SNOWSHOE HARE (*LEPUS AMERICANUS*) HABITAT USE IN THE SUB-BOREAL FORESTS OF NORTH-CENTRAL BRITISH COLUMBIA

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ABSTRACT

Understanding a species' habitat use allows researchers and managers to identify areas and/or features essential to management and conservation. For populations that cycle in abundance, habitat associations may change through time complicating our understanding of how different habitat metrics may be related to preferences shown by the species. Snowshoe Hares (*Lepus americanus*) are a keystone species as they are a major food source for a diverse array of predators. Understanding their specific habitat associations provides for broader management planning (e.g., the conservation of associated predators). Although hare habitat use has been well studied, gaps in our knowledge still exist including how habitat use differs with ecological scale or throughout their population cycles. In this thesis I examined hare habitat use in the sub-boreal forests of the John Prince Research Forest and surrounding area in north-central British Columbia, Canada. I assessed this relationship at multiple scales, with multiple methods and at varying hare occupancy and densities in order to address these knowledge gaps. I used wildlife camera trapping (2015, 2016 and 2020) and hare pellet counts (2018 – 2020) to passively collect hare detection data and used LIDAR data to quantify habitat variables. My study population also showed evidence of being cyclical and cameras proved useful at detecting population oscillations. I detected a large decline in camera-detection rates during winter from 0.09 (SD = 0.13) in 2015 to 0.03 (SD = 0.05) in 2020. Naive occupancy declined during the period from 0.42 to 0.21. Pellet detections also declined between 2018/2019 and 2020. Distance to riparian area appeared to be the best metric for explaining hare camera detections in 2015, versus canopy closure in 2016 and distance to edge in 2020. Model selection using pellet counts was similar between the two years but canopy closure proved the most useful at explaining hare use at the landscape-scale, versus distance-to-edge for the within-stand models. Habitat use appeared to be density-dependent and also varied at different ecological scales and this should be considered in future habitat studies of Snowshoe Hare, as it has often gone unaddressed in the past.

Keywords: Snowshoe Hare, *Lepus americanus*, camera trapping, pellet count, occupancy, density estimation, habitat use, habitat biology, population cycle, sub-boreal forests.

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CHAPTER 1: INTRODUCTION

Wildlife habitat can most broadly be defined as the natural environment an animal occurs in (Grebner et al. 2013) and may include any space that provides food, shelter, or breeding grounds (Sharpe and Undersander 2019). Densities and patterns of landscape occupancy vary across heterogenous landscapes for many wildlife species based on habitat requirements that increase each individual's chance of survival and fitness (Stirnemann et al. 2015, Zhang et al. 2018). For example, many small rodents (e.g., mice, voles, shrews) are more active and abundant in areas with taller vegetation as it may provide protection from predators (Jacob 2008). Female White-Tailed Deer (*Odocoileus virginianus*) may seek areas of their home ranges with the greatest cover during and following parturition (Hasapes and Comer 2017). All species, sub-species and local populations have these types of habitat associations that may change during different life-stages, seasons or with population cycles and understanding them is key to studying and managing most wildlife.

Studies that examine how habitat quality affects the distribution and abundance or occupancy of species across a landscape have been a foundation of ecological research (Royle and Nichols 2003, Weir et al. 2003, Fuller et al. 2016). By combining species detection data and local habitat data we can assess how different biotic and abiotic factors influence habitat use (MacKenzie et al. 2002, 2006). These types of studies are commonly used by researchers and managers to assess habitat quality while identifying important features and/or habitats essential to long-term conservation and management (MacKenzie et al. 2002, Di Marco et al. 2017).

Assessing habitat use is difficult for species or local populations that cycle in abundance over time (Mordecai et al. 2011). Many species are known to exhibit density-dependent habitat use, in which they exploit different habitats during population highs versus lows (Wolff 1980, van Beest 2014). As populations increase high-quality habitat can become oversaturated forcing some individuals into lower-quality habitat (Fretwell and Lucas 1969). For example, high-quality habitats are known to sustain healthy and stable cyclical vole (subfamily Arvicolinae) populations, whereas marginal habitats are only occupied during population peaks (Sundell et al. 2012). Habitat studies undertaken at population highs and lows may lead to different and even conflicting results and interpretations so there is a need to standardize surveys at known points within the cycle.

The well-known 8 – 11-year population cycle of Snowshoe Hare (*Lepus americanus*) has been recognized by scientists for over a century and is one of the most studied ecological phenomena in the world (Meslow and Keith 1968, Keith and Windberg 1978, Krebs et al. 2018). I undertook a hare habitat use study, using passive detection methods, to answer some key questions about the relative importance of different habitats and features to hares and the local hare cycle in north-central British Columbia (BC), Canada.

In this chapter I give an overview of Snowshoe Hare ecology and habitat use, highlight much of what is already known about Snowshoe Hares and identify knowledge gaps. I then lay out the objectives of my study and how it aims to address some of these gaps. Finally, I introduce my dynamic study site area in north-central BC.

SNOWSHOE HARE ECOLOGY

Snowshoe Hares are medium-sized (~1.1 – 1.5 kg; Black 1965, Sullivan and Sullivan 1988, Murray 2002, Ellsworth et al. 2016) lagomorphs, native to North America. They occupy a range of habitat types and are distributed from the boreal forests of Alaska to Newfoundland and Labrador (introduced to the island of Newfoundland), south through the sub-boreal forests of southern Canada and into the montane forests of the Rocky, Sierra Nevada and Appalachian Mountains. They are absent from the far north of the Arctic, prairie grasslands and coastal islands of BC.

Snowshoe Hares draw their name from their recognizably large hindfeet that help them move across snow. The soles of their feet have dense fur, another anatomical feature that hints to their evolution in and for the cold snowy winter conditions of their northern and montane range. Across most of their range they are known to turn from a rusty- or grayish-brown colour in summer to white in winter; this provides camouflage from predators (Mills et al. 2018, Zimova et al. 2020) and may also increase the insulating properties of hair to assist thermoregulation in winter (Russell and Tumlison 1996, Gigliotti et al. 2017).

Behaviour and Reproduction

Snowshoe Hares are nocturnal and/or crepuscular and active year-round (Keith 1964, Feierabend and Kielland 2014, Studd et al. 2019). During the day they hide under dense brush, in hollow trees and logs, or anywhere else that provides structural protection. They eat a large variety of woody and non-woody plant species across their range (Brooks 1955, Telfer 1972, Smith et al. 1988) and also are known to scavenge carrion (Peers et al. 2018).

Most Snowshoe Hare populations have multiple litters per breeding season; the average is typically around three (Dodds 1965, Meslow and Keith 1968, O'Donoghue and Krebs 1992). Breeding begins in early-spring followed by a 35 – 40-day gestation period, with the first litter occurring in May followed by short intervals between subsequent litters (Severaid 1945, Dodds 1965, Kuvlesky and Keith 1983). Litter sizes can vary from one to 14 leverets but the typical average is three to five per litter (Meslow and Keith 1968, O'Donoghue and Krebs 1992, Stefan and Krebs 2001). Leverets usually are weaned in under a month with females often giving birth to a new litter shortly afterwards (Severaid 1942, Rongstad and Tester 1971). Litters generally are synchronized among females so that distinct litter groups occur within a population (Meslow and Keith 1968, O'Donoghue and Boutin 1995, Peers et al. 2021).

Pregnancy rates vary with each litter group but generally exceed 90% (Kuvlesky and Keith 1983, O'Donoghue and Krebs 1992, Krebs et al. 2001*a*). Females normally first breed as yearlings, this group making up approximately 70% of the breeding population, given that Snowshoe Hares have a short average life span of one year (Krebs et al. 2018). Surprisingly the main cause of leveret mortality is predation by other small mammals such as American Red Squirrels (*Tamiasciurus hudsonicus*) and Arctic Ground Squirrels (*Urocitellus parryii*; O'Donoghue 1994, Krebs et al. 2018).

The Role of Snowshoe Hares as a Keystone Species

The International Union for the Conservation of Nature (IUCN) presently lists Snowshoe Hares as a species of Least Concern (LC - G5), which corresponds to their appearance on the Yellow List in BC (secure - S5). While there is currently not broad concern for their conservation, they are widely recognized as playing a critical role in food webs. Snowshoe Hares, particularly during periods of high abundance, represent a substantial amount of the vertebrate biomass available to many mesocarnivores, including Canada Lynx (*Lynx canadensis*), American Marten (*Martes americana*), Fisher (*Pekania pennanti*), Wolverine (*Gulo gulo*), Coyote (*Canis latrans*), Red Fox (*Vulpes vulpes*) and others. This is especially true in winter when other small mammals are hibernating or have reduced activity (Krebs et al. 2018). Overall, the main cause of Snowshoe Hare mortality is predation (Boutin et al. 1986, Feierabend and Kielland 2015, Majchrzak et al. 2022).

Larger apex predators, such as Gray Wolves (*Canis lupus*) and Cougars (*Puma concolor*), also are known to occasionally consume hares (Spalding and Lesowski 1971, Floyd et al. 1978, Gable et al. 2018). Avian predators, such as the Great Horned Owl (*Bubo virginianus*; Rohner and Krebs 1996) and Northern Goshawk (*Accipiter gentilis*; Boutin et al. 1995), as well as other members of Orders Accipitriformes and Strigiformes also predate hares (Luttich et al. 1970, Krebs et al. 2018, Schmidt et al. 2018). In fact, avian predation can account for up to 40% of predation events in some hare populations (Krebs et al. 1995, Feierabend and Kielland 2015). Other species prey on leverets during spring and summer, including squirrels. This critical and significant role played by Snowshoe Hares in food webs is why they are considered a keystone species in many parts of their range (Bois et al. 2012, Morris and Vijayan 2018, Jensen et al. 2022).

Canada Lynx are known to be a specialist predator of Snowshoe Hares across much of their range and account for a significant proportion of hare mortality; hares in fact often constitute the primary prey species of lynx (Breitenmoser et al. 1993, O'Donoghue et al. 1997, Boutin 1998). Lynx are a medium-sized felid species that have evolved large snowshoe-like feet and other features for the snowy winter climates they inhabit. Their range overlaps almost completely with that of Snowshoe Hares but they are absent from the southernmost portions of the hare's range in the contiguous United States of America (USA). The connection between lynx and hares is so strong that their populations are known to cycle together, with lynx typically demonstrating a time-lag behind hare numbers, across much of their joint range (Breitenmoser et al. 1993, Vik et al. 2008, Tyson et al. 2010).

The Snowshoe Hare Cycle

The hare-lynx association is a classic ecological tale found in many textbooks. It often is used to demonstrate the Lotka-Volterra equation that describes the dynamics of interacting predator-prey species (Krebs et al. 2001*a*). Reports of regular oscillations in Snowshoe Hare populations were made by fur trappers in the 18th and 19th centuries (Krebs et al. 2001*a*). The hare-lynx cycle was first detected by scientists in the early 20th century when The Hudson Bay Company's detailed fur trading records were analyzed by biologists (Elton and Nicholson 1942). These records demonstrated approximately 10-year intervals between population peaks in many discrete locations across Canada (Elton and Nicholson 1942). The amplitude of the population peaks also fluctuates between cycles (Ginzburg and Krebs 2015, Myers 2018). The Snowshoe Hare cycle was thereafter confirmed with field studies (Green and Larson 1938, Green and Evans 1940, Dodds 1965).

The documentation of the hare cycle has led to considerable work seeking to explain the underlying cause for such an extensive, synchronous cycle (Keith and Windberg 1978, Breitenmoser et al. 1993, O'Donoghue et al. 1997 and reviewed in Krebs et al. 2018). Hypotheses have included predation (Krebs et al. 1995, 2018, Sheriff et al. 2011), food availability (Pease et al. 1979, Vaughan and Keith 1981, Keith 1983), secondary plant compounds (Fox and Bryant 1984, Sinclair and Smith 1984, Sinclair et al. 1988), solar activity (Sinclair et al. 1993, Ranta et al. 1997, Sinclair and Gosline 1997) and parasites, diseases and other stressors (Green and Larson 1938, Erickson 1944, Keith et al. 1985). Studies across their range, but especially those in Alberta (Keith 1966, Meslow and Keith 1968, Cary and Keith 1979) and Southern Yukon (reviewed in Krebs et al. 2001*a* and 2018), have helped explain this phenomenon, with predation now appearing to be the primary cause of the cycle (Krebs et al. 2018). Predators not only cause direct mortality but interactions with them cause stress in reproductive females that is passed down via the maternal effect and sustains the low-phase of the hare cycle by decreasing reproductive output (Sheriff et al. 2009, 2010, 2011). The constant threat of predation influences Snowshoe Hare habitat use as they select habitats that offer the greatest levels of protection.

SNOWSHOE HARE HABITAT USE

Snowshoe Hare habitat use has received considerable research attention across much of their range (Sullivan and Sullivan 1988, Ferron and Ouellet 1992, Kawaguchi and Desrochers 2018). Snowshoe Hares generally are restricted to continuous forested habitats, avoiding open grasslands, coastal beaches, alpine habitats and tundra. They do, however, occupy a diverse array of forest types: middle- to mature-aged conifer-predominated forests in western North America (Ausband and Baty 2005, Griffin and Mills 2007, Sullivan et al. 2012), black spruce (*Picea mariana*) forests of northern and eastern Canada (Ferron et al. 1998, St-Laurent et al. 2008), mixed hardwood-softwood forests of their southeastern range (Litvaitis et al. 1985, Homyack et al. 2006, Gigliotti et al. 2018) and subalpine fir (*Abies lasiocarpa*) stands found in the southern extent of the species' range in southwestern USA (Frey and Malaney 2006, Malaney and Frey 2006). Hares also use stands and patches of deciduous species such as trembling aspen (*Populus tremuloides*; Wolfe et al. 1982, Strong and Jung 2012), red maple (*Acer rubrum*; Conroy et al. 1979) and scrub oak (*Quercus ilicifolia*; Gigliotti et al. 2018).

The Importance of Cover for Snowshoe Hares

Despite the wide range of forest types used by hares, there appear to be some commonalities. Cover, primarily provided by vegetation, often is cited as the most important determinant and predictor of hare habitat use, as it provides visual obstruction from predators (Litvaitis et al. 1985, Bois et al. 2012, Simard et al. 2018). Given the intensity of predation on hare populations, it is not surprising that individuals select habitats that provide protection and increase their fitness. This relationship supports the so-called "Landscape of Fear" theory that postulates the perceived threat or fear of potential predators cause animals to choose habitats that offer protection, even if doing so requires the sacrifice of optimal foraging (Brown et al. 1999, Laundré et al. 2001). Cover also could be correlated with other important life-history requirements of hares, such as thermoregulation and food quantity and/or quality.

Horizontal cover, also called lateral, understory or shrub cover, frequently has been found to be the most important type of cover for Snowshoe Hares (Litvaitis et al. 1985, Bois et al. 2012, Gigliotti et al. 2018). Dense understories provide places where hares can feed and rest while reducing their susceptibility to terrestrial predators (Bois et al. 2012, Suffice et al. 2015). This type of cover also may visually obstruct hares from aerial predators, although canopy closure is likely more important in this role (Thomas et al. 2019). Increased canopy closure has been found to be correlated with increased hare use (Roy et al. 2010, Thornton et al. 2013, Cheng et al. 2015). However, Bois et al. (2012) did not find a strong correlation between canopy closure and hare use, suggesting canopy closure in fact may reduce horizontal cover, possibly by reducing light availability (Simard et al. 2018). Another habitat feature that may impart protection to hares is tree density, with hares being more abundant in areas with greater numbers of trees and/or volume (i.e., basal area) of trees (Hodson et al. 2010*a*, Ewacha et al. 2014, Thomas et al. 2019).

The relationship between hares and distance to habitat edges also has been explored. Some of this work has suggested hares use edge habitats (Conroy et al. 1979), while others lean towards avoidance (Roy et al. 2010, Sultaire et al. 2016). In winter, when hares feed more on woody browse, they are known to forage in densely vegetated interior sites. In summer, however, it is the interspersion of interior habitat (providing protection) and open habitat and gaps (providing herbaceous foliage) that may drive habitat use (Wolff 1980). Although edge habitat may provide an important interspersion of foraging and cover habitat (Conroy et al. 1979), predation rates of some prey species are known to be greater closer to edge habitat (Andrén and Angelstam 1988, Andrén 1995).

Factors Influencing Snowshoe Hare Habitat Use

In addition to cover, other site factors known to influence hare use include elevation and slope (Berg et al. 2012, Thornton et al. 2013). Coarse woody debris also has been positively associated with hare use (Berg et al. 2012). The local soil type may influence vegetation and subsequently hare use (Berg et al. 2012). Stand-age and silviculture practices have also been linked to hare habitat use patterns (Sullivan 1994, Sullivan et al. 2007, Bois et al. 2012). All told, there appears to be a multitude of factors and interactions that influence hare habitat use and patterns of landscape occupancy. Snowshoe Hare habitat use also varies regionally and more studies have occurred in the northern boreal and southern extents of their range.

Despite the relatively large number of hare habitat studies, we still lack a clear picture of how habitat use changes throughout and between population cycles. Snowshoe Hares are known to exhibit density-dependent habitat use (Wolff 1980, Hodson et al. 2010*b*). When the population is low, during the crash and recovery phase of the cycle, the remaining individuals only may occupy the best quality habitat, usually areas with dense vegetation (Wolff 1980). During population highs, however, the higher density of hares may result in occupancy across a wider array of available habitats. This would conform to the "Ideal Free Distribution" theory that predicts the occupancy of suboptimal habitat at population peaks (Fretwell and Lucas 1969). This in turn raises the question of when is the right time to survey cyclic populations to quantify and assess habitat use. Studies undertaken at different points during a population cycle may yield different and even conflicting results and interpretations. Short-lived occupancy patterns (i.e., patch colonization and extinction) also may render it harder to classify what is or is not hare habitat in variegated landscapes (Thornton et al. 2013). If Snowshoe Hares do retreat to high-quality refugia during cyclic lows, then those habitats may be relatively important when managing for hares and their many predators.

Hare habitat use also can vary at different ecological scales (Lewis et al. 2011, Fuller and Harrison 2013, Gigliotti et al. 2018). Most hare studies have been at landscape- or stand-level and only a few have examined within-stand or plot-level habitat use (Ausband and Baty 2005, Fuller and Harrison 2013, Holbrook et al. 2017). Horizontal cover has been found to drive within-stand habitat selection with structure/visual obstruction being more important than species composition (Gigliotti et al. 2018). Holbrook et al. (2017) found that horizontal cover drove habitat use at the within-stand and landscape-scale but that snow depth was significant only at the landscape-level. Similarly, Sultaire et al. (2016) found that horizontal cover was the only significant predictor of habitat use at the plot-scale but not at the landscape-level. Selection for forested and lower edge density areas at the landscape-scale showed how the effects of habitat fragmentation outweighed the influence of horizontal cover at a broader scale. This illustrates how studies undertaken at multiple scales can be important in determining the full scope of hare habitat use (Thornton et al. 2013, Holbrook et al. 2017).

Holbrook et al. (2017) pointed out that not only does hare habitat use differ at varying scales but with different response variables (e.g., occupancy, density, detection rates, etc.). Most ecological studies focus only on a single response but it has been shown that habitat factors can influence both occupancy and density in different ways (Holbrook et al. 2016 and 2017). They suggest studies that evaluate multiple responses may be able to improve our understanding of habitat use by Snowshoe Hares. They further suggest that study areas should be in continuous habitat with a gradient of natural conditions over type-based or stratified approaches (e.g., sampling only pre-defined high-quality habitat based on existing cover maps; Holbrook et al. 2017).

Snowshoe Hare home range size varies across different habitat types but is typically 7 – 14 ha and averages around 9 ha, of which hares spend 80% or more of their time in a core-area of less than 3 ha (Wolff 1980). Male hares generally have larger home ranges than females (Wolff 1980). Snowshoe Hares exhibit seasonal patterns of habitat use (Wolff 1980, Ferron and Ouellet 1992, Ivan et al. 2014). In winter they may spend their time in densely vegetated interior forests that provide not only the cover they require but also winter diet items such as spruce, willow, birch and alder species (Wolff 1980). During summer they may move to areas with a mix of open and densely vegetated areas (e.g., near forest edges or gaps) to access herbaceous foliage that grows in areas where increased light penetration encourages growth (Wolff 1980, Ferron and Ouellet 1992).

WILDLIFE CAMERA TRAPPING STUDIES

Over the years various methods have been used to collect detection, movement, density and other data in to assess Snowshoe Hare habitat use. Mark-recapture studies historically were a common way to gather this type of information, but they remain labour intensive and invasive (Meslow and Keith 1968, Mills et al. 2005). The attachment of VHF- and GPS-collars provides detailed movement data that can give insights into fine-scale habitat use (Feierabend and Kielland 2014, Majchrzak et al. 2022) but similarly requires invasive capture, restraint and handling. Pellet (scat) counts provide a relative measure of use that has most commonly been used at the stand-level. Wildlife camera studies have become common over the last two decades and have also been used to assess hare habitat use (Thomas et al. 2019).

The use of wildlife camera trapping (CT) began with the development of new technology in the 1990s and quickly became a common way to passively monitor wildlife species (Shannon et al. 2014, Newey et al. 2015, Neilson et al. 2018). Cameras can be deployed remotely to passively gather detection data on one or more focal species. They also may be used in place of labour intensive and stress-inducing traditional trapping studies, depending on the objectives of the study. Historically these studies were limited by camera battery life and storage capacity but both of these features have continued to improve over time. They have been used to assess wildlife abundance and distribution (Linkie et al. 2013, Rich et al. 2017, Evans et al. 2019), habitat use (Fuller et al. 2016, Thomas et al. 2019, Wilson et al. 2020), behaviour (Peers et al. 2018), to detect rare species (Linkie et al. 2013) and even to estimate density (Rowcliffe et al. 2008, Jensen et al. 2022).

Many different sampling designs and types of analyses have been used for CT studies and several papers have stressed the importance of standardizing and validating the different approaches (Meek et al. 2014, Burton et al. 2015, Newey et al. 2015). For example, using multiple cameras, with a minimum of two per station, may greatly improve detection rates and reduce false negatives (O'Connor et al. 2017, Evans et al. 2019). However, it is challenging to standardize approaches when habitats or species ecology require different methods (Burton et al. 2015). It is critical to assess the relationship between camera detections and abundance because if this relationship does not exist, or if it is heavily affected by animal movements or other factors, then research conclusions may not be valid (Burton et al. 2015).

Once CT data have been collected, they must be categorized into discrete presence/absence detection histories that can vary from a day to weeks (Burton et al. 2015, Rich et al. 2017, Neilson et al. 2018). The detection history data can then be used in models to assess habitat use. Occupancy modelling commonly has been used with CT data as it incorporates detection probabilities that account for false negatives (Shannon et al. 2014, Fuller et al. 2016, Neilson et al. 2018). This may not, however, be necessary if you can assume high levels of detection, especially with abundant species and other modelling approaches, such as logistic regression, also may be appropriate (Ngoprasert et al. 2012, Chaiyarat et al. 2019)

Researchers can add covariates to models to assess the use of different habitat types and features or factors influencing detection (Burton et al. 2015, Neilson et al. 2018). Several Snowshoe Hare studies have used CT recently for a variety of objectives including multi-species monitoring (Foresman and Pearson 1999, Evans et al. 2019, Jensen et al. 2021). Thomas et al. (2019) investigated the effects of salvage logging induced structural changes on hare habitat use. Wilson et al. (2020) used cameras to study a population of translocated hares and their colonization and extinction of different habitats. Other aspects of Snowshoe Hare ecology have been studied using cameras including risk management strategies (Morris 2019), molting and camouflage (Zimova et al. 2020) and carrion scavenging (Peers et al. 2018). Recently Jensen et al. (2022) used CT to estimate Snowshoe Hare density, suggesting that with further refinement, CT studies may replace traditional pellet counts.

HARE PELLET COUNTS

The technique of fecal pellet counts has been used by wildlife biologists to estimate abundance for many years (Neff 1968, White and Eberhardt 1980, Litvaitis et al. 1985). Originally the use of pellet data was considered inappropriate for estimating density (Wolfe et al. 1982); however, the work of Krebs et al. (1987) set out a method of estimating Snowshoe Hare density through pellet counts, creating a standard for hare population assessments. In their seminal paper the researchers used Jolly-Seber mark-recapture estimates from a hare trapping study along with pellet counts to create an equation (the “Yukon Equation”) that could be used to estimate hare density (i.e., hares/ha). They determined the relationship between pellet and mark-recapture estimates to be so close as to recommend the use of pellet counts as a precise and accurate way to estimate hare density.

Some studies simply have used pellet counts to determine the abundance and distribution of hares (Homyack et al. 2006, Hodges et al. 2009). Other studies have used pellet counts to assess habitat use generally, or more specifically the impacts of different forestry treatments (e.g., precommercial thinning, fertilization) on hares (Sullivan et al.

2006, Griffin and Mills 2007, Homyack et al. 2007). Pellet counts have been used as a stand-alone approach (Newbury and Simon 2005, Thornton et al. 2013, Sultaire et al. 2016), or combined with complimentary methods such as mark-recapture and snow-tracking (Ferron et al. 1998, Homyack et al. 2006, Hodges et al. 2009).

Since the publication of the Yukon Equation other studies have developed their own regression models linking pellet count data to hare habitat use (Mills et al. 2005, McCann et al. 2008, Berg and Gese 2010). Mills et al. (2005) found that the Yukon Equation provided comparable density estimates to their locally derived equation despite the fact that their study took place in very different habitat in Montana. They suggested that the Yukon Equation may be applicable across a broader spectrum of habitats, especially if studies do not require highly accurate measure of absolute abundance. The Yukon Equation has since been revised by some of the original researchers and other collaborators (Krebs et al. 2001*b*).

The precise method of collecting Snowshoe Hare pellet counts has involved a variety of study designs and plot sizes. Hodges and Mills (2008) suggested using long thin rectangles (5.08 cm x 305 cm = 0.155 m^2) or circles (1 m^2). The original Yukon Equation papers used 0.155 m^2 rectangular plots (Krebs et al. 1987, Krebs et al. 2001*b*) and subsequently it has been suggested that using different plot sizes with this equation may not be appropriate (McKelvey et al. 2002, Mills et al. 2005). It has been suggested the optimal number of plots per site is between 50 – 100 and shown that increasing the number past that does not improve estimates (Krebs et al. 2001*b*, Hodges and Mills 2008). Increasing the number of sites, however, can improve accuracy and a minimum of three sites per study (150 – 300 plots) was suggested by Krebs et al. (2001*b*).

THESIS OBJECTIVES

After an in-depth review of over a century worth of Snowshoe Hare research, with a particular focus of hare habitat use, it was clear several knowledge gaps still exist. While it is known that hares exhibit density-dependent habitat use, few studies have directly compared habitat use at different population densities or occupancy. Snowshoe Hare studies also have been mainly concerned with habitat use at a stand-level scale and the nuances of within-stand habitat use have often gone ignored. In this thesis I address both these issues and also expanded on traditional hare habitat use studies by using multiple ecological responses (i.e., occupancy and density) in a range of habitats and methods newer to hare research (i.e., wildlife CT).

For this thesis I partnered with the John Prince Research Forest (JPRF) in north-central BC. A primary focus of the JPRF is to monitor multiple species, particularly mesocarnivores, over time. This has made understanding the relationship between hares, their population cycles and habitat particularly relevant. Staff at JPRF and I collected passive hare detection data between 2015 and 2020, which I then analyzed for this thesis.

In consultation with JPRF researchers and following Holbrook et al. (2017) I chose to conduct a multi-scale, multi-response study of hare occupancy patterns over a heterogenous landscape that represented a gradient of potential habitat. In a broad sense my goal was to establish baseline population and habitat analysis that could be used to aid further Snowshoe Hare research at the JPRF. Additionally, this analysis may be useful to others studying hare predators or larger ecosystem dynamics at the JPRF and more broadly.

My specific objectives were to determine what habitat components were most important to hares in my study area and to develop models that could predict hare use. Additionally, I wanted to compare habitat use at the stand- and within-stand-scale. Furthermore, I wanted to determine if the local hare population oscillated in abundance over time and whether cameras were useful in detecting that change. If a population oscillation did occur, I was curious to determine whether the local hare population exhibited density-dependent habitat use.

In the following chapter I use overlapping CT and pellet counts to assess hare habitat use using logistic regression models. I further used the pellet data to assess whether habitat use differed at the landscape compared to the within-stand-scale. With the camera data I also evaluated whether cameras can detect population oscillations to assess their use for monitoring the Snowshoe Hare cycle. In the final chapter of this thesis, I summarize the results of my work, discuss management implications, highlight limitations encountered during my study and suggest areas for future research.

STUDY SITE

In addition to field work, I also utilized historical data collected at the JPRF. The JPRF is located in north-central BC approximately 45 km north of Fort St. James and served as the main study area for this thesis (Figure 1.1).

The JPRF is cooperatively managed by the Tl'azt'en Nation, Binche Whut'en First Nation and the University of Northern British Columbia but works with other academic institutions across BC and beyond. Their primary objective is to "*develop innovative approaches to natural resource conservation and management that combines First Nations' traditional and western scientific approaches to understanding the natural world*". For over twenty years researchers with the JPRF and their external partners have carried out a diverse array of wildlife and environmental studies in the region. Some of the species previously studied at the JPRF include River Otter (*Lontra canadensis*; Crowley et al. 2013*b*, 2018), Canada Lynx (Crowley et al. 2013*a*, Crowley and Hodder 2017), Moose (*Alces alces*; Chisholm et al. 2021), American Mink (*Neovison vison*; Hodder et al. 2018), American Marten (Seip et al. 2018) and others.

The JPRF and the surrounding region is within the Sub-Boreal Spruce biogeoclimatic zone, typical of north-central BC, that experiences cold snowy winters and relatively short cool summers (Meidinger and Pojar 1991). Mean daily average temperatures (1981 – 2010) were 3.5 ºC; the lowest monthly mean daily average occurred in January (-9.5º C) while the warmest occurred in July (15.4º C) (Environment and Climate Change Canada 2022). Mean annual precipitation (1981 – 2010) was 487 mm, with more than a third of it falling as snow (173 cm) (Environment and Climate Change Canada 2022).

The JPRF is bordered to the north by Tezzeron Lake and Pinchi Lake to the south (see Figure 1.1). Both year-round and ephemeral streams of varying size criss-cross much of the landscape. Wetlands, bogs and small lakes are numerous. The valley bottoms sit at approximately 700 m above sea level with rolling terrain and low mountains to 1500 m (Crowley and Hodder 2017). Land-use operations in the area include forestry, ranching and historically, mining. There are no major highways or urban areas within the study area but there are several active logging roads and backroads for access to remote recreation sites and rural properties.

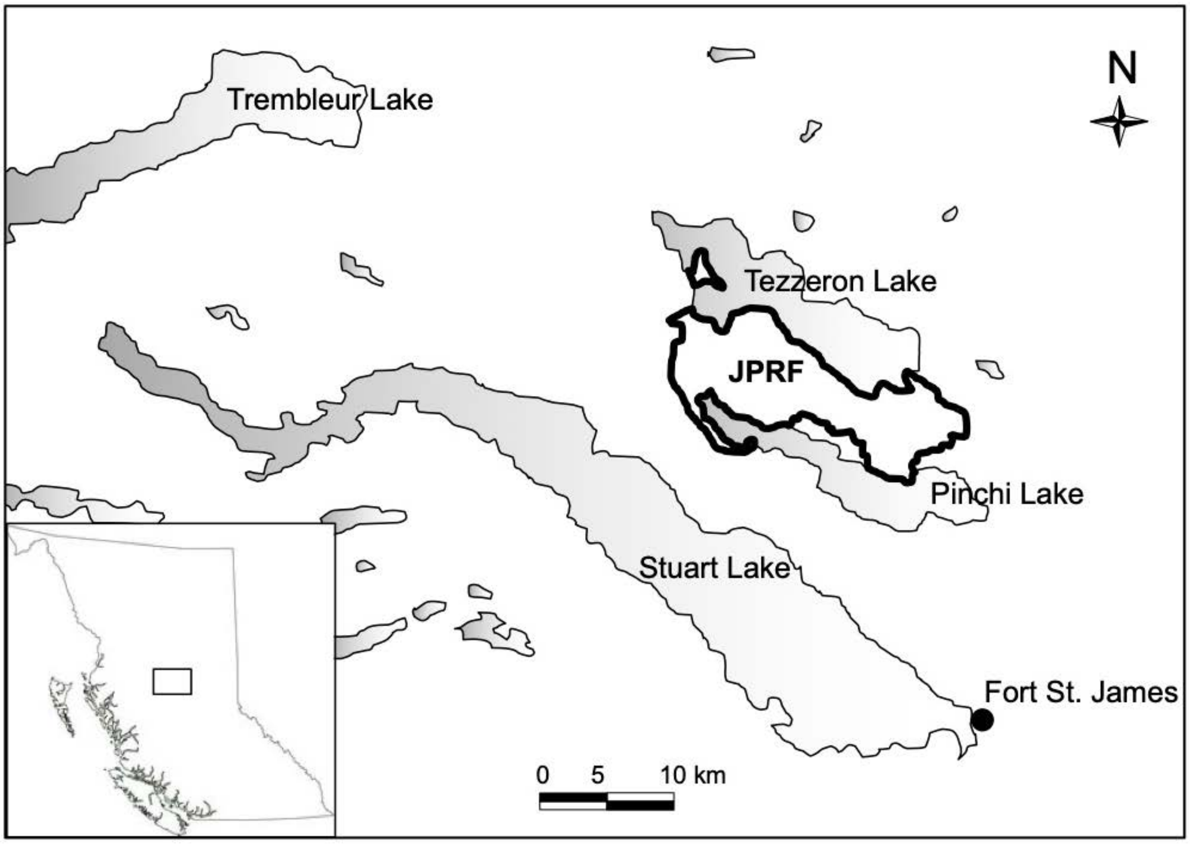

Figure 1.1. Location of the John Prince Research Forest (JPRF) and surrounding Snowshoe Hare (*Lepus americanus*) study area in north-central British Columbia, Canada (UTM Zone 10 – NAD83).

Much of this region is predominated by hybrid white spruce (*Picea x albertiana*) and subalpine fir (*Abies lasiocarpa*) (Meidinger and Pojar 1991; See Figure 1.2 for examples). Lodgepole pine (*Pinus contorta*) is an early-seral species but also occurs frequently on drier mature sites (Bedford and Sutton 2000). Black spruce (*Picea mariana*) is the dominant species in bogs and saturated areas (Wali and Krajina 1973).

Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) is less predominant but occurs on dry warm sites throughout the region (Meidinger and Pojar 1991) where the species is at its northern limit (Crowley and Hodder 2017). Smaller patches and stands of deciduous trees occur throughout the area. Trembling aspen stands are fairly common in moist historically harvested areas (Wali and Krajina 1973). Other deciduous species such as paper birch (*Betula papyrifera*) and poplar (*Populus balsamifera*) also are common but less abundant (Wali and Krajina 1973).

Close to a century of forestry has created a patchwork of seral stages in the JPRF and it is now predominantly composed of regenerating-to-mature conifer stands with patches of deciduous and clear-cut areas (Crowley and Hodder 2017). In the summer of 2015, JPRF staff conducted a variety of timber cruising and vegetation field surveys at all camera stations confirming the description of sub-boreal spruce forest composition was accurate for my study area. Hybrid spruce was by far the predominant tree and accounted for nearly half (41%) of all trees counted in cruise plots. Several other species occurred in varying amounts: lodgepole pine (16%), subalpine fir (13%), trembling aspen (8%), paper birch (6%) and Douglas-fir (5%) with minor amounts of black spruce and poplar.

A dense understory is found throughout much of the study area (Crowley and Hodder 2017). Visual obstruction cover pole measurements at camera stations ranged from 0 to 90% with an average of 35%. Common shrub species counted during brush cover surveys included willows (*Salix* spp.), red osier dogwood (*Cornus sericea*), black huckleberry (*Vaccinium membranaceum*), saskatoon berry (*Amelanchier alnifolia*), twinberry (*Lonicera involucrata*), highbush-cranberry (*Viburnum edule*), soopolallie (*Shepherdia canadensis*), devil’s club (*Oplopanax horridus*) and alders (*Alnus* spp.).

Figure 1.2. Example of common forest types found in and around the John Prince Research Forest in north-central, British Columbia, Canada. Outer (clockwise from the top left): Mature warm and dry Douglas-fir site, moist aspen stand, saturated bog-like black spruce stand (note the presence of the bog species Labrador tea (*Rhododendron groenlandicum*)) and mature open park-like lodgepole pine stand. Centre: Typical predominant hybrid spruce-fir stand.

A diverse terrestrial mammalian mesocarnivore community is found in the JPRF and includes Canada Lynx, Coyote, Fisher*,* American Marten, American Mink, Red Fox, Short-Tailed Weasel (*Mustela erminea*), Striped Skunk (*Mephitis mephitis*) and Wolverine. Several species of raptors also are known to inhabit the area including known hare predators such as Great Horned Owls (Rohner and Krebs 1996) and Northern Goshawks (Boutin et al. 1995), as well as other members of the Orders Accipitriformes and Strigiformes. Wolves, Cougars, Black (*Ursus americanus*) and Grizzly (*Ursus arctos horribilis*) Bears also occasionally prey on hares (Spalding and Lesowski 1971, Floyd et al. 1978, Gable et al. 2018) and have all been observed locally. The American Red Squirrel (*Tamiasciurus hudsonicus*) also occurs locally.

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CHAPTER 2: DENSITY-DEPENDENT HABITAT USE IN A CYCLICAL SNOWSHOE HARE (*LEPUS AMERICANUS*) POPULATION IN THE SUB-BOREAL FORESTS OF NORTH-CENTRAL BRITISH COLUMBIA.

INTRODUCTION

Species and populations have different habitat requirements for survival and reproduction that cause their densities to vary across different habitat types (Stirnemann et al. 2015, Zhang et al. 2018). Consequently, many ecological studies have assessed habitat quality in an attempt to explain wildlife distribution, abundance or occupancy across a landscape (Royle and Nichols 2003, Weir et al. 2003, Fuller et al. 2016). Modeling species detection and habitat data allows for the assessment of relative use and identification of important habitat components (MacKenzie et al. 2002, 2006). This common type of study can inform wildlife managers by identifying high-quality or important habitats for protection or management action (MacKenzie et al. 2002, Di Marco et al. 2017).

For species or local populations that cycle in abundance over time, assessing habitat use becomes more challenging. Studies completed during population peaks may yield different results and interpretations compared to those undertaken during population lows and long-term studies across many predictable population cycles may offer the greatest insights (e.g., the Southern Yukon hare studies – reviewed in Krebs et al. 2018) Additionally, the amplitude of cycles may vary over time (Ginzburg and Krebs 2015, Myers 2018) furthering complicating the issue of when to study these populations.

The population cycle of Snowshoe Hares (*Lepus americanus*) is one of the most well documented and studied ecological phenomena in the world (Meslow and Keith 1968, Keith and Windberg 1978, Krebs et al. 1986). Across much of their range, populations of this species are known to fluctuate on a predictable 8 – 11-year interval with varying amplitudes (Krebs et al. 2014). Snowshoe Hares account for a large proportion of the vertebrate prey biomass in the boreal and sub-boreal forests of Canada and thus are critical links in the complex food webs of these ecosystems (Krebs et al. 2018). Canada Lynx (*Lynx canadensis*) specialize on Snowshoe Hares, and populations of this small felid cycle in accordance with hare populations over much of their shared range (Breitenmoser et al. 1993, O'Donoghue et al. 1997, 1998). Predation has been recently argued to be the main driver of the Snowshoe Hare cycle (Krebs et al. 2018).

Many studies have evaluated Snowshoe Hare habitat use across their range and cover, particularly horizontal/understory cover, is often considered the most important predictor of use (Litvaitis et al. 1985, Thornton et al. 2013, Simard et al. 2018). Horizontal cover provides visual obstruction so that hares can feed and rest without being easily seen and preyed upon by terrestrial predators. Canopy closure also may be important as it provides protection from avian predators (Gigliotti et al. 2018, Thomas et al. 2019); this is significant given raptors can be responsible for up to 40% of predatory losses (Southern Yukon – see Krebs et al. 1995). Other habitat features that may be correlated with Snowshoe Hare habitat use include tree density (Thomas et al. 2019) or volume, distance to edge habitat (Roy et al. 2010) and other regionally significant factors.

Although it is known that Snowshoe Hares exhibit density-dependent habitat use (Wolff 1980, Hodson et al. 2010) few studies have investigated how hare habitat use changes throughout a population cycle. Wolff (1980) found that when hare populations were low, the remaining individuals only occupied the best quality habitat, usually areas with dense vegetation, but during a population high they occupied a wider array of available habitats. This type of density-dependent habitat use and occupancy of suboptimal habitat at population peaks is predicted by the "Ideal Free Distribution" theory (Fretwell and Lucas 1969). If during population lows Snowshoe Hares retreat to high quality refugia those habitats may be important when managing for hares and their predators. If habitat use does change during the cycle, then the timing of population surveys is important. Studies undertaken at different points during a population cycle may yield different and even conflicting results and interpretations. Short-lived occupancy patterns (i.e., patch colonization and extinction) also make it harder to determine what is or is not hare habitat (Thornton et al. 2013) and this is why there is a need to better understand how habitat use changes with population cycles.

Most Snowshoe Hare studies have been at landscape- or stand-level and only a few have examined within-stand or plot-level habitat use (Ausband and Baty 2005, Fuller and Harrison 2013, Holbrook et al. 2017); therefore, there is still a need to better understand hare habitat use at a fine-scale as it is known to vary across ecological scales (Lewis et al. 2011, Fuller and Harrison 2013, Gigliotti et al. 2018). For example, horizontal cover has been found to drive hare within-stand habitat selection while other factors may influence stand-level selection (Holbrook et al. 2017, Gigliotti et al. 2018). This is why studies undertaken at multiple scales can be important in determining the full scope of hare habitat use (Thornton et al. 2013, Holbrook et al. 2017).

I assessed Snowshoe Hare habitat use in the sub-boreal forests of north-central British Columbia (BC), Canada, using habitat metrics known to be of importance to hares (e.g., canopy closure, tree volume, distance to edge). I conducted this work using camera trapping (CT) and pellet counts, in a region where Snowshoe Hares exist alongside a diverse community of mesocarnivores including mustelid, felid and canid mammals, as well as raptors. I used cameras partly to assess their efficacy in detecting hare population changes and also carried out pellet counts to confirm population oscillations detected by the cameras and to compare and contrast the results of the two methods. An additional motivation for adding in pellet surveys was to be able to compare this study with existing hare habitat use studies that have primarily used pellet surveys as their detection and/or enumeration method.

My main objective was to determine what habitat components were most important to hares in the region and to develop models using fine-scale habitat covariates that could predict habitat use. I also wanted to assess and compare habitat use at the landscape- and within-stand-scale. An additional objective was to determine if the local hare population oscillated in abundance over time. Given that the landscape was highly fragmented by forestry, a condition suggested to lead to non-cyclical hare populations (Wirsing et al. 2002), it was unknown whether the local hare population followed a typical cyclical pattern. The hare cycle can have far reaching impacts on other species and the ecosystem as a whole and it was important to know to what extent the local population cycled over time. If a population oscillation was detected, I wanted to assess whether there was a concomitant density-dependent change in habitat use.

I developed several hypotheses based on commonalities that ran through existing hare habitat literature. I predicted hare use would increase with increasing horizontal cover and canopy closure. I also expected hare use to increase with tree volume (i.e., basal area) and I additionally assumed that hare use would increase closer to habitat edges. Since vegetation is usually denser in riparian areas, I predicted hare use would increase closer to them. Finally, I assumed that, if hare occupancy were to increase or decrease appreciably, I would observe a density-dependent change in habitat use.

Snowshoe Hare habitat use has been well studied but some gaps in our knowledge still exist including how habitat use inferences change with scale or at varying hare densities throughout their population cycles. These data were collected over a period of time when Snowshoe Hare occupancy ranged considerably across the landscape allowing me to assess density-dependent habitat use. I also evaluated hare habitat use at the within-stand-scale, which has gone understudied, and was able to compare this to landscape-scale models to assess hare habitat use at multiple scales. Thus, this work adds to our understanding of Snowshoe Hare habitat use across landscapes and fluctuations of population occupancy or density.

METHODS

Study Site

In this study I utilized Snowshoe Hare detection data from 2015 to 2020 in the John Prince Research Forest (JPRF) and neighbouring provincial lands, approximately 45 km north-east of Fort St. James, BC (54° 40’ 14” N, 124° 25’ 13” W; Figure 2.1, also see Figure 1.1). This region occurs within the Sub-Boreal Spruce biogeoclimatic zone of the province and experiences cool summers and long cold winters (Meidinger and Pojar 1991). Over 70 years of forestry has altered the landscape, creating a patchwork of seral stages predominantly composed of regenerating-to-mature conifer stands of hybrid white spruce (*Picea x albertiana*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*) and Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*; Crowley and Hodder 2017). Smaller deciduous-predominant patches of trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*) and poplar (*Populus balsamifera*) also occur, as well as newly harvested areas. A dense understory of willows, alders and other shrubs is found throughout most of the study area (Crowley and Hodder 2017; See Chapter 1 for species description). There also is a diverse mesocarnivore community that includes Canada Lynx, Marten (*Martes americana*), Fisher (*Pekania pennanti*), Wolverine (*Gulo gulo*), Coyote (*Canis *latrans*), Red Fox (*Vulpes vulpes*), American Mink (*Neogale vison*) as well as several species of avian predators (Orders Accipitriformes and Strigiformes). Known hare leveret predators, American Red Squirrels (*Tamiasciurus hudsonicus*) are common in the area.

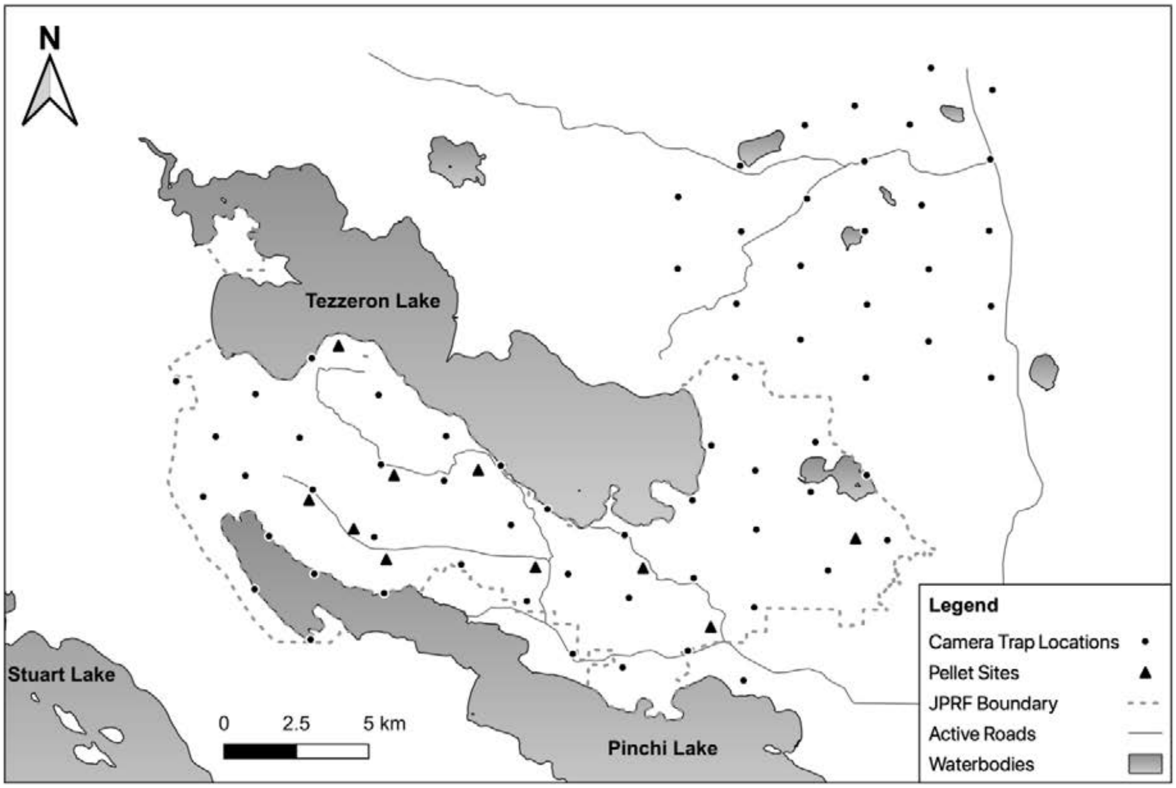

Figure 2.1. Study area with the locations of the 66 camera trapping stations and 10 pellet sites used for the five-year (2015 – 2020) Snowshoe Hare (*Lepus americanus*) habitat study in the John Prince Research Forest (JPRF) and surrounding area in north-central, British Columbia, Canada (UTM Zone 10 – NAD83).

Snowshoe Hare Detection Data

Camera Data

Researchers at the JPRF divided the study area into a grid of 66 hexagons with 2.5 km between the center of each 5.41 km^2 hexagon, creating a 357 km^2 study area. They positioned one digital infrared trail camera at the center of each hexagon; if this was not possible (e.g., centre was in the middle of a stream) they chose the nearest suitable location to establish a camera station. In 2015 and 2016 they deployed Bushnell Trophy Cameras (models 119467 and 11947; Bushnell Outdoor Products, Missouri, USA). They programmed the cameras to record a 30-second video when motion was detected, with a one-second interval between videos. In 2020 they switched out all cameras for Browning Dark Ops HD Pro model BTC-6HDP (Browning, Utah, USA) with video lengths of 10 seconds, with a one-second interval between videos or continuous recording if motion was detected.

Snowshoe Hares are nocturnal and/or crepuscular (Feierabend and Kielland 2014, Studd et al. 2019); therefore, I considered my independent sampling event to be one camera-day: the 24-hour period of active camera recording starting at 12:00:00 and ending at 11:59:59 the following calendar day. Doing this fully encompassed one active period rather than splitting a single active period over two sampling events. I used camera data from January 20 in 2015 and from January 21 in 2016 and 2020 until March 31st to create a 70 camera-day study period for each year, while accommodating for leap years. I reviewed the camera footage and recorded whether a hare was detected or not during each camera-day. I also gathered detection data over a single 26-week spring-summer session from 12:00:00 on April 1, 2016 to 11:59:59 on September 30, 2016 at 49 camera stations. Staff at JPRF accessed camera stations by snowmobile in winter. During spring and summer, they could not access all 66 stations due to changing conditions (e.g., ephemeral streams and wetlands) so for my analyses I only included data from cameras that were functioning for a minimum of 75% of camera-days.

Since all camera stations were not equally surveyed due to camera malfunctions, battery issues, etc., I used the detection rate (camera-days with hare detections/camera-days per camera station) to determine whether hares were present or absent at each station. I used detection rates greater than the 50th percentile of all detection rates for the first year (2015 = 0.04) to set a threshold for classifying hares as present (1) at a station, whereas hares at stations with detection rates equal to or less than 0.04 were classified as absent (0). This allowed me to distinguish between stations with moderate to high detection rates, likely because the station fell within an individual's home range (i.e., suggesting some level of habitat use) and stations where hares were completely absent or had low detection rates, suggesting less and possibly only temporary use (e.g., a foray out of its home range for predator avoidance). In addition to using the above system to create a binary database (1 = present, 0 = absent for each camera-day), I also calculated occupancy (stations with hare present/total number of stations), sometimes referred to as naïve occupancy as it does not incorporate detection probabilities (Nichols et al. 2007), to compare trends between study years.

Pellet Data

I established a total of 10 hare pellet sites in a variety of forest types (e.g., mature forests (>50 years old), regenerating forests (15 – 50 years old), clearcuts (<15 years old)) across the study area from 2017 – 2019. Each pellet site consisted of four transects located 100 m apart; each transect was composed of 25 pellet plots, located 15 m apart, for a total of 100 pellet plots per site. Each plot was positioned directionally (first plot = north-south, the second = northeast-southwest, third = east-west, fourth = northwest-southeast). I cleared each 0.155 m^2 (305 cm x 5 cm) rectangular plot (Krebs et al. 2001, Hodges and Mills 2008) of all pellets when I first established six sites in fall 2017 and added an additional four sites in spring 2018. Following establishment of each site, I counted pellets in spring and fall of 2019 and 2020. I also counted pellets at six of the 10 sites in 2018, which I used to estimate density for each site but did not include in my models. I established these pellet sites to provide a way to corroborate population trends or habitat use conclusions drawn from the camera data.

I removed pellets from each plot after counting to avoid recounting. I combined spring and fall pellet count totals to estimate density over a one-year time span that ranged from the clearing of pellets in fall of one year to the counting of pellets in fall of the subsequent year (e.g., the 2019 study year went from the clearing of pellets in September 2018 to the second counting of pellets in September 2019, representing the total of the spring and fall 2019 counts). This ensured the results were comparable with other pellet studies where a one-year sampling period is most common (McCann et al. 2008). I obtained forest stand age estimates for each pellet site from the publicly available Vegetation Resource Inventory (VRI; Ministry of Forests, BC) and confirmed them with timber harvest records from the JPRF.

In order to estimate hare density from the pellet counts I used the revised "Yukon Equation" ($hares/ha = -1.203 + 0.889 \log_e (mean\ no.\ of\ pellets) \times 1.567$; Krebs et al. 2001). Other local equations have been created from paired pellet and mark-recapture studies across Snowshoe Hare range (Mills et al. 2005, Homyack et al. 2006, Berg and Gese 2010). Mills et al. (2005) found that the Yukon Equation provided comparable density estimates to their locally derived equation even though it was in different habitat in Montana. They also suggested that it may be appropriate to use at moderate hare densities if absolute density is not needed. That was less important in this study than obtaining a measure of relative use to assess hare habitat. I used 0.155 m^2 rectangular plots to align with the methods of Krebs et al. (2001) as this may be important for producing reliable density estimates from the Yukon Equation (McKelvey et al. 2002, Mills et al. 2005).

Habitat Metrics

The JPRF had remote-sensing LIDAR data collected from a fixed-winged aircraft for the entire study area in August 2015. This provided high-resolution habitat data (10 m x 10 m pixel) that allowed for the quantification of dozens of candidate site and habitat covariates to use in models. LIDAR data were initially processed by Forsite Consultants Ltd., Salmon Arm, BC. Out of the dozens of candidate covariates I selected nine that had been previously identified as important to Snowshoe Hares, allowing me to explore my hypotheses (Table 2.1). I obtained basal area for the camera models and distance to edge for the camera and pellet models from the publicly-available VRI. I treated canopy closure from 0 to 1 m as a surrogate for horizontal cover, as it was highly correlated with cover pole measurements taken at camera stations.

Table 2.1. Habitat and site covariates used in Snowshoe Hare (*Lepus americanus*) logistic regression models for camera and pellet detection data (2015 – 2020) from the John Prince Research Forest and surrounding area in north-central, British Columbia (BC), Canada. Data collected using remote sensing LIDAR with additional data from the Vegetation Resource Index (VRI; Ministry of Forests, BC). Canopy closure is in meters (m) above the ground. *Used in camera models only.

Covariate	Abbreviation	Definition	Data Source
Basal Area*	BA	Estimated BA (m^2/ha) from VRI polygon for each location.	VRI
Canopy Closure 0 – 1 m 1 – 3 m 3 – 10 m > 10 m	 CC0–1 CC1–3 CC3–10 CC>10	• Camera Models: percent canopy closure using raster zonal statistics for each height category within 50 m-radius buffer around each camera station • Pellet Models: percent canopy closure for each height category for each pellet plot within 10 x 10 m LIDAR tile it occurs in.	LIDAR
Distance to Edge	DistEdge	Distance (m) to VRI polygon stand edge.	VRI
Distance to Riparian Area*	DistRip	Distance (m) to the closest wetland, stream or lake.	LIDAR
Elevation (m)*	Elev	Mean elevation using raster zonal statistics within 50 m-radius buffer.	LIDAR
Slope		• Camera Models: slope (%) using raster zonal statistics within 50 m-radius buffer surrounding the camera. • Pellet Models: slope (%) for each pellet plot within 10 x 10 m LIDAR tile it occurs in	LIDAR

Habitat Modelling

Camera Habitat Models

To explore habitat relationships between binary detection data (present vs. absent) I chose logistic regression over occupancy models, although both are commonly used in analyses of detection data (Fuller et al. 2016, Pease et al. 2016, Thomas et al. 2019). The cameras provided near-continuous monitoring and had good sightlines that made false negatives unlikely. I performed preliminary occupancy modelling that confirmed the addition of detection probabilities was not necessary as they did not change occupancy estimates for any of the years. Given this, I used more parsimonious logistic regression models (i.e., less parameters). To explore for multicollinearity between the habitat metrics, I generated and visibly inspected a correlation matrix of all the variables. Any variables that appeared to be correlated were not included in the same model.

I fitted all logistic regression models using R version 4.2.1 (R Foundation Statistical Computing, Vienna, Austria). I used corrected Akaike's Information Criterion (AIC_c) and AIC model averaging to assess the relative rank of each model (Hurvich and Tsai 1989, Burnham and Anderson 2002) using the R package "AICcmodavg." I considered models that were within two AIC units of the top model to be competitive (Burnham and Anderson 2002). To assess goodness-of-fit for the models I calculated the area under the curve (AUC) for the Receiver Operating Characteristic (ROC) curve (Boyce et al. 2002) using the R package "pROC." I used the commonly referenced 0.7 AUC threshold (Boyce et al. 2002) for defining models that have acceptable predictive power for assessing habitat use. From these models, I compared the explanatory covariates between stations where hares were present with those where they were absent using Mann Whitney *U* tests (non-parametric t-tests).

Pellet Habitat Models

I pooled the data from the plots at each site together to assess habitat use across the entire landscape, where hares were both present and absent. Hereafter I refer to these models as “landscape models.” To investigate use at a finer-scale I looked at 7/10 sites where hares were present above 0.3 hares/ha, a threshold necessary to prevent an overestimation of density through the Yukon Equation (Mills et al. 2005). This set of models (based on 700 plots) I refer to as “within-stand models.” I decided to only use covariates that varied at similar levels among plots as they did among sites to eliminate potential bias. I therefore used fine-scale covariates that were measured at the plot-level, resulting in the exclusion of basal area and elevation from the pellet analysis. Additionally, I omitted the distance to riparian area metric from the fine-scale analysis based on the fact it was not considered biologically meaningful at this scale.

I used logistic regression models for pellet analysis, by assigning all pellet plots to a binary category (plots with pellets (i.e., hares present) = 1; plots without pellets (i.e., hares absent) = 0). This was appropriate because, although it was possible to estimate density at a site by averaging many plots, it was impossible to equate the number of pellets at each individual plot with intensity of use due to variation in pellet deposition rates and topography. Logistic models also fit better, had less parameters and allowed for some comparison with the camera models. I performed all pellet logistic regression models for 2019 and 2020 using the same software and model averaging methods as the camera data (See *Camera Habitat Models*).

Model Set

I generated a set of eight models for the camera detection data and seven for the pellet data to evaluate the relationship among hare use and cover, tree volume, edge and riparian habitat (Table 2.2). The “Site” models contained only geographic features while the “Cover” models contained only canopy closure. The “Hyp1” model, short for hypothesis, combined near-ground canopy closure and site covariates, with the idea that near-ground cover provides protection from terrestrial predators while overstorey cover covariates contained in “Hyp2” may protect from avian predators. The “Hyp3” and “Hyp4” combine all site and canopy closure covariates to investigate whether all levels of cover may interact to influence use. Finally, models “Esc1” and “Esc2,” short for escape, included features that could provide quick escape cover from predators such as horizontal cover (i.e., canopy closure from 0 to 1 m), cover provided by larger tree stems (i.e., basal area) and the distance to edge and riparian area. I did not include basal area, distance to riparian area or elevation in the pellet models; this made Hyp3 and Hpy4 equivalent so I eliminated Hyp4.

Table 2.2. Models used in logistic regression analysis of camera (2015, 2016 and 2020) and pellet (2019 and 2020) detection data from the John Prince Research Forest and surrounding area in north-central, British Columbia, Canada. BA = basal area, CC = canopy closure between 0 – 1 m, 1 – 3 m, 3 – 10 m and greater than (>) 10 m, DistEdge = distance to edge, DistRip = distance to riparian area and Elev = elevation.

Name	**Camera Models**	**Pellet Models**
Site	Elev + Slope + DistEdge + DistRip	Slope + DistEdge
Cover	CC0–1 + CC1–3 + CC3–10 + CC>10	CC0–1 + CC1–3 + CC3–10 + CC>10
Hyp1	Elev + Slope + CC0–1 + CC1–3 + BA	Slope + CC0–1 + CC1–3
Hyp2	Elev + Slope + CC3–10 + CC>10 + BA	Slope + CC3–10 + CC>10
Hyp3	Slope + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	Slope + CC0–1 + CC1–3 + CC3–10 + CC>10
Hyp4	Elev + Slope + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	
Esc1	CC0–1 + DistEdge + DistRip + BA	CC0–1 + DistEdge
Esc2	Elev + Slope + CC0–1 + DistEdge + DistRip + BA	Slope + CC0–1 + DistEdge

RESULTS

Camera Detection Variance Across Years

I detected hares during 885 out of a total of 12,840 winter camera-days (7%) across all three study years (Table 2.3). The mean detection rate was three times greater in 2015 ($\bar{X}$ = 0.09 (SD = 0.13)) than in 2020 ($\bar{X}$ = 0.03 (SD= 0.05)). Detection rates decreased at 41/66 camera stations between 2015 and 2020. I detected hares at least once at 59 stations across all three study years in winter and at 25 out of 49 in spring-summer 2016.

Detection rates in 2015 ranged from zero at 19/66 camera stations to a maximum of 0.66, while the majority (71%) of stations had detections rates of less than 0.10. I did not detect hares at 19 stations in winter 2016, whereas one camera station had the study maximum detection rate of 0.77. Detection rates were the lowest overall in 2020 with hares only detected at half (52%) of the stations and a maximum detection rate of 0.23 at one.

Although detection rates generally declined over the three years of study, the majority of camera stations retained the same relative position when compared to other stations within the same year (i.e., most stations that had the lowest/highest detection rates in 2015 also had the lowest/highest in 2016 and 2020). The 50th percentile of detection rates for 2015 was 0.04 and I used it as the threshold for classifying hares present (detection rate > 0.04) or absent (detection rate ≤ 0.04) at each station. Using this threshold, I classified hares as present at 28/66 camera stations in 2015, 27/66 in winter 2016, 25/49 in spring-summer 2016 and 14/66 in 2020. This meant occupancy also decreased by half, from a winter high of 0.42 in 2015 to a low of 0.21 in 2020.

Table 2.3. Total camera-days (maximum of 4620 per year for winter (W) and 8918 for spring-summer (SS)), mean camera-days per camera station (maximum of 70 per station for W, 182 for SS) (SD), total camera-days with detections, mean detection rate (total camera-days with detections/total camera-days) (SD) and occupancy (stations with hares present/total stations) for Snowshoe Hare (*Lepus americanus*) camera trapping study during W (February and March) 2015, 2016 and 2020 and SS (April – September) 2016 in the John Prince Research Forest and surrounding area, north-central British Columbia, Canada.

	2015 - W	**2016 – W**	**2016 - SS**	**2020 - W**
Total camera-days	4254	4453	8621	4133
Mean camera-days per station	64 (8)	68 (7)	176 (12)	63 (8)
Total camera-days with detections	389	361	628	135
Mean detection rate	0.09 (0.13)	0.08 (0.10)	0.08 (0.11)	0.03 (0.05)
Occupancy	0.42	0.41	0.51	0.21

Camera Habitat Models

Most of the 2015 models had a level of predictive power that made them useful for assessing habitat use (AUC > 0.7; Table 2.4). The majority of the model averaged weight was from models containing the distance to riparian area covariate, which was significant in all models it was included in. These models also had the greatest predictive power (i.e., AUC scores) and suggested hare use was positively associated with increasing distance from riparian areas (Table 2.5). The median distance to riparian areas for stations where hares were present was 41 m (Interquartile range (IQR) = 11 – 78 m) and was over four times greater than the 9 m median at the absent stations (IQR = 3 – 21 m; $W_{28,38} = 328$, $P = 0.008$).

Table 2.4. Logistic regression models for Snowshoe Hare (*Lepus americanus*) camera trapping study in the John Prince Research Forest and surrounding area, north-central British Columbia, Canada. Only models deemed competitive with the top model (i.e., within two Delta AIC units) are displayed. *K* = number of parameters, $\mathrm{AIC}_{\mathrm{ci}}$ = corrected Akaike's Information Criterion, $\mathrm{AIC}_{\mathrm{c\Delta i}}$ = Delta AIC = difference in AIC score between top model and each model, $\mathrm{AIC}_{\mathrm{cWi}}$ = AIC weight = proportion of the total amount of predictive power of each model when assessing the full set of models, AUC = area under the curve for the receiver operating characteristic. See Table 2.2 for model abbreviations. * Denotes significant coefficient ($P < 0.05$).

Model		*K*	$\mathrm{AIC}_{\mathrm{ci}}$	$\mathrm{AIC}_{\mathrm{c\Delta i}}$	$\mathrm{AIC}_{\mathrm{cWi}}$	AUC
2015 – Winter (n = 66)						
Esc2	Elev + Slope* + CC0–1 + DistEdge + DistRip* + BA	7	82.96	0.00	0.30	0.84
Hyp2	Elev + Slope* + CC3–10* + CC>10 + BA	6	83.58	0.62	0.22	0.80
Esc1	CC0–1 + DistEdge + DistRip* + BA*	5	84.03	1.06	0.18	0.79
Site	Elev + Slope* + DistEdge + DistRip*	5	84.36	1.40	0.15	0.81
2016 – Winter (n = 66)						
Hyp2	Elev* + Slope + CC3–10* + CC>10 + BA	6	85.80	0.00	0.28	0.77
Hyp1	Elev*+ Slope + CC0–1 + CC1–3* + BA	6	85.82	0.01	0.28	0.70
Cover	CC0–1 + CC1–3 + CC3–10 + CC>10	5	86.28	0.48	0.22	0.65
Hyp4	Elev* + Slope + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	8	87.28	1.48	0.13	0.80
2016 – Spring-Summer (n = 49)						
Cover	CC0–1 + CC1–3* + CC3–10* + CC>10*	5	64.56	0.00	0.37	0.80
Hyp3	Slope + CC0–1* + CC1–3 + CC3–10* + CC>10* + BA	7	64.68	0.12	0.35	0.83
2020 – Winter (n = 66)						
Esc1	CC0–1 + DistEdge* + DistRip + BA	5	66.55	0.00	0.44	0.76
Site	Elev + Slope + DistEdge* + DistRip	5	67.19	0.64	0.32	0.76

Table 2.5. Coefficients (β) for significant variables in logistic regression models for Snowshoe Hare (*Lepus americanus*) camera detections in the John Prince Research Forest and surrounding area, north-central British Columbia, Canada. See Table 2.2 for model abbreviations.

Study Period	**Model**	**Covariate**	**β**	**SE**	***P***
2015	Esc2	Slope	-0.12	0.06	0.04
2015	Esc2	DistRip	0.03	0.01	0.01
2015	Hyp2	Slope	-0.14	0.05	0.01
2015	Hyp2	CC3–10	0.05	0.02	0.01
2015	Esc1	DistRip	0.03	0.01	0.004
2015	Esc1	BA	-0.06	0.03	0.013
2015	Site	Slope	-0.11	0.05	0.025
2015	Site	DistRip	0.02	0.01	0.039
2016 – Winter	Hyp2	Elev	0.01	0.01	0.037
2016 – Winter	Hyp2	CC3–10	0.05	0.02	0.021
2016 – Winter	Hyp1	Elev	0.01	0.01	0.039
2016 – Winter	Hyp1	CC1–3	0.06	0.02	0.024
2016 – Winter	Hyp4	Elev	0.01	0.01	0.050
2016 – SS	Cover	CC1–3	-0.11	0.05	0.027
2016 – SS	Cover	CC3–10	0.09	0.04	0.014
2016 – SS	Cover	CC>10	-0.08	0.03	0.004
2016 – SS	Hyp3	CC0–1	0.08	0.04	0.033
2016 – SS	Hyp3	CC3–10	0.09	0.04	0.024
2016 – SS	Hyp3	CC>10	-0.09	0.03	0.010
2020	Esc1	DistEdge	0.03	0.01	0.009
2020	Site	DistEdge	0.02	0.01	0.045

In 2015 slope was significant in all models where it was included, being negatively associated with hare use. In fact, the median slope was almost twice as steep for camera stations where hares were absent (14% (IQR = 8 – 18%)) than camera stations where they were present (8% (IQR = 6 – 12%); $W_{28,38} = 744$, $P = 0.005$) in 2015. I also observed a similar difference in 2020 with flatter median slopes at stations where hares were present (8% (IQR = 5 – 11%)) than at stations where they were absent (12% (IQR = 7 – 17%); $W_{14, 52} = 495$, $P = 0.041$). In winter 2016 there was no difference in slope ($W_{27,39} = 645$, $P = 0.124$); however, median elevation was greater at stations where hares were present (809 m (IQR = 781 – 851 m)) than where they were not (786 m (IQR = 767 – 810 m); $W_{27,39} = 321$, $P = 0.007$). In Winter 2016, elevation was positively and significantly associated with hare use in all models it was included.

Canopy closure from 3 – 10 m was significant in the Hyp2 model in 2015 and in the top ranked model of winter 2016, was in several of the models with the highest AUC values and was positively associated with hare use in all models. It was also significant in the top two ranked models in spring-summer 2016. Median canopy closure from 3 – 10 m was greater at camera stations where hares were present than where they were absent in both 2015 (58% (IQR = 44 – 70 %) vs. 48% (IQR = 38 – 57%); $W_{28,38} = 364$, $P = 0.029$) and winter 2016 (57% (IQR = 48 – 70%) vs. 49% (IQR = 38 – 58%); $W_{27,39} = 351$, $P = 0.022$).

Model selection differed in winter 2016 from winter 2015 as many of the models with the highest AUC and lowest AIC contained canopy closure covariates, with distance to riparian area seeming less influential. Canopy closure from 1 – 3 m was significant in the Hyp3 model in winter 2016 and camera stations with hares present also had greater median canopy closure from 1 – 3 m (49% (IQR = 40 – 59%)) than where they were absent (42% (IQR = 32 – 53%); $W_{27,39} = 374$, $P = 0.047$). It was also significant in the top model in spring-summer 2016 but was negatively associated with hare use.

Distance to edge appeared to drive model selection in 2020. It was significant and positively associated with hare use and included in the top three ranked models. Median distance to edge where hares were present was almost double (29 m (IQR = 17 – 59 m)) that of camera stations where they were absent (16 m (IQR = 5 – 35 m); $W_{14, 52} = 219$, $P = 0.023$). An almost two-fold increase in this metric also was seen at stations where hares were present (15 m (IQR = 5 – 25 m) vs 29 m (IQR = 12 – 50 m); $W_{24,25} = 415$, $P = 0.021$) in spring-summer 2016 but did not seem as important to model selection as it was only included in models with relatively low model average weight.

Canopy closure over 10 m was significant in the Hyp3 model and negatively associated with hare use in 2020. It was also significant in all models in spring-summer 2016 and the median was 23% greater at camera stations where hares were absent (54% (IQR = 32 – 62%)) than where they were present (31% (IQR = 21 – 50%); $W_{24,25} = 180$, $P = 0.015$). Canopy closure from 0 – 1 m was not significant in any models in winter in any of the three years but it was in two models in spring-summer 2016 and positively associated with hare use. However, there was no difference in the median between stations where they were present or absent ($W_{24,25} = 242$, $P = 0.254$).

Pellet Detections Across Multiple Scales

I detected hare pellets at 408/1000 plots in 2019 and 322/1000 plots in 2020. When I eliminated recently cut and mature sites pellet detection rates increased to 403/700 plots in 2019 and 320/700 plots in 2020. I also used pellet counts from each site to estimate annual hare density for 2019 and 2020 and for the six sites that were also sampled in 2018 (Table 2.6). These numbers suggested density dropped at 7/10 sites from 2019 to 2020. Density also decreased or was unchanged at five out of six sites from 2018 to 2019. Density was the lowest at the mature sites (>80 years) and the recently clear-cut site (~ six years old).

Table 2.6. Estimated hare density (hares/ha) using the Yukon Equation (Krebs et al. 2001) for Snowshoe Hare (*Lepus americanus*) pellet sites in the John Prince Research Forest (JPRF) and surrounding area, north-central British Columbia (BC), Canada. Each site contained 100 plots for a total of 1000 plots (600 plots in 2018) counted twice annually and combined to obtain a single annual estimate. *These sites were eliminated from the within-stand model analysis. **Forest stand age estimates obtained from the BC Vegetation Resource Inventory and confirmed by JPRF harvest records.

Site	**2018 Density**	**2019 Density**	**2020 Density**	**Age***
1	0.18	0.16	0.07	43
2	1.74	2.19	0.71	16
3	0.47	0.26	0.16	48
4*	0.01	0.00	0.00	>80
5*	0.16	0.05	0.06	>80
6*	0.00	0.01	0.00	6
7		0.47	0.66	23
8		2.04	1.52	34
9		1.20	1.43	35
10		1.54	0.92	40

Pellet Habitat Models

Model selection outcomes were different when comparing high-ranking habitat covariates at the within-stand-scale to those at the landscape-scale (Table 2.7). The landscape models had the same AIC ranking in 2019 and 2020 with the majority of the AIC weight held by the same top ranked model (Hyp3 AIC_{cWi}: 2019 = 0.83, 2020 = 0.96) that contained all four canopy closure categories and slope. The cover covariates in combination with slope seems to have driven model selection at the landscape-scale, whereas the distance to edge seemed more important for within-stand models.

Table 2.7. Logistic regression habitat models for Snowshoe Hare (*Lepus americanus*) derived from pellet counts in 2019 and 2020 within the John Prince Research Forest and surrounding area, north-central British Columbia, Canada. All four study periods used the same set of seven models (See Table 2.2 for model abbreviations) but only those deemed competitive with the top model (i.e., within two Delta AIC units) are displayed. *K* = number of parameters in model including the intercept, Akaike's Information Criterion scores ($\mathrm{AIC}_{\mathrm{ci}}$), Delta AIC ($\mathrm{AIC}_{\mathrm{c\Delta i}}$) = difference in AIC score between top model and each model, AIC weight ($\mathrm{AIC}_{\mathrm{cWi}}$) = proportion of the total amount of predictive power provided by each model when assessing the full set of models, and area under the curve (AUC) for the receiver operating characteristic. *Denotes significant coefficient ($P < 0.05$).

Model		***K***	**$\mathrm{AIC}_{\mathrm{ci}}$**	**$\mathrm{AIC}_{\mathrm{c\Delta i}}$**	**$\mathrm{AIC}_{\mathrm{cWi}}$**	**AUC**
2019 – Within-stand Models (n = 700)						
Site	Slope + DistEdge*	3	810.61	0.00	0.54	0.73
Esc2	Slope + CC0–1 + DistEdge*	4	811.98	1.37	0.27	0.74
Esc1	CC0–1 + DistEdge*	3	812.65	2.04	0.19	0.73
2020 - Within-stand Models (n = 700)						
Site	Slope* + DistEdge*	3	858.10	0.00	0.68	0.69
Esc2	Slope* + CC0–1 + DistEdge*	4	860.11	2.01	0.25	0.69
2019 - Landscape Models (n = 1000)						
Hyp3	Slope* + CC0–1 + CC1–3* + CC3–10* + CC>10*	6	983.09	0.00	0.83	0.84
2020 - Landscape Models (n = 1000)						
Hyp3	Slope* + CC0–1 + CC1–3* + CC3–10* + CC>10*	6	981.17	0.00	0.96	0.81

Canopy closure from 1 – 3 m was significant in all landscape models and also was positively associated with hare use. Median canopy closure from 1 – 3 m was one-third greater for plots with hares present for the landscape data in 2019 (58% (IQR = 19 – 52%) vs. 44% (IQR = 43 – 78; $W_{408,592} = 59870$, $P < 2.2\text{e-}16$) and more than two-thirds greater in 2020 (61% (IQR = 46 – 80%) vs. 35% (IQR = 20 – 57%); $W_{322,678} = 54136$, $P < 2.2\text{e-}16$; Table 2.8). Canopy closure from 3 – 10 m was significant in all models and was positively associated with hare use. Canopy closure over 10 m was significant in all models as well but was negatively associated with hare use. Median canopy closure over 10 m was two-thirds greater for plots with hares absent in 2019 (37% (IQR = 0 – 87%) vs. 22% (IQR = 0 – 48%); $W_{408,592} = 157197$, $P = 2.3\text{e-}16$) and nearly three times greater in 2020 (53% (IQR = 0 – 85%) vs. 20% (IQR = 0 – 46%); $W_{322,678} = 140946$, $P = 5.1\text{e-}14$) for the landscape data. It was also over two times greater for plots with hares absent in 2019 (53% (IQR = 5 – 83%) vs. 22% (IQR = 0 – 47%); $W_{403,297} = 77822$, $P = 8.1\text{e-}12$) and 2020 (43% (IQR = 2 – 79%) vs. 19% (IQR = 0 – 46%); $W_{320,380} = 77135$, $P = 6.3\text{e-}10$) for the within-stand data.

It was harder to determine the relationship between hare use and canopy closure from 0 – 1 m, as even in those models where the covariate was significant, there was both positive and negative values. For the within-stand data in both years, canopy closure from 0 – 1 m was not significantly different for hare present sites from absent sites (2019 - $W_{403,297} = 55705$, $P = 0.113$, 2020 - $W_{320,380} = 55777$, $P = 0.059$).

The within-stand models were similarly ranked in 2019 and 2020. The distance to edge covariate was significant for both years and was also included in the top three AIC ranked models in both years as well, accounting for all of the model averaged AIC weight. The AUC values for 2020 were low, however, suggesting not all the models may have had adequate predictive power to use for assessing habitat use (6/7 below 0.7 AUC value). Median distance to edge was almost three times less for plots with hares present (50 m (IQR = 22 – 101 m)) than for those with hares absent in 2019 (149 m (IQR = 44 – 282 m); $W_{403,297} = 122792$, $P = 0.001$) and over two times less in 2020 (50 m (IQR = 33 – 103 m) vs. 116 m (35 – 257 m); $W_{320,380} = 82141$, $P = 1.25\text{e-}15$) for hare habitat plots.

Table 2.8. Coefficients for significant variables in logistic regression models for Snowshoe Hare (*Lepus americanus*) pellet detections in 2019 and 2020 in the John Prince Research Forest and surrounding area, north-central British Columbia, Canada. WS = Within-stand-scale and LS = Landscape-scale models, see Table 2.2 for model abbreviations.

Study Period	**Model**	**Covariate**	**β**	**SE**	***P***
2019 – WS	Site	DistEdge	-0.010	0.001	<2e-16
2019 – WS	Esc2	DistEdge	-0.010	0.001	< 2e-16
2019 – WS	Esc1	DistEdge	-0.010	0.001	< 2e-16
2020 – WS	Site	Slope	-0.014	0.001	0.0283
2020 – WS	Site	DistEdge	-0.009	0.001	< 2e-16
2020 – WS	Esc2	Slope	-0.015	0.007	0.0307
2020 – WS	Esc2	DistEdge	-0.009	0.001	< 2e-16
2019 – LS	Hyp3	Slope	-0.015	0.006	0.022
2019 – LS	Hyp3	CC1–3	0.018	0.005	0.006
2019 – LS	Hyp3	CC3–10	0.043	0.004	< 2e-16
2019 – LS	Hyp3	CC>10	-0.031	0.004	< 2e-16
2020 – LS	Hyp3	Slope	-0.018	0.006	0.005
2020 – LS	Hyp3	CC1–3	0.026	0.005	6.23E-07
2020 – LS	Hyp3	CC3–10	0.031	0.004	4.98E-16
2020 – LS	Hyp3	CC>10	-0.023	0.004	2.89E-10

DISCUSSION

My results showed that habitat use changed at different scales and population densities and occupancy. For example, habitat model selection and fit differed for all three years of CT as Snowshoe Hare occupancy declined by almost half; this suggested density-dependent habitat use. It was also different at the within-stand- compared to the landscape-scale for the pellet counts. This study furthers the understanding of Snowshoe Hare habitat use by demonstrating some of the shortcomings of previous hare habitat surveys that have primarily focused on the stand-level and either ignored or did not discuss the impact density-dependent habitat use on their results and conclusions (Holbrook 2017). Furthermore, I was able to produce habitat models that were biologically realistic and had good predictive accuracy that help deepen our understanding of hare habitat use in the sub-boreal forests of north-central BC.

Habitat Use

In 2015, when occupancy was highest, increased distances to riparian areas seemed to drive camera model selection. This is counter to what I predicted as I believed the dense vegetation and abundance of winter food species (e.g., willows) provided by riparian areas would be associated with increased hare use. Tape et al. (2016) discovered that changes to the Arctic climate have allowed riparian ecosystems to expand north and these habitats may have further supported the expansion of Snowshoe Hare range north as well. I was not, however, able to identify other studies that specifically looked at hare habitat use in relation to riparian areas. It is possible that hares avoid riparian areas and this was most apparent in 2015 when they occupied more available habitat. This needs further investigation to confirm as many species, including mesocarnivores, use riparian areas as travel corridors (Hilty and Merenlender 2016, Santos et al. 2016) and it is possible predation is greater for hares in these habitats.

In 2016 camera model selection and fit appeared to be influenced by canopy closure. I predicted hares in my study area would use areas with greater horizontal cover (i.e., canopy closure from 0 – 1 m) but it was not significant in any winter camera or pellet models. This

LIDAR variable was highly correlated with cover pole visual obstruction measurements taken at each camera station; therefore, I believed it was a robust measure of understory/horizontal cover. This type of cover has been found to be the most important to Snowshoe Hares, especially in winter, and is often the biggest predictor of use (Sullivan et al. 2007, Berg et al. 2012, Sultaire et al. 2016).

Snow may explain the fact canopy cover from 0 – 1 m was significant and positively associated with hare use in spring-summer 2016 but was not in many of the winter models, when 1 – 2 m of snow on the ground is common. Snow also could have influenced this layer in the pellet models, which span a year of pellet counts, as there is generally snow on the ground in the region for about half the year (Environment and Climate Change Canada 2022). Canopy closure from 1 – 3 m was significant and positively associated with hare use in one 2016 camera model and in many pellet models. It is possible that this height category acted as horizontal cover in these models as it represented the crucial 0 – 2 m above ground horizontal cover layer (Conroy et al. 1979, Litvaitis et al. 1985) when there was snow on the ground. Potvin et al. (2005) did not find a significant effect of horizontal cover on hare use and suggested the uniformity of cover across their study area may be the cause. That could also be true for my study but it is more likely snow caused the 1 – 3 m layer to be more representative of horizontal cover in the winter than the 0 – 1 m layer, indicating horizontal cover is important to hares in the region.

Canopy closure above the understory provides a different type of cover (e.g., visual obstruction from aerial predators) and is often correlated with increased hare use (Roy et al. 2010, Cheng et al. 2015, Holbrook et al. 2016), which my data also supported. Canopy closure from 3 – 10 m was a significant predictor of hare use for several camera models in 2015 and 2016 and many of the pellet models. Thomas et al. (2019) found canopy closure more important to hares than horizontal cover and suggested this could be due to hares avoiding the risk of avian predation. A diverse and abundant raptor community is found in the area with several known hare predators, including Great Horned Owl (*Bubo virginianu*s) (Rohner and Krebs 1996) and Northern Goshawk (*Accipiter gentilis*) (Boutin et al. 1995), and it is possible hares use areas with increased canopy closure to reduce the risk of aerial predation. Canopy closure also could be correlated with thermoregulation, food quality and/or quantity or other benefits.

Mature forests do not always provide suitable habitat for hares even though canopy closure is often greatest in these habitats (Sullivan et al. 2012). Canopy closure over 10 m was significant and negatively associated with hare use in camera models in spring-summer 2016 and winter 2020 as well as several pellet models. In 2020 population pressure to occupy all available, including suboptimal, habitat was likely reduced and so it is possible the remaining hares avoided sites with the greatest canopy closure over 10 m, indicating they avoided mature sites. This idea was further supported by very low pellet detections at mature sites in all years.

For the camera models in 2020 and the pellet within-stand models the distance to edge seemed to be an important predictor of use and was significant in the top three models. Interestingly, hares were positively associated with distance to edge for the camera models in 2020 but negatively associated for the pellet models. The difference between the pellet and camera models could be due to differences in scale but could also be attributed to seasonality. Hares often forage in more densely vegetated interior sites in winter when they feed on more woody browse; whereas in summer it is the interspersion of edge and open habitat that provides seasonally available herbaceous foliage (Wolff 1980). The 2016 spring-summer data contradicts this, however, as distance to edge also was significant and positive but was not highly influential on model selection. Although edge habitat may provide the interspersion of foraging and cover habitat required by hares in some populations (Conroy et al. 1979) it may also be correlated with greater predation for some species (Andrén 1995).

Several studies have associated sites with lower edge density or greater distances from edge habitat with higher Snowshoe Hare occupancy and use (Roy et al. 2010, Sultaire et al. 2016). Distance to edge was not significant in winter 2015 or 2016 but as occupancy substantially decreased it became highly influential in the 2020 cameras models. It is possible in 2020 that the remaining hares stayed in or moved to areas further from habitat edges, potentially to avoid predation (Wolff 1980). This highlights the differences in model selection in winter 2015 and 2016 compared to 2020 that suggest density-dependent habitat use. Furthermore, the different model selection and importance of distance to edge in the within-stand compared to the landscape pellet models suggests a potential difference in use at varying ecological scales.

Habitat Use Across Ecological Scales

As evidenced in many species, but largely unexplored with Snowshoe Hares, model selection appears to vary across different ecological scales. In the current study, pellet model selection was similar for 2019 and 2020 and was more influenced by scale (within-stand vs. landscape). At the landscape-scale canopy closure appeared to have had the greatest influence on model selection. This contrasts with the finer-scale within-stand models where distance to edge drove model selection and fit but aligns with the few other studies that have investigated and found a change in hare habitat use at different scales (Lewis et al. 2011, Fuller and Harrison 2013, Gigliotti et al. 2018).

The concept of ecological scale is fundamental to wildlife research yet most habitat studies focus on a single scale without exploring or addressing the impact of scale on their results and conclusions (Wheatley and Larsen 2018). One approach is to test all the same independent and dependent variables at each scale measured (Wheatley and Larsen 2018); a continuum of scales is ideal for this as it may allow for cross-scale predictability (Wheatley and Johnson 2009). Wheatley and Larsen (2018) demonstrated how model selection varied for Northern Flying Squirrels (*Glaucomys sabrinus*) across 14 observational scales and showed how the effect differed between sex and age classes. Unfortunately, I was not able to do this type of in-depth scale analysis but it may be possible in the future with a long-term hare dataset and LIDAR, which allows for the quantification of the same habitat variables at different scales.

I only examined hare habitat use at two scales but I was able to demonstrate differences in model selection between the two. This illustrates how studies undertaken at multiple scales can be important in determining the full scope of hare habitat use (Thornton et al. 2013, Holbrook et al. 2017) and further supports the recommendations of others to expand beyond typical stand-level hare habitat studies (Ausband and Baty 2005, Fuller and Harrison 2013, Holbrook et al. 2017).

Density-Dependent Habitat Use and the Snowshoe Hare Cycle

I observed a large decline in camera detections between the first two years of study and the third; this population oscillation suggested to me that my study population may follow a cyclical pattern observed in many other Snowshoe Hare populations (Keith and Windberg 1978, Krebs et al. 2018, Sullivan and Sullivan 1988). Pellet counts also declined between 2018 and 2020 and subsequent pellet counts in 2022 have shown the population is beginning to rebound (unpublished JPRF data); this further corroborated a local hare cycle. It is also worth noting that lynx detections decreased during this same period to their lowest levels in 2020 and 2021 (unpublished JPRF data). This also suggested the occurrence of the classic hare-lynx cycle in my study area.

Without observations spanning the entirety of a typical cycle length, or multiple cycles, I was unable to determine if 2015 represented the peak and 2020 the low of the cycle. I did, however, believe it was useful to compare the camera models in winter 2015 and 2016, which had similar occupancy, to 2020 when occupancy was significantly reduced. Occupancy was highest in spring-summer 2016. This was not surprising as hare populations generally are higher in summer when many offspring are produced before many young-of-the-year and adults do not survive winter (Kielland et al. 2010). The winter models supported my hypothesis that if occupancy and/or density changed so would habitat use and supported the theory that hares exhibit density-dependent habitat use.

Determining the most effective time to quantify and assess habitat and life history characteristics of species that cycle in abundance has long been a question of debate in ecology. The Ideal Free Distribution theory suggests that as a population increases, some individuals will have to move to lower quality habitat (Fretwell and Lucas 1969). Snowshoe Hares are known to exhibit density-dependent habitat preferences and occupy most available habitat during population peaks and retreat to refugium during lows (Wolff 1980, Hodson et al. 2010). These refugia appear to be high-quality areas with dense vegetation (Wolff 1980). This change in landscape occupancy could potentially lead to conflicting results and interpretations when assessing habitat use for hare or other cyclic populations that exists in a heterogenous environment. This could explain the differences in model selection for the three years of camera data. More broadly it could explain the varying and sometimes contrasting hare habitat use inferences from previous studies, in addition to their broad distribution across many habitat types and varying methods used.

Conclusions and Management Implications

My comparisons are limited in that the camera and pellet studies did not have complete temporal overlap. Also, the spring-summer data only represented a subset of all camera stations. A useful continuation of this study would be to monitor hares in my study area over the entire cycle. Cameras proved to be a useful tool for collecting hare detection data that I used to look at habitat use but they could be used to examine other aspects of their ecology. The detection data we passively gathered with cameras allowed me to develop models that seemed to fit the data (i.e., AUC > 0.7). With my study design and cameras, I was also able to detect a large decline in the population confirmed by more traditional and widely-tested hare pellet plots. This supports the argument that CT is a useful way to monitor the Snowshoe Hare cycle, especially with new methods for estimating hare densities from cameras (Jensen et al. 2022).

My results suggested that both horizontal cover and canopy closure influence habitat use. It should be a priority of anyone managing forests for Snowshoe Hares, or one or more of their many predators, to ensure contiguous areas with abundant horizontal cover and canopy closure (Holbrook et al. 2017). In practice this might include dividing forestry operations over a larger area to avoid large clearcuts, retaining more trees, or longer harvest intervals (Thomas et al. 2019). Managing for a mosaic of different interconnected habitat types (e.g., stand ages, composition) may allow both forestry and conservation priorities to be met as long as some contiguous forested patches with dense cover are maintained. This will also provide the diversity of habitats that allow hares to avoid or use areas near habitat edges and riparian areas.

My results showed that habitat modelling can be heavily influenced by the method and scale used in each study and hence the results of this and other studies need to be interpreted within their own confines. This in turn supports the recommendations of Holbrook et al. (2017) to assess habitat use at multiple ecological scales (e.g., assess within-stand use in addition to the traditional stand-level approach), with multiple response variables (e.g., density and occupancy) and across a gradient of potential habitats not just those assumed to be high quality.

Density-dependent habitat use can occur in cyclic populations and further complicate the interpretations of these studies (Kawaguchi and Desrochers 2018). Habitats that provide refugia during population lows may be the most important to protect and manage for Snowshoe Hares (Wolff 1980, Hodson et al. 2010) and their many obligate and opportunistic predators, especially lynx. Similar to Wolff (1980) my results suggested interior sites (i.e., further from habitat edges) with abundant horizontal cover and canopy closure may provide this type of refugia. Multi-year studies that span the entirety, with regular intermittent sampling, of one or more population cycles may provide better insights into Snowshoe Hare habitat use and may also be important for other species or populations that cycle in abundance over time as well.

Camera trapping proved useful in detecting changes in the local hare population and for evaluating habitat use. Deploying cameras and maintaining storage devices and batteries across a fairly large study area was labour intensive. As storage and battery technology continues to improve and easier and cheaper remote access wildlife cameras become available, they may provide a more effective way to monitor cyclic populations like Snowshoe Hares. These populations may also require more frequent monitoring to fully understand habitat use, especially if it is density-dependent, to ensure proper management. This is important for a keystone species like Snowshoe Hares that sustain so many other species and are an integral part of their local ecosystems.

This study has expanded our understanding of hare habitat use in the sub-boreal forests of north-central BC. It also has confirmed the need for more hare habitat studies to go beyond the stand-level and explore hare habitat use at a fine-scale. I have also been able to provide more support for the idea that Snowshoe Hares exhibit density-dependent habitat use; this is useful as it needs to be addressed more frequently in hare habitat studies. Finally, I was able to provide some evidence that the local hare population cycles in abundance and that wildlife CT studies were useful in detecting population changes. This project contributes to the long-term conservation and understanding of this keystone species that is integral to the healthy functioning of northern forested ecosystems.

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CHAPTER 3: CONCLUSION

HIGHLIGHTS OF THE STUDY

I produced Snowshoe Hare (*Lepus americanus*) habitat models that were biologically realistic and had good predictive accuracy. Model selection and fit aligned with many other hare habitat studies in that cover and canopy closure were important predictors of hare use. My results, however, showed that habitat modelling can be influenced by scale and also by changes in population density or occupancy. For example, distance to edge was positively associated with hare use for the within-stand pellet models but it appeared they avoided edges for the camera models in the same year (2020). In the landscape pellet models distance to edge was not significant highlighting differences in use at varying ecological scales. It was also not significant in the 2015 or 2016 camera models potentially showing density-dependent habitat use in Snowshoe Hares.

Other significant site and habitat variables included elevation, slope and distance to riparian areas in some years/models. This study has helped to deepen our understanding of hare habitat use in the sub-boreal forests of north-central British Columbia (BC). It also furthers the understanding of Snowshoe Hare habitat use in general by addressing some of the previous knowledge gaps by assessing hare habitat use at different scales with two methods over a gradient of potential habitats and while hare occupancy and density was declining. I was also able to document density-dependent habitat use.

MANAGEMENT IMPLICATIONS

Implications of Study to Snowshoe Hare Ecology

My results showed that a variety of site and habitat components influenced hare habitat use. Cover often is cited as the single most important determinant and predictor of hare habitat use (Litvaitis et al. 1985, Bois et al. 2012, Gigliotti et al. 2018). My results supported this conclusion although other variables such as distance to edge also influenced model selection. Horizontal/understory often is cited as the most important type of cover to hares (Sullivan et al. 2007, Berg et al. 2012, Simard et al. 2018), while my models suggested it did influence habitat use they also showed the importance of canopy closure higher in the canopy (i.e. >3 m).

Canopy closure is known to influence hare habitat use (Roy et al. 2010, Thornton et al. 2013, Cheng et al. 2015). Thomas et al. (2019) found canopy closure to be more important to hares than horizontal cover and suggested hares used areas with greater canopy closure to avoid aerial predation. Although Canada Lynx (*Lynx canadensis*) are known to predate hares in the area (as evidenced by the camera footage), the exact proportion each predator species contributes to hare mortality in the area is unknown. In the Yukon, Krebs et al. (1995) found that avian predators accounted for 40% of hare predation. It is possible hares select for different types of cover based on the composition of the local predator community. It is, therefore, important to include several measures of cover when modelling hare habitat use including both horizontal and canopy closure. My models indicated hares were positively associated with canopy closure under 10 m but negatively associated with it over 10 m so it may also be useful for other studies to stratify canopy closure to assess its influence at multiple levels.

Distance to edge was an important predictor of use and was significant in the top three camera models in 2020 and the within-stand pellet models in both years. Hare habitat use was positively associated with distance to edge for the camera models in 2020 but negatively associated for the pellet models. This may have indicated that the relationship with distance to edge changes with scale and/or hare abundance. Other significant site and habitat variables included elevation, slope and distance to riparian areas in some years/models.

Snowshoe Hare densities vary greatly across their range and throughout the hare cycle so it can be difficult to compare them. In the southern part of their range in Colorado, Ivan et al. (2014) estimated densities in different forest stands that ranged from 0.01 to 0.66 hares/ha. Whereas Krebs et al. (1995) documented densities in the southern Yukon as high as 7 hares/ha near a population peak that later crashed to 1 hare/ha. Estimated densities at my pellet sites ranged from 0 to 2.2 hares/ha and generally declined from 2018 to 2020 but appeared to be rebounding in 2021 and 2022 (unpublished JPRF data). Originally it was believed that the hare cycle was synchronized across their range but fur trapper data from the 1930s and -40s suggested population peaks travelled in a wave across Canada with delays between peaks up to four years (Krebs et al. 2018). Hare densities most recently hit their peak at the famous Kluane Lake study area in 2017 (Oli et al. 2020). Krebs et al. (2018) suggested about a two-year delay in peak number between north-central BC, where this study was located, and the Kluane Lake study area in Southern Yukon. If 2015 was, or was close to, the peak for my study population then it would align with that suggestion, adding support to my conclusion that it cycles in abundance over time.

As emphasized throughout this thesis, Snowshoe Hares have received considerable research attention. Studies across their range and especially long-term studies, such as those in the Southern Yukon (Krebs et al. 1986, 2001*a*, Smith et al. 1988) are not just important for understanding hare ecology but are also landmark ecological studies. Some knowledge gaps still exist though; for example, most hare habitat studies have been conducted at the stand- or patch-level and it is important that future research broadens the focus to multiple scales (e.g., within-stand; Thornton et al. 2013, Holbrook et al. 2017). With my pellet models I assessed hare habitat use at the landscape-scale (i.e., a representative selection of all habitat types) vs. areas with moderate to high hare use and demonstrated a difference in model selection between the two scales. Although camera and pellet models were not directly comparable, model selection differed between the 7854 m^2 camera trapping (CT) scale and the 100 m^2 pellet plot scale. I believe this shows it is important that those managing forests for hares and their predators or any other species to assess habitat use at multiple scales or conservation planning may leave important habitats unprotected (Wheatley and Larsen 2018, Wheatley and Johnson 2009).

Another common practice in hare habitat studies has been to use type-based approaches where habitats are predefined and sampled accordingly (e.g., using forest cover maps to stratify habitats and only sampling areas with high hare use potential) but it has been argued surveying a gradient of potential habitats may be more appropriate (Holbrook et al. 2017). The CT grid was randomly generated in order to capture a representative sample of the broader landscape. This included areas where hares were more likely to occur (e.g., regenerating hybrid spruce-fir forests or lodgepole pine stands) and where they likely were not (e.g., open habitats, mature stands). With the pellet counts I also included a variety of sites with varying hare use potential, such as clear-cuts and old-growth stands that are not commonly included. By dropping these sites for part of the pellet analysis I was able to show that model selection, and therefore likely habitat use, differed when assessing all sites or just those that supported moderate to high hare population densities. This leads me to agree with the conclusions of Holbrook et al. (2017) and recommend biologists survey a broader range of habitat types not just those assumed to support high hare densities.

With this study I was able to demonstrate density-dependent habitat use that also has been observed in other Snowshoe Hare populations (Wolff 1980, Hodson et al. 2010). Although it has been acknowledged by other hare researchers, the impacts of this shift in landscape occupancy throughout the hare cycle largely goes undiscussed. Studies that are able to investigate hare habitat use over the course of a cycle, or several cycles, may provide better insights than short-term studies. It would therefore be useful for researchers to explicitly state which phase of the cycle their study took place in, as habitat conclusions made at population peaks can differ from those made during lows, as I demonstrated. I state this with the understanding that long-term research funding is rare and planning studies that may span decades is very challenging (e.g., a graduate study typically lasts two to four years).

Implications of Study to Passive Snowshoe Hare Surveys

The cameras used in this study also detected many other species and these data are currently being analyzed by JPRF researchers and other graduate students. Their data showed population and/or detection declines in hare predators and changes in the composition of the mesocarnivore community (unpublished JPRF data). I believe my study can help inform this ongoing work. First, I would suggest including cover (horizontal and canopy closure) and distance to edge covariates in any habitat models, as it is reasonable to assume overlap in habitat use between hares and their predators. I would also recommend assessing whether local predator species also experience density-dependent habitat use as exhibited by hares in this study.

The use of CT for Snowshoe Hare density estimation (Jensen et al. 2022) may provide a logistically and economically feasible way to assess hare habitat cycles alone or in conjunction with other types of surveys. I was able to detect a large decline in occupancy

(50%) with cameras alone and confirmed this decline with traditional pellet counts. This could eliminate the need for labour intensive and invasive mark-recapture trapping, except in certain circumstances; these might include studies where more accurate measures of abundance are required (e.g., addressing conservation concerns) or investigations into diet, movement or other factors.

We also might see CT density estimation replace labour intensive pellet surveys, especially with continuing technological improvements and new methods discussed in Jensen et al. (2022). I also was able to demonstrate that traditional pellet surveys can be used to explore hare habitat use at different scales; this also could be done using CT methods, especially when combined with LIDAR data, which can allow for the quantification of the same variable at a variety of scales. I believe the combination of camera and pellet methods allowed me to address my hypothesis without the need for challenging mark-recapture surveys. I also demonstrated the CT can be used to monitor the Snowshoe Hare cycle, which could be very useful to researchers looking for a non-invasive way to do that.

Forest Management of a Keystone Species

Many aspects of Snowshoe Hare ecology have been studied over the years. This is due to both their critical importance as a food source for many other species and also their dramatic population cycles that allows for the exploration of many key ecological concepts (e.g., Lotka-Volterra predator-prey dynamics). I chose to focus on hares due to their importance to the local ecosystem in the sub-boreal forests of north-central BC and because preliminary camera analysis suggested a change in the composition of the local predator community (e.g., decreases in Canada Lynx and American Marten (*Martes americana*) detections and increases in detections of rarer species such as Fisher (*Pekania pennanti*) and Wolverine (*Gulo gulo*)). This study will help JPRF researchers further explore these dynamics and determine whether they are related to the Snowshoe Hare cycle.

These results support the idea that a mosaic of seral stages and habitat types may provide the interspersion of interior and open sites that hares require at different scales and at varying points along the hare cycle (Conroy et al. 1979, Wolff 1980). Snowshoe Hares occupy a variety of forested habitats across their range and so it is up to land managers to determine what harvest regimes and combination of different age patches best support local hare populations.

It was clear that recent clear-cut sites, with no or low cover, and mature sites, with lower shrub and tree densities, did not support as many hares as sites of intermediate ages. This has also been observed in other studies and hares usually do not recolonize harvested areas for 15 – 30 years (Paragi et al. 1997, de Bellefeuille et al. 2001). My models indicated both cover and canopy closure influenced habitat use so patches that provide both (e.g., mid-successional conifer- or mixed-stands) should be maintained, preferably they also should be connected within a mosaic of other seral stages and land uses. Therefore, for my study region, and most likely others, I would recommend staggering harvest timing geographically so that the appropriate composition of seral stages exist for hares and avoiding large clear cuts, increasing tree retention in and adjacent to harvested areas and allowing for longer harvest intervals (Thomas et al 2019).

LIMITATIONS AND FUTURE RESEARCH

Most of the biggest limitations of this study revolved around timing. With the data series I was unable to fully determine which years represented the absolute hare population peak and low. I had camera data for 2015 and 2016, then a three-year data gap and then pellet data in 2019 and both pellet and camera data in 2020. This five-year period did not cover the span of a typical hare cycle, which is around 10 years and sometimes presented as a range from 8 – 11 years (Krebs et al. 2018). Camera trapping and pellet counts completed subsequent to my study, in 2021 and 2022, seem to indicate that the local hare population is beginning to recover (unpublished JPRF data). This does suggest that 2020 was the population low and further implies that the population was near its peak in 2015. Another limitation was that the camera and pellet data did not fully align temporally. A longer-term dataset would have enabled me to plot out the entire cycle but I do believe I was still able to draw conclusions about density-dependent hare habitat use during or near a population peak and low. Linden et al. (2017) concluded that models using detection data can be used in place of other methods (e.g., measure of abundance such as density) as they often offer similar habitat inferences, while remaining more cost effective.

Going forward the JPRF will have annual hare density estimates and CT every three to five years. This dataset will allow them to determine and predict hare population highs and lows. Using the analysis framework in this thesis, it should be relatively simple to use the same models to assess hare habitat use for subsequent years. As I established with this study, the hares in this region exhibit density-dependent habitat use. It would be very interesting to not only assess habitat use near the population peak and crash but also during the recovery and decline phase. Furthermore, it has been established that the amplitude of each population cycle can vary (Ginzburg and Krebs 2015, Myers 2018) and it would be interesting to determine whether habitat use also varies with cyclic amplitude.

The use of CT wildlife studies has grown exponentially over the last 20 years and a variety of field methods and analytical approaches have been used. Although some have advocated for the standardization of CT methods it is challenging when habitats and species ecology vary so much; also, rare species may require specialized approaches (Burton et al. 2015). One commonly cited issue with CT studies is that researchers must organize continuous detection data into discrete presence/absence “surveys” that are analogous to independent sampling events and can vary from a day to weeks (Burton et al. 2015, Rich et al. 2017, Neilson et al. 2018). This subjectivity can bias results and interpretations and different survey lengths could led to different estimates of abundance or conflicting model selection. Cameras also do not allow the identification of individuals, with the exception of some species (e.g., distinct markings), and this makes estimating density difficult. Camera data is also time consuming to process and so traditional mark-recapture studies are still useful for many research questions.

In order to define what constituted an independent sampling event I considered the ecology of my model species. Snowshoe Hares are mostly active at night, dawn and dusk and are almost completely sedentary during the day (Keith 1964, Feierabend and Kielland 2014, Studd et al. 2019). This meant that their activity already was organized into discrete time periods and hence I chose a 24-hour camera-day that ran from noon on one calendar day until noon the next. Of course, this did not eliminate all biases and the results of this study must be interpreted within the confines of the methods used. This includes the fact that I further defined presence/absence using the 50th percentile of detection rates for the first year of study (2015), during the studies’ population high. This may seem subjective but the detection rate data was clearly bimodal, where the stations with detections either had very few (one or two camera-days out of 70) or moderate to high detections (10 – 40 camera-days out of 70). The approach I chose helped to delineate between the two clear categories. Another reason I chose to do this was because a common weakness of CT studies is that they fail to established a clear relationship between camera detections and abundance (Burton et al. 2015). I believed by delineating very low use stations I could be more confident that stations where hares were classified as present represented stations they actually used.

I chose not to incorporate detection probabilities into my models, which has been cited as a flaw of some camera studies (Burton et al. 2015). I did, however, perform exploratory occupancy modeling with my data and the occupancy estimates were not different for any of the years. I chose to use logistic regression models because they have less parameters and I sought to compare, in whatever capacity, the pellet and camera models. Another weakness of some camera studies is the arbitrary definition of scale as detections at a single camera are often broadened and interpreted in the context of a much larger geographic unit (e.g., a forest stand). To limit this type of bias I paired the camera detection data with fine-scale habitat data (50-m radius), which was only possible due to the LIDAR data.

The LIDAR data were collected in 2015, given it is expensive to collect and analyze these data it was not feasible to update it for the later models. I visited each camera station in summer of 2019, as did JPRF researchers in winter 2020, and did not observe any major disturbances or habitat changes within the buffer of any camera. My study area experiences long cold winters that limit annual plant growth and rapid changes in vegetative biomass so I believe that it was still appropriate to use the 2015 LIDAR for all my study years.

One final limitation of the pellet models was that I used the Yukon-derived regression equation (Krebs et al. 1987, Krebs et al. 2001*b*) to estimate density and not a locally derived equation because that would have required an entire hare trapping and tagging mark-recapture study. As shown by Mills et al. (2005) the Yukon Equation may provide comparable density estimates across a wider geographic range, especially if studies do not require highly accurate measures of absolute abundance, which I did not. I also followed similar pellet count methods to limit bias (McKelvey et al. 2002, Mills et al. 2005).

A hare mark-recapture study in the JPRF would answer this question. More broadly other future research that would complement my thesis includes verifying new methods for estimating hare density from cameras (Jensen et al. 2022) and directly comparing them to pellet studies. Eventually this could eliminate the need for labour intensive pellet and mark-recapture studies and standardize Snowshoe Hare density estimating methods across their range. As suggested by Wheatley (2009) I also believe a more in-depth study of hare habitat use over a larger scale-domain continuum would be beneficial instead of just the two I investigated in this study. The JPRF LIDAR dataset may provide the opportunity to do this in the future.

CONCLUSION

Although Snowshoe Hares have been heavily researched this study is one of a few that has assessed hare habitat use at multi-scales, with multiple responses and field methods and sampled a wide-range of habitats, not just those suspected to be high-quality (Holbrook et al. 2017). With this study I was able to show that hares exhibit density-dependent habitat use that varied at different scales. I was also able to confirm that cameras can be useful in detecting oscillations in hare populations such as those occurring over the full population cycle. I also showed that cover, especially horizontal cover and canopy closure under 10 m, distance to edge and several other site and habitat features were important and useful in predicting hare use.

I believe this study expands our understanding of Snowshoe Hare ecology potentially leading to better management of not only hares but the many predators who rely on them. My ability to demonstrate the effects of different detection methods, scale and density/occupancy on habitat model selection influences not only Snowshoe Hare studies but also those of their predators and other species who cycle in abundance overtime. I showed that cameras were useful in detecting changes in occupancy/density associated with population cycles and this has implications for species other than hares as CT studies could be used to monitor their cycles as well. This study increases the scope and depth of our knowledge of this important keystone species, and in turn provides for better management and conservation of forest processes.

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APPENDIX 1 – FULL SET OF LOGISTIC REGRESSION CAMERA MODELS (N = 8 PER CAMERA TRAPPING SESSION).

Table 1. Full set of logistic regression models with number of parameters (*K*), corrected Akaike's Information Criterion (AIC$_{ci}$), Delta AIC (AIC$_{c\Delta i}$) = difference in AIC score between top model and each model, AIC weight (AIC$_{cWi}$) = proportion of the total amount of predictive power of each model when assessing the full set of models, and area under the curve (AUC) for the receiver operating characteristic = a measure of predictive accuracy, for Snowshoe Hare (Lepus americanus) camera trapping study during winter 2015, 2016 and 2020 and during spring-summer 2016 in the John Prince Research Forest and surrounding area, north-central British Columbia, Canada. BA = basal area, CC = canopy cover between 0 – 1 m, 1 – 3 m, 3 – 10 m and over 10 m, DistEdge = distance to edge, DistRip = distance to riparian and Elev = elevation. * Denotes significant coefficient ($P < 0.05$).

Model		***K***	**AIC$_{ci}$**	**AIC$_{c\Delta i}$**	**AIC$_{cWi}$**	**AUC**
2015 – Winter (n = 66)						
Esc2	Elev + Slope* + CC0–1 + DistEdge + DistRip* + BA	7	82.96	0.00	0.30	0.84
Hyp2	Elev + Slope* + CC3–10* + cc>10 + BA	6	83.58	0.62	0.22	0.80
Esc1	cc0–1 + DistEdge + DistRip* + BA*	5	84.03	1.06	0.18	0.79
Site	Elev + Slope* + DistEdge + DistRip*	5	84.36	1.40	0.15	0.81
Hyp3	Slope* + CC0–1 + CC1–3 + CC3–10 + cc>10 + BA	7	85.72	2.76	0.08	0.79
Hyp4	Elev + Slope* + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	8	86.06	3.09	0.06	0.81
Hyp1	Elev + Slope* + CC0–1 + CC1–3 + BA	6	89.13	6.16	0.01	0.76
Cover	CC0–1 + CC1–3 + CC3–10 + CC>10	5	93.40	10.44	0.00	0.67
2016 – Winter (n = 66)						
Hyp2	Elev* + Slope + CC3–10* + CC>10 + BA	6	85.80	0.00	0.28	0.77
Hyp1	Elev*+ Slope + CC0–1 + CC1–3* + BA	6	85.82	0.01	0.28	0.70
Cover	CC0–1 + CC1–3 + CC3–10 + CC>10	5	86.28	0.48	0.22	0.65

Hyp4	Elev* + Slope + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	8	87.28	1.48	0.13	0.80
Hyp3	Slope + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	7	89.16	3.36	0.05	0.76
Site	Elev* + Slope + DistEdge + DistRip	5	91.20	5.40	0.02	0.70
Esc2	Elev* + Slope + CC0–1 + DistEdge + DistRip + BA	7	92.23	6.43	0.01	0.74
Esc1	CC0–1 + DistEdge + DistRip + BA*	5	93.30	7.49	0.01	0.69
2020 – Winter (n = 66)						
Esc1	CC0–1 + DistEdge* + DistRip + BA	5	66.55	0.00	0.44	0.76
Site	Elev + Slope + DistEdge* + DistRip	5	67.19	0.64	0.32	0.76
Esc2	Elev + Slope + cc0–1 + DistEdge* + DistRip + BA	7	69.66	3.11	0.09	0.78
Cover	CC0–1 + CC1–3 + CC3–10 + CC>10*	5	70.01	3.46	0.08	0.72
Hyp2	Elev + Slope + CC3–10 + CC>10 + BA	6	72.31	5.76	0.02	0.74
Hyp3	Slope + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	7	72.57	6.02	0.02	0.76
Hyp1	Elev + Slope + CC0–1 + CC1–3 + BA	6	73.28	6.73	0.02	0.72
Hyp4	Elev + Slope + CC0–1 + CC1–3 + CC3–10 + CC>10 + BA	8	74.60	8.05	0.01	0.76
2016 – Spring-Summer (n = 49)						
Cover	CC0–1 + CC1–3* + CC3–10* + CC>10*	5	64.56	0.00	0.37	0.80
Hyp3	Slope + CC0–1* + CC1–3 + CC3–10* + CC>10* + BA	7	64.68	0.12	0.35	0.83
Hyp4	Elev + Slope + CC0–1* + CC1–3 + CC3–10* + CC>10* + BA	8	67.53	2.97	0.08	0.83
Site	Elev + Slope + DistEdge* + DistRip	5	67.80	3.24	0.07	0.75
Hyp2	Elev + Slope + CC3–10 + CC>10* + BA	6	67.93	3.38	0.07	0.79
Esc1	CC0–1 + DistEdge* + DistRip + BA	5	69.29	4.74	0.03	0.73

Esc2	Elev + Slope + CC0–1 + DistEdge* + DistRip + BA	7	70.22	5.66	0.02	0.78
Hyp1	Elev + Slope* + CC0–1 + CC1–3 + BA	6	72.99	8.43	0.01	0.72

APPENDIX 2 – FULL SET OF LOGISTIC REGRESSION PELLET MODELS (N = 7 PER CAMERA TRAPPING SESSION).

Table 1. Full set of logistic regression models with the number of parameters (*K*), Akaike's Information Criterion scores (AIC_{ci}), Delta AIC ($AIC_{c\Delta i}$) = difference in AIC score between top model and each model, AIC weight (AIC_{cWi}) = proportion of the total amount of predictive power provided by each model when assessing the full set of models, and area under the curve (AUC) for the receiver operating characteristic = a measure of predictive accuracy for each model, for Snowshoe Hare (Lepus americanus) pellet study for 2019 and 2020 in the John Prince Research Forest and surrounding area, north-central British Columbia, Canada. CC = canopy cover between 0 – 1 m, 1 – 3 m, 3 – 10 m and over 10 m, DistEdge = distance to edge. * Denotes significant coefficient ($P < 0.05$).

Model		*K*	AIC_{ci}	$AIC_{c\Delta i}$	AIC_{cWi}	AUC
2019 –Within-stand Models (n = 700)						
Site	Slope + DistEdge*	3	810.61	0.00	0.54	0.73
Esc2	Slope + CC0–1 + DistEdge*	4	811.98	1.37	0.27	0.74
Esc1	CC0_1 + DