steps but browsed more often very likely spent more time on the pathway because eating takes time. A hare would have to remain stationary for longer when eating lots of twigs. Since hares in open patches ate less and took the least number of steps, they very likely spent minimal time in those patches.

Pathway tortuosity was unaffected by patch type. Regardless of whether snowshoe hares moved faster or browsed more, they made roughly the same pathway angles while foraging. In a similar study, Hodges et al. (2014) also found no differences in hare tortuosity between stands. They also noted large variation in hare tortuosities in the mature stands, a pattern I also found. Movement patterns while foraging are highly variable and species-dependent (Pearce-Duvet et al. 2011) so it is not surprising that I found no differences in the tortuosities of foraging hares in the different patches. Even in patches with high sapling density, it may be in a hare's best interest to not stay in a given area and consume all available browse. Doing so would mean the hare has to remain in a small patch for longer, which could expose it to predation (Keith et al. 1993, Vitense et al. 2016). Therefore, even in areas with dense sapling growth, it is likely that snowshoe hares do not move more tortuously because staying in an area and eating all available browse is not a better foraging option than moving through a patch, especially when the patch is large and consistently rich in food (Barbour and Litvaitis 1993, Beaudoin et al. 2004, Vitense et al. 2016).

Here, I found that hares optimized their foraging in burned forests by spending less time eating in open patches and more time eating in regenerating patches without changing tortuosity. The risk of foraging in open patches as opposed to sapling or mature forests could be incurred either through the lower availability of browse or the potential risks of getting eaten themselves (Lima and Dill 1990, Hodson et al. 2010a, b, Hodson et al. 2011, Hodges et al. 2014). I found minimal differences in the pathway-level vegetation at the different patches. Understory cover did not differ between patches and canopy cover was only lower in open patches. The number of trees counted along the pathways was not difference between patches. Since the vegetation along pathways does not differ between stands, snowshoe hares may be selecting for pathways that are more similar than would be a random vegetation sample in the patch would predict.

Most estimates place snowshoe hare home ranges around 5-10 ha (Hodges 1999, Hodges 2000b) so it is unlikely that the hares use only one type of patch. Previous studies have indicated that predator risk strongly affects both snowshoe hare home range size (Beaudoin et al 2004) and reproduction (Boonstra et al. 1998), with home ranges being smaller and reproduction lower when predation risk increases. Hares very likely use all patch types at some point while foraging, and indeed, Feierabend and Kielland (2014) found that radio-collared hares routinely use multiple vegetation types, even when food and cover are readily available in a single area.

### **3.5 Summary**

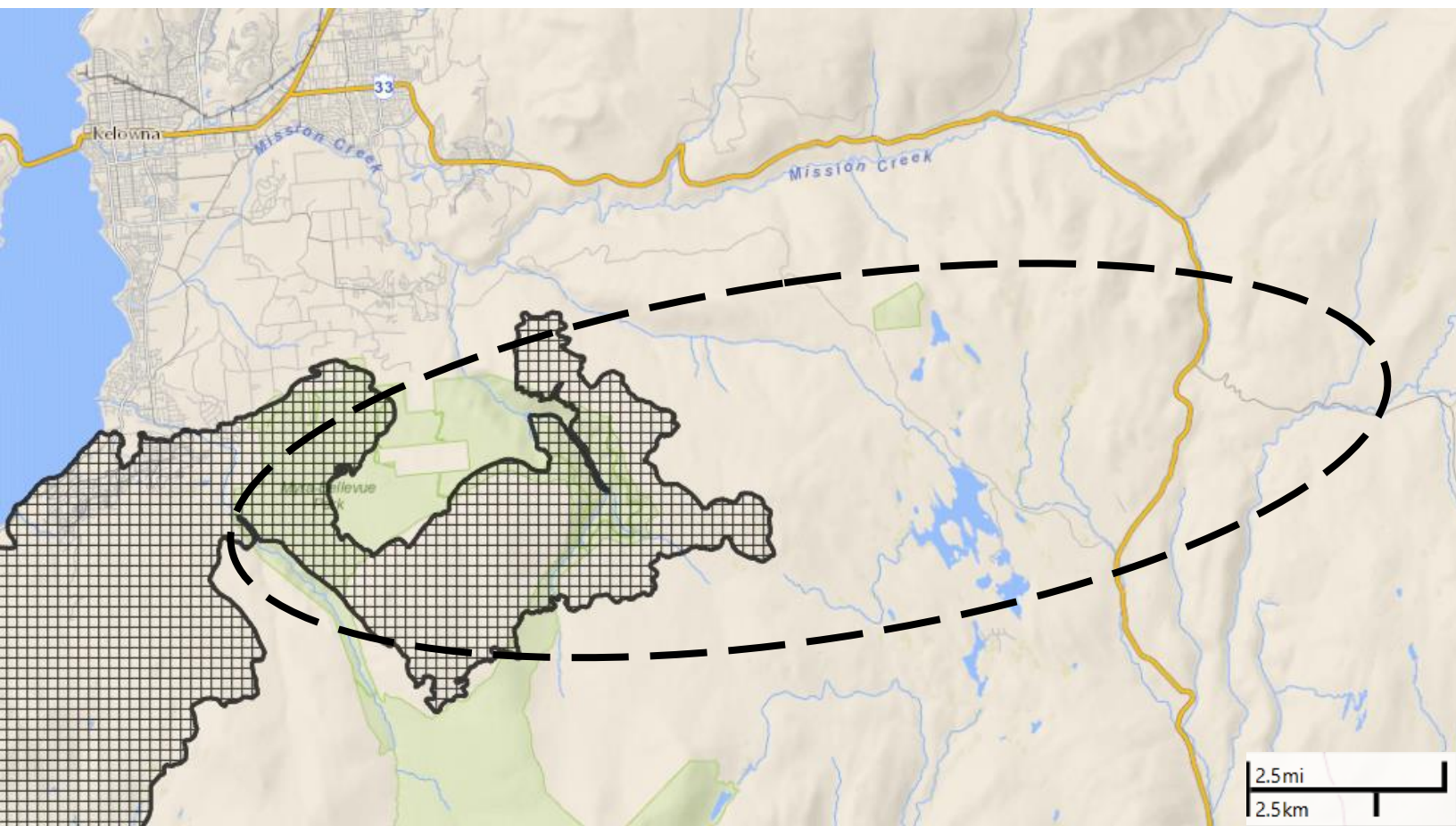
Wildfires are heterogenous disturbances that are influenced by a host of factors (including topography, weather, and seed banks) and the data presented in this chapter show



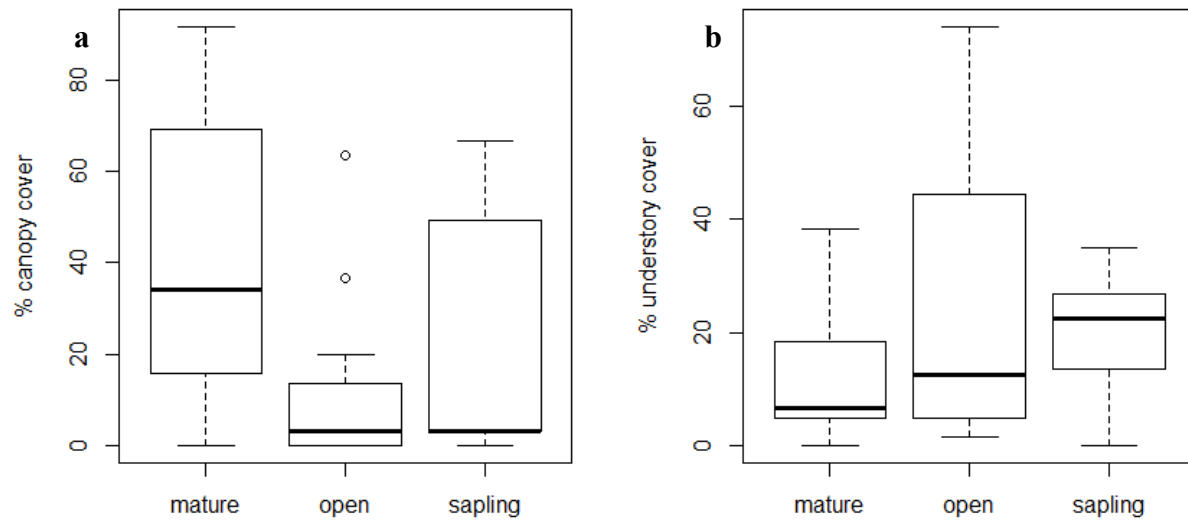
that the vegetative growth following a wildfire is important in understanding how foraging hares use their available habitat. Snowshoe hares adapted their speed and the amount they foraged depending on the stands they were in. These data highlight the need for more consideration of within-burn heterogeneity in post-fire studies of small mammals, rather than the common burn vs. unburned study design (Hutchen et al. 2017). Despite no observable differences in the understory cover, or number of trees, at the pathway scale hares moved the fastest and ate the least in open burned patches. This study shows that the internal heterogeneity within the burn scar matters greatly to snowshoe hares because hares respond to the vegetation and habitat, not the direct disturbance.

**Table 3.1.** Relationships of cover type and hare movement patterns. The only significant regression was speed and canopy cover in sapling forests, where hares took more steps (moved slower) with increasing canopy cover ( $R^2=0.78$ ).

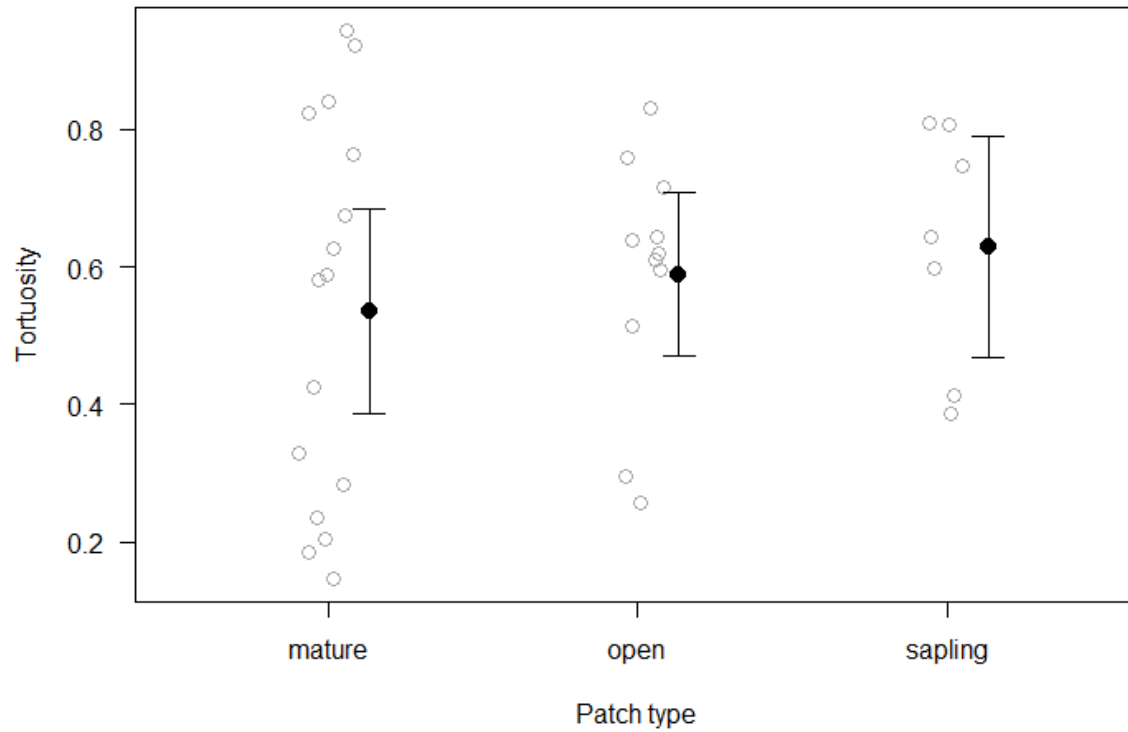
Cover Type	Variable	Stand Type		
		Open	Sapling	Mature
Understory Cover	Tortuosity	$F_{1,9}=0.22$	$F_{1,5}=0.26$	$F_{1,14}=0.19$
		$p=0.64$	$p=0.63$	$p=0.67$
	Speed	$F_{1,9}=3.52$	$F_{1,5}=0.23$	$F_{1,14}=0.71$
		$p=0.09$	$p=0.65$	0.41
	Browse	$F_{1,9}=0.34$	$F_{1,5}=0.02$	$F_{1,14}=2.40$
		$p=0.57$	$p=0.89$	$p=0.14$
Canopy Cover	Tortuosity	$F_{1,9}=2.43$	$F_{1,5}=2.50$	$F_{1,14}=0.12$
		0.15	$p=0.18$	0.74
	Speed	$F_{1,9}=0.32$	<b><math>F_{1,5}=17.63</math></b>	$F_{1,14}=0.10$
		0.58	<b><math>p &lt; 0.05</math></b>	$p=0.75$
	Browse	$F_{1,9}=0.50$	$F_{1,5}=0.12$	$F_{1,14}=0.90$
		$p=0.50$	$p=0.74$	$p=0.36$



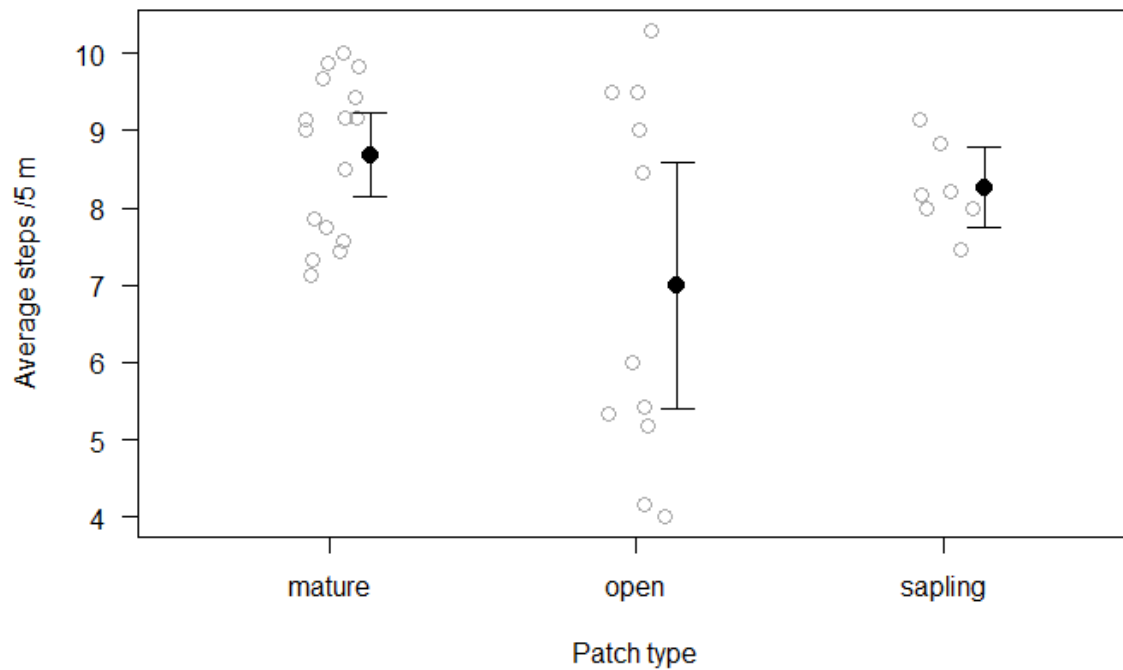
**Figure 3.1.** Spatial range of the Okanagan Mountain Park Wildfire. Thick dashed line shows the approximate range of where field work occurred.



**Figure 3.2a.** Canopy and understory cover in forest patches on foraging pathways. Canopy cover was significantly lower in open stands than in mature stands, but was not different in sapling/open or sapling/mature stands ( $F_{2,31}=3.59$ ,  $p=0.039$ ). **3.2b.** Understory cover was not significantly different in open, sapling, or mature stands ( $F_{2,31}=1.50$ ,  $p=0.238$ ).

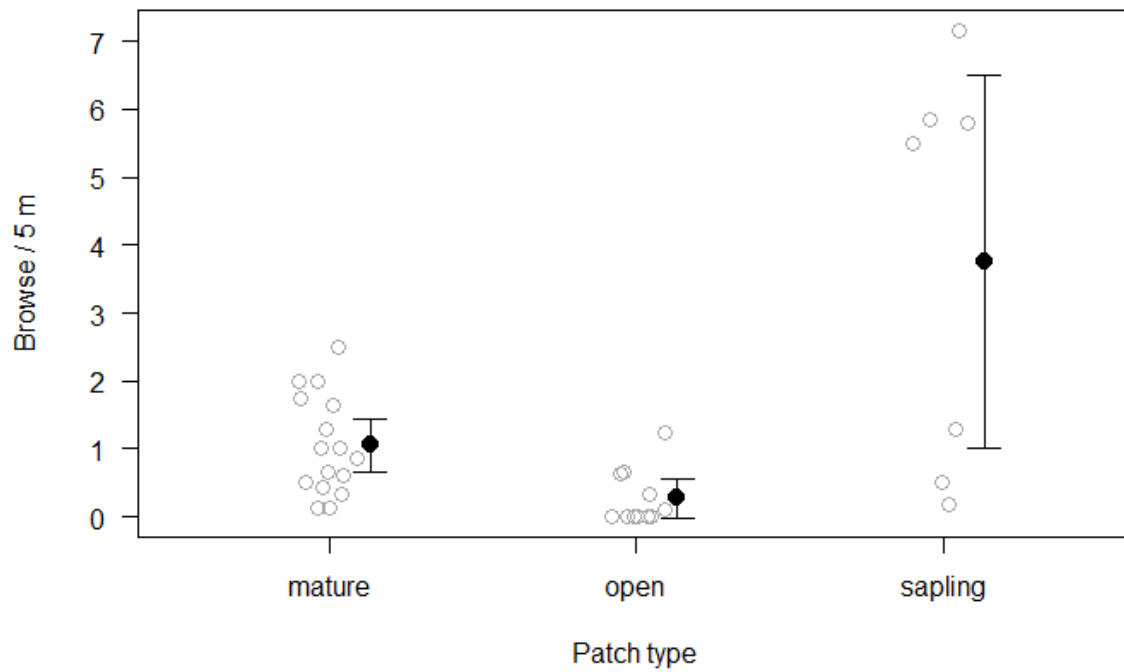


**Figure 3.3.** Snowshoe hare tortuosity in forest patches. Hares moved at similar tortuosities in all patches. High values indicate more tortuous movement. Open circles show individual pathways, filled circles are the mean, and whiskers are 95% confidence intervals.

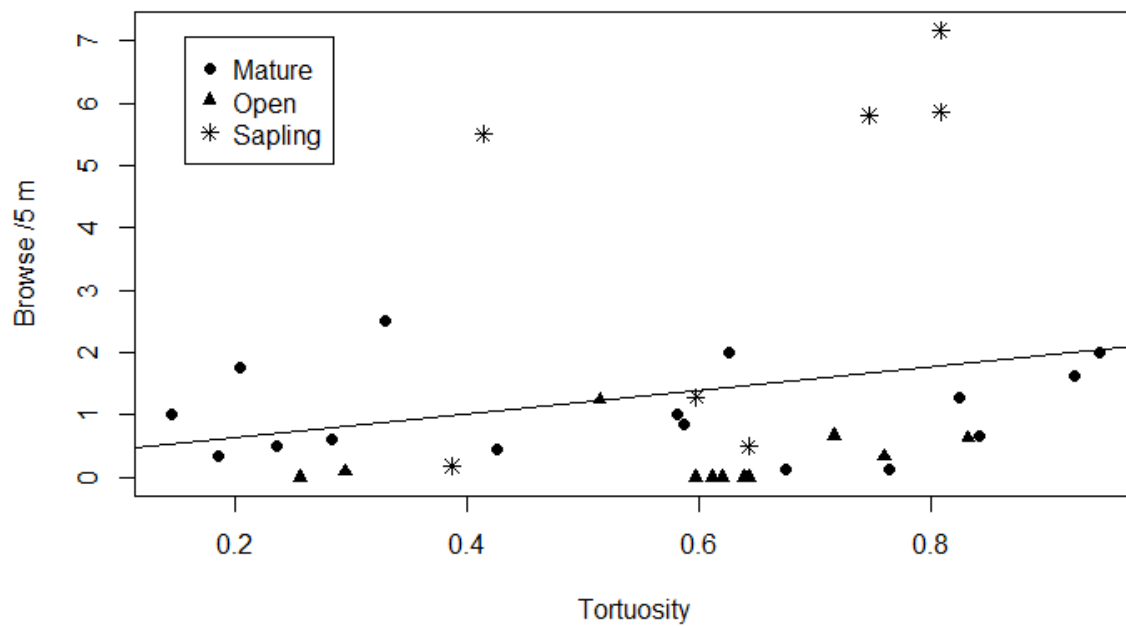


**Figure 3.4.** Snowshoe hare step numbers along foraging pathways in forest patches.

Snowshoe hare speed along foraging pathways differs between open, sapling, and mature stands ( $F_{2,31}=4.04$ ,  $p < 0.05$ ). Open circles show individual pathways, filled circles are the mean, and whiskers are 95% confidence intervals.

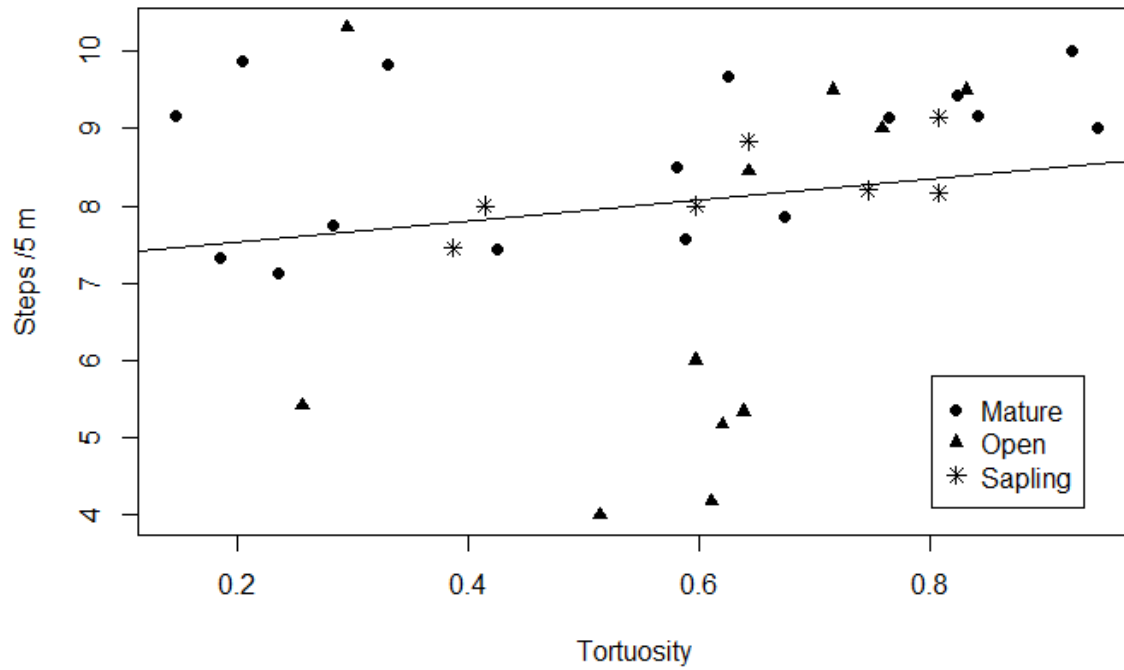


**Figure 3.5.** Snowshoe hare browse points in forest patches. Snowshoe hare browse points along foraging pathways were significantly different in open, sapling, and mature patches. Open circles show individual pathways, filled circles are the mean, and whiskers are 95% confidence intervals.

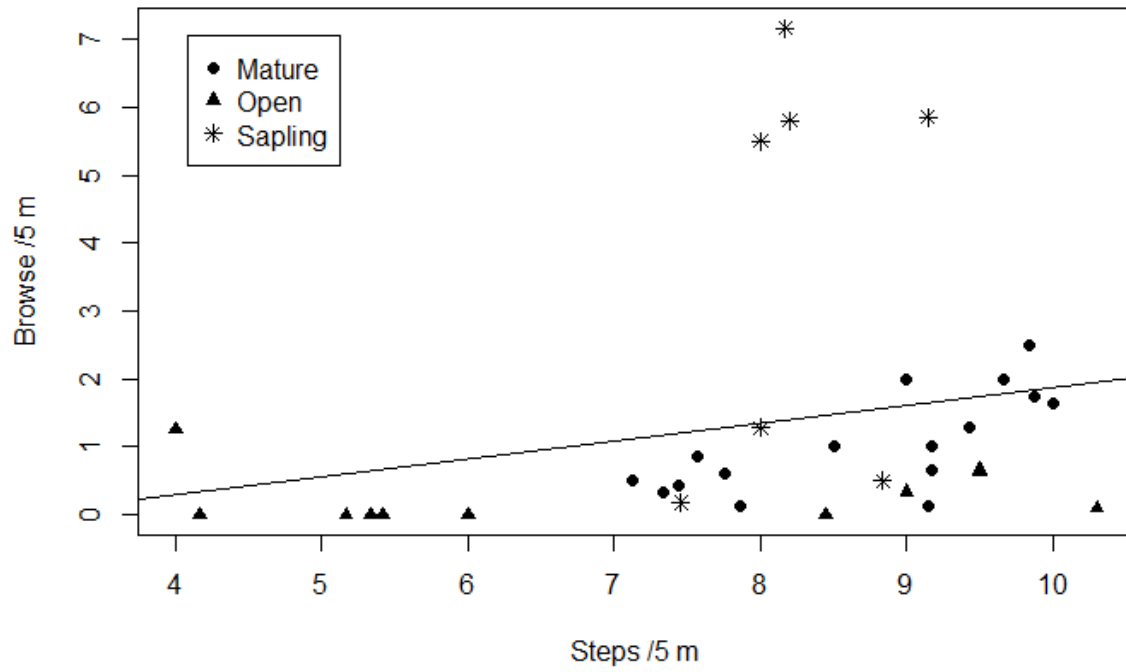


**Figure 3.6.** Hare tortuosity and browse on foraging pathways. Hare tortuosity and browse along foraging pathways are uncorrelated in open, sapling, or mature patches ( $R^2=0.05$ ,  $p=0.19$ ).





**Figure 3.7.** Hare tortuosity and speed on foraging pathways. Hare speed and tortuosity along foraging pathways are uncorrelated in open, sapling, mature patches ( $R^2=0.035$ ,  $p=0.29$ ).



**Figure 3.8.** Hare speed and browse on foraging pathways. Hare speed and browse along foraging pathways are uncorrelated in open, sapling, and mature patches ( $R^2=0.05$ ,  $p=0.18$ )

## Chapter 4 Conclusion

My overarching objective in this thesis was to assess snowshoe hare population responses and behavioral responses to wildfire. Unsurprisingly, my results have shown that snowshoe hare response is complex and not easily described as positive or negative. Past studies that showed population declines in snowshoe hares following fire may have oversimplified natural post-fire complexity (Keith and Surrindi 1971, Strong and Jung 2012).

My first objective in this thesis was addressed in Chapter 2: Does fire size affect population response of snowshoe hares? My field data clearly showed that snowshoe hares are found more frequently after large wildfires than they were following small or medium fires, or in mature forest. When snowshoe hares are found after larger fires, they occur at far higher densities than in mature forest. Cheng et al. (2015) and Hodges et al. (2009) found similar results, with snowshoe hares either being not present or present at very high densities after a wildfire. In the one medium fire where I found hare pellets, the densities were comparable to mature forests. No pellets were found in small fires. Hare abundances were higher in densely regenerating lodgepole pine sapling patches within those large fires and large fires were the only sites that had this degree of sapling regrowth. Sapling tree number was a strong predictor of hare abundance in all forest types (burn sizes and mature). These results highlight that the structure of the post-burn landscape is of critical importance when understanding how a species will respond to wildfire.

In Chapter 3, I examined if snowshoe hares modify foraging behaviour in burned forests. I found no evidence to suggest that hares change their tortuosity of movement when foraging in open or regenerating saplings patches in burns when compared to mature forests.

These results suggest that the variation in foraging pathways shown by Hodges et al (2014) may be conserved behaviour to optimize food intake and that hares may change movement patterns only when directly fleeing a predator. Hares did move faster in open patches, suggesting that they are spending less time in less desirable habitat,

Understanding how wildfire impacts an animal species requires more than just an assessment of population changes. With this thesis, I have shown that when studying large wildfires it is very important to study post-fire heterogeneity because of how variable the post-fire vegetation can be. Snowshoe hares have also shown different foraging behaviour in open and regenerating burned patches, showing that mammal response to wildfire is more nuanced than the decision to enter a patch or not. In southern British Columbian conifer forests, snowshoe hare abundance is correlated to sapling tree density, which in turn is linked to higher availability in food. This thesis is unique in its characterization of both population and behavioural responses of an animal to wildfire. As wildfires grow larger, more frequent, and more severe in the years to come (Westerling et al. 2006) studies of wildlife's responses to fire will become more important because they can allow us to predict how different species respond to an increasingly fire-disturbed landscape.

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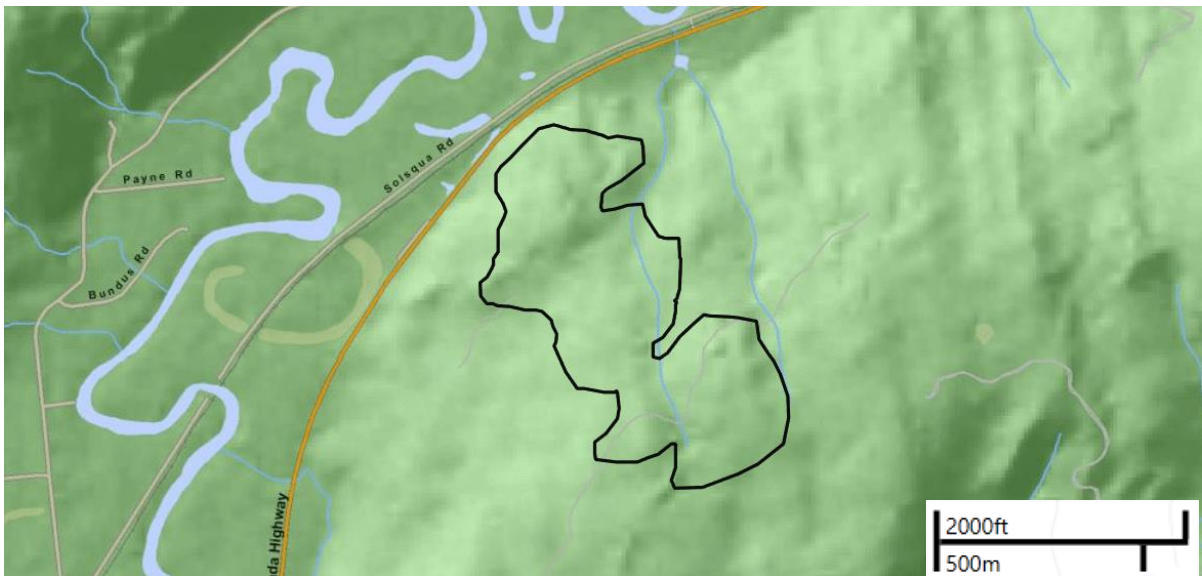
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## Appendices

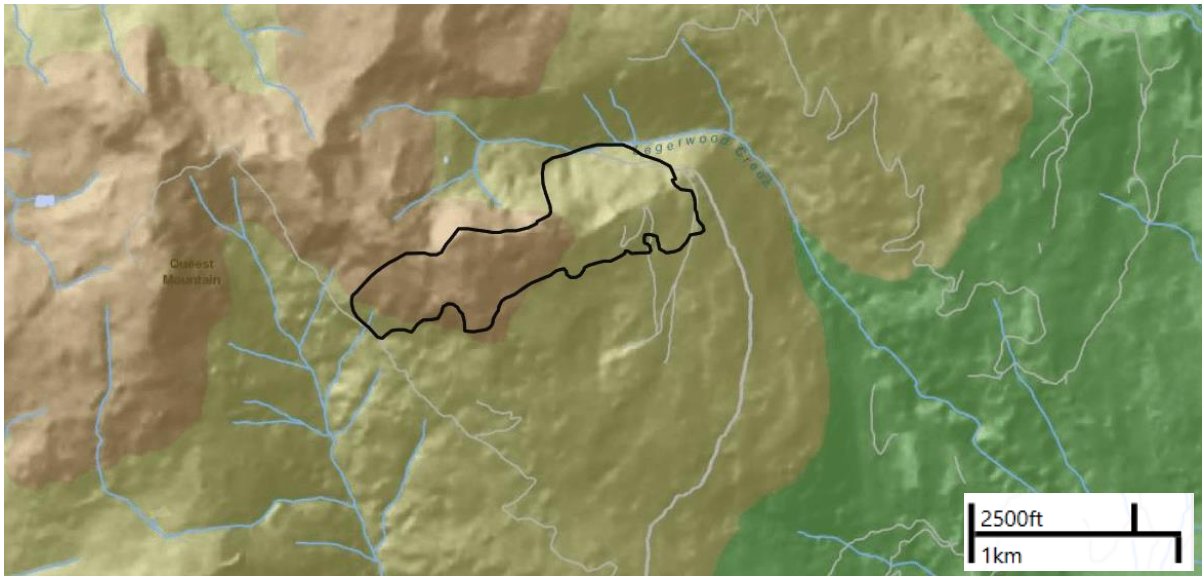
### Appendix A: Field maps and supplementary vegetation graphs for snowshoe hare density studies (Chapter 2)



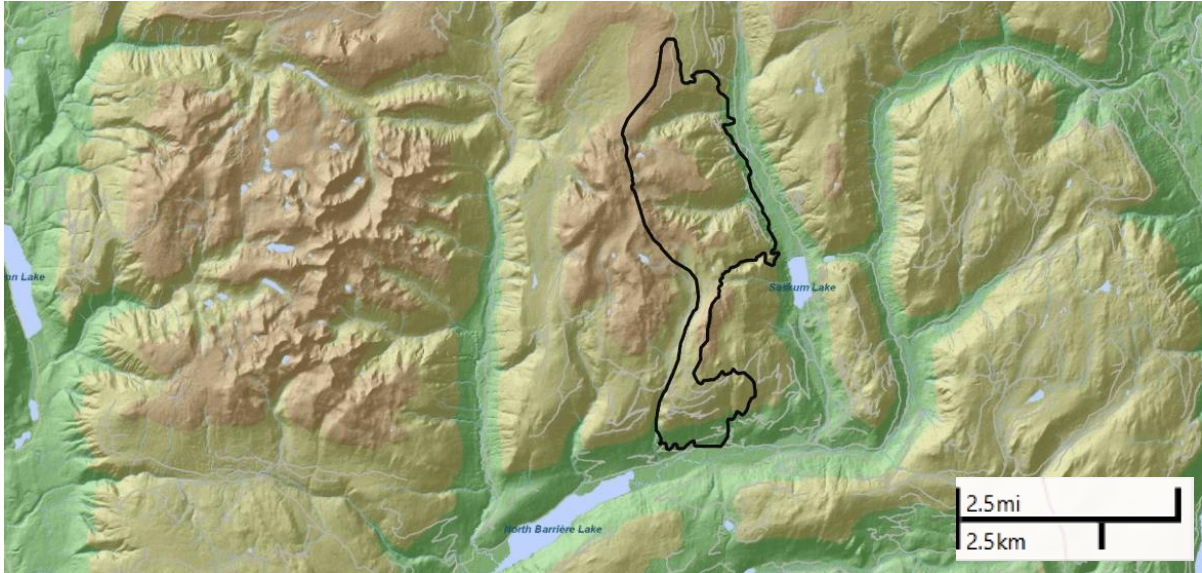
**Figure A.1.** Chase. 1:20,000. South of Highway 1, east of the town of Chase.



**Figure A.2.** Owlhead. 1:20,000. Northeast of Sicamous. South of Highway 1.

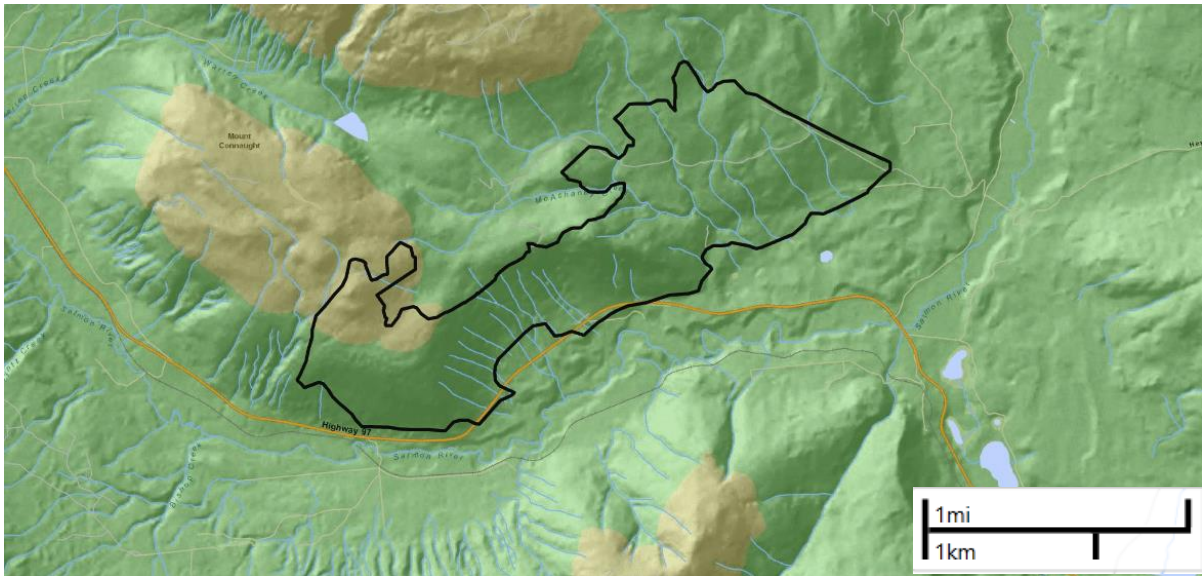


**Figure A.3.** Quest 1:40,000. On Quest Mountain, Northwest of the town of Malakwa

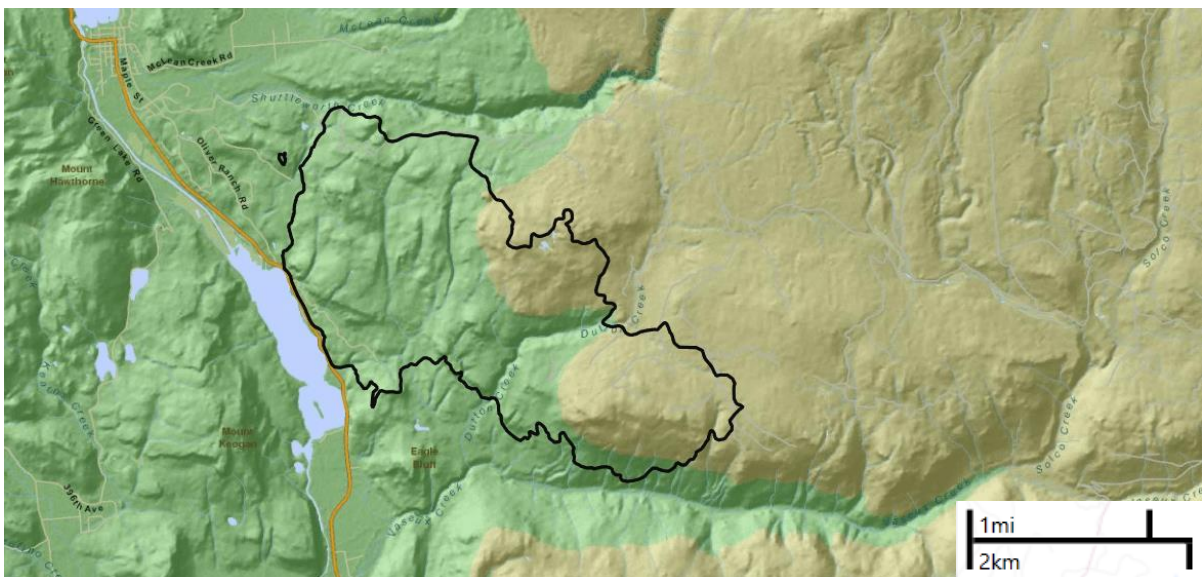


**Figure A.4.** Vermillion 1:150,000. Northeast of the town of Barriere. Only the low elevation southern portion of the wildfire near North Barriere Lake was accessible for field work. The large upper area may only be safely accessed in the winter via discontinued snowmobile trail.

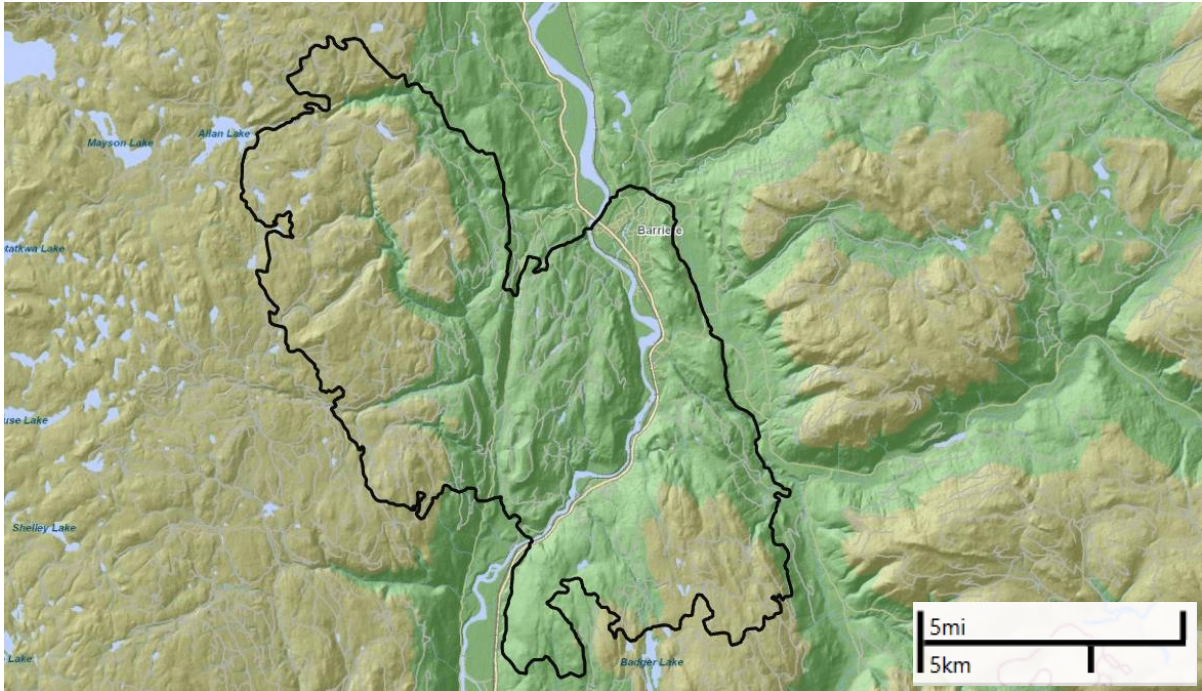




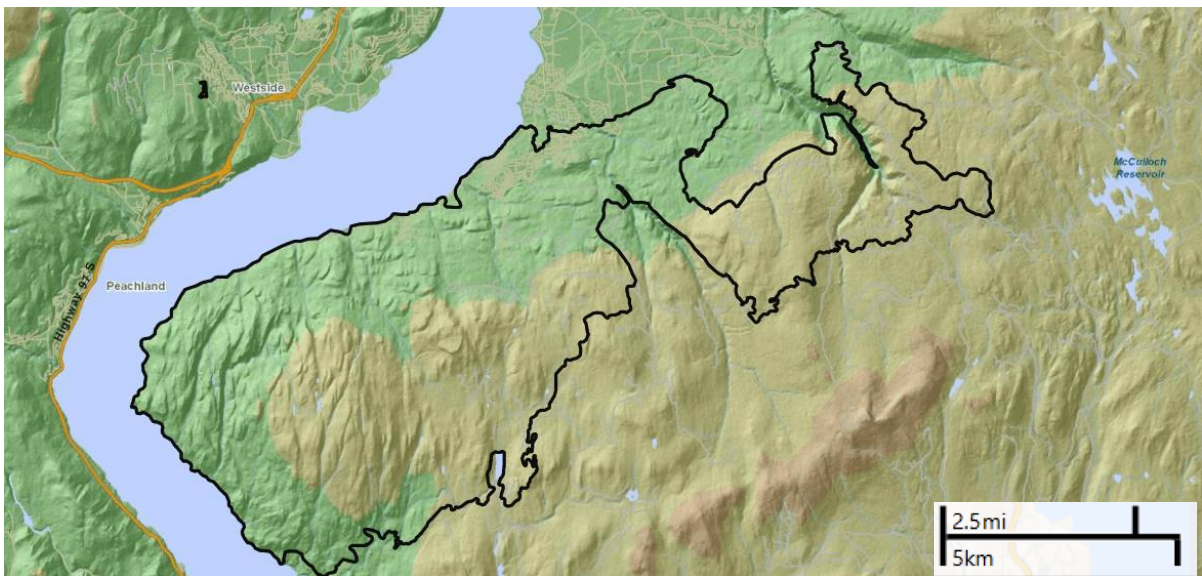
**Figure A.5.** Falkland 1:50,000. Southeast of the town of Falkland. North of highway 97.



**Figure A.6.** Vaseux 1:75,000. Southwest of Vaseux Lake and Highway 97.



**Figure A.7.** McClure wildfire. 1:250,000. North of Kamloops on Highway 5, on the towns of McClure and Barriere. The McClure fire is bisected by the North Thompson river, effectively creating two wildfires for the purposes on snowshoe hare movement.



**Figure A.8.** Okanagan mountain park wildfire. 1:175,000. South of Kelowna, on Okanagan Mountain



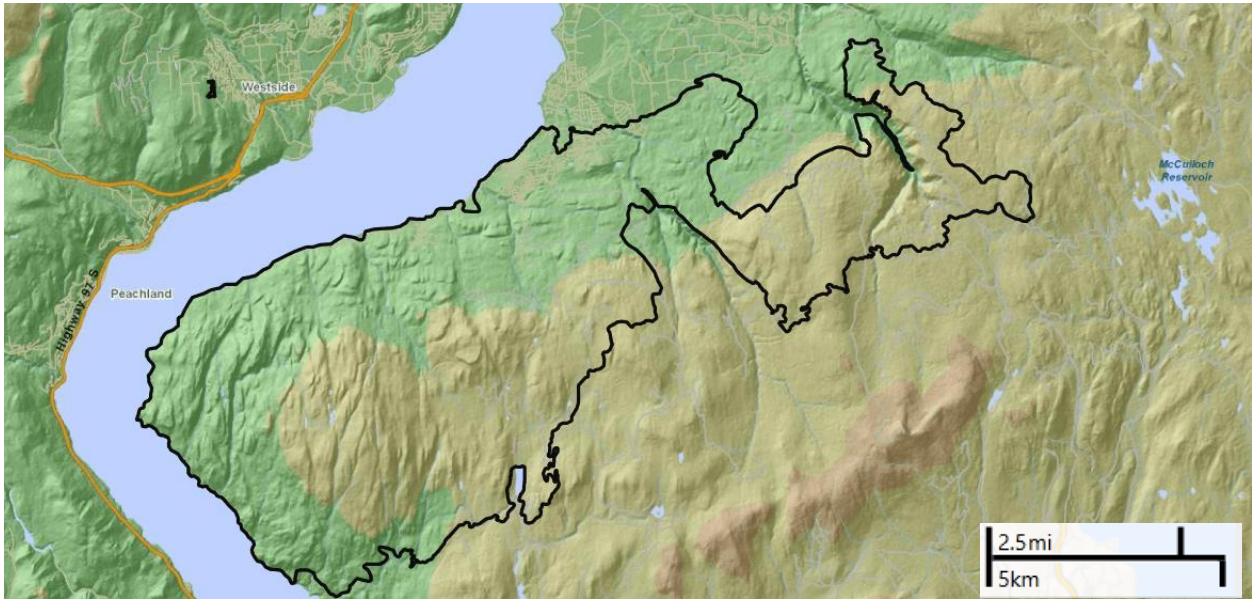
**Table A.1.** Regression results for all vegetation variables considered in analysis of snowshoe hare pellet correlations other than sapling and lodgepole pine sapling densities, which are presented in Figure 2.2 and 2.3.

Variable	R <sup>2</sup>	F <sub>1,31</sub>	p
Living canopy trees	0.03	0.84	0.37
Snag trees	0.02	0.49	0.48
Total canopy trees	0.05	1.49	0.23
Canopy cover	0.01	0.42	0.52
Understory cover	0.04	1.39	0.25
Shrub cover	0.006	0.02	0.66
Coarse woody debris	0.02	0.28	0.49
Total tree basal area	0.1	3.41	0.07

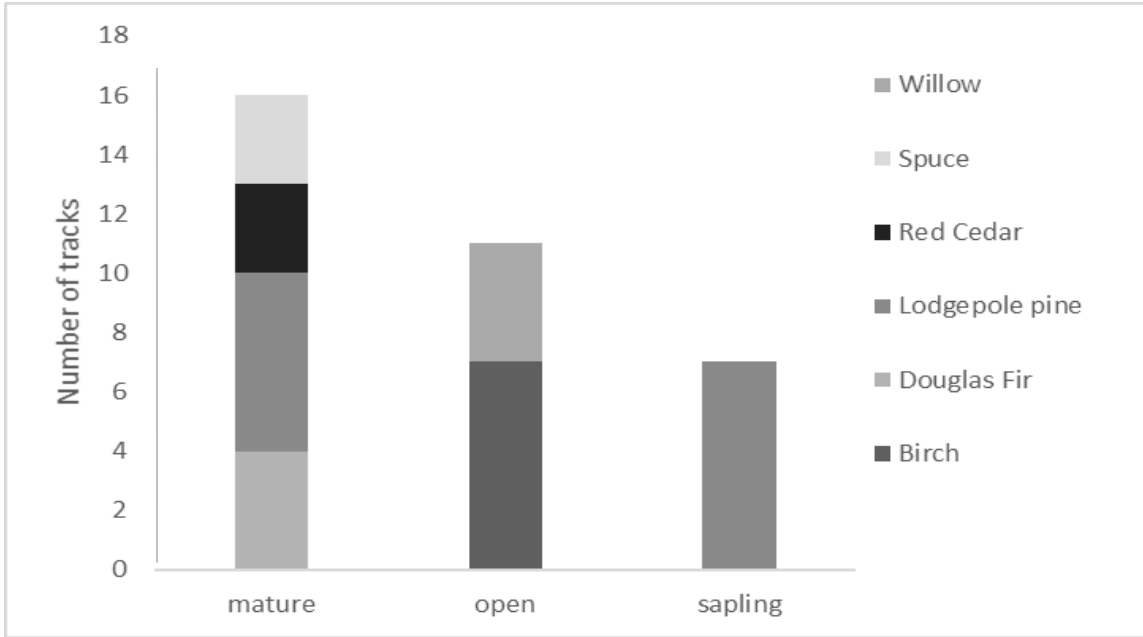
**Table A.2** Regression results for all vegetation variables in relation to fire size, other than sapling trees, which are presented in Figure 2.4.

Variable	R <sup>2</sup>	F <sub>2,29</sub>	p
Living canopy trees	0.66	18.90	< <b>0.01</b>
Snag trees	0.13	1.50	0.23
Canopy cover	0.78	35.04	< <b>0.01</b>
Understory cover	0.14	1.60	0.21
Shrub cover	0.17	1.94	0.15
Coarse woody debris	0.23	2.97	0.05

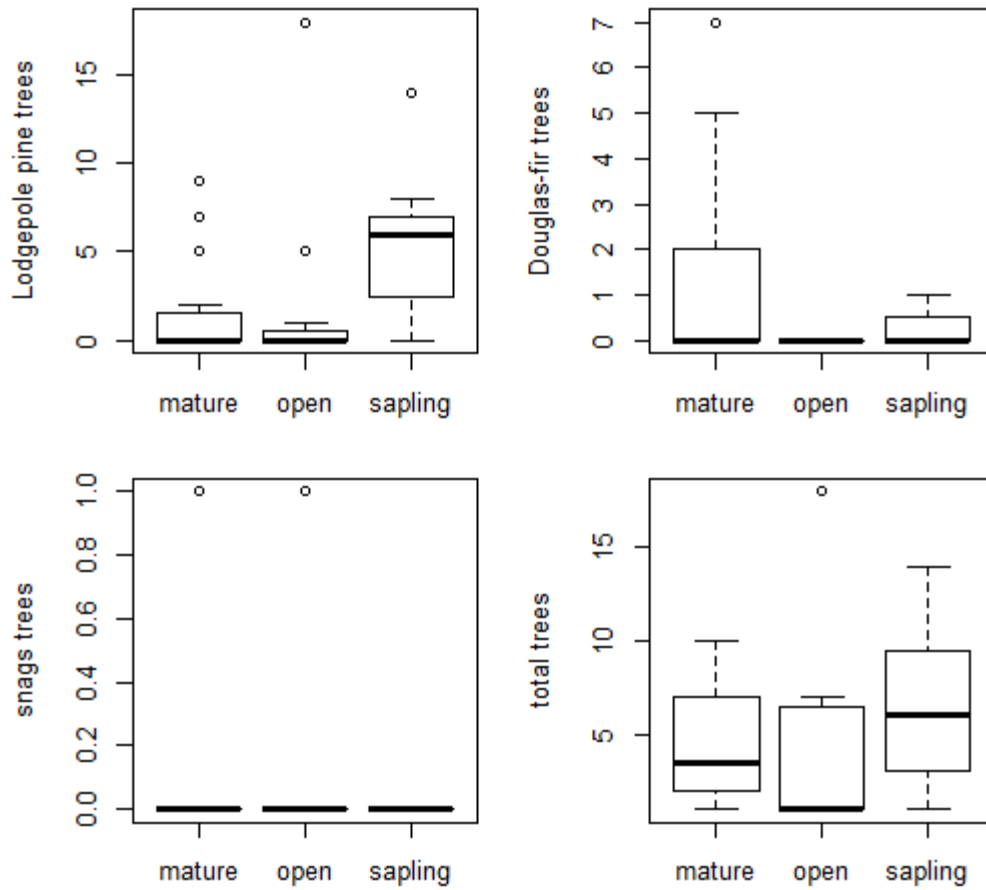
**Appendix B: Site map of snowshoe hare behavioural study (Chapter 3) and additional vegetation variable graphs**



**Figure B.1** Okanagan mountain park wildfire. 1:175,000. South of Kelowna, on Okanagan Mountain.



**Figure B.2.** Snowshoe hare tracks by dominant forest type in different patches.



**Figure B.3.** Variation in canopy tree number across stands. The number of lodgepole pine trees, Douglas-fir trees, snag trees, or total trees was not significantly different between open, sapling, or mature stands (Lodgepole:  $F_{2,31}=0.2.29$ ,  $p=0.12$ ; Douglas-fir:  $F_{2,31}=2.60$ ,  $p=0.09$ ; Snags:  $F_{2,31}=0.30$ ,  $p=0.74$ ; Total trees:  $F_{2,31}=0.30$ ,  $p=0.74$ ).

**Table B.1** Number of browse points per species eaten by snowshoe hares in the different stand types.

Common name	Scientific name	# of browse points eaten		
		Sapling	Open	Mature
<b>Conifers</b>				
Douglas-fir	<i>Pseudotsuga menziesii</i>	9	0	1
Lodgepole pine	<i>Pinus contorta</i>	152	5	22
Red cedar	<i>Thuja plicata</i>	0	0	7
Western hemlock	<i>Tsuga heterophylla</i>	0	0	2
<b>Shrubs</b>				
Alder	<i>Alnus spp.</i>	0	0	8
Ceanothus	<i>Ceanothus sanguineus</i>	0	1	0
Currant	<i>Ribes spp.</i>	0	0	3
Falsebox	<i>Paxistima myrsinites</i>	0	0	1
Oregon grape	<i>Mahonia aquifolium</i>	0	0	3
Paper birch	<i>Betula papyrifera</i>	9	9	0
Rose	<i>Rosa spp.</i>	44	9	23
Willow	<i>Salix spp.</i>	0	0	27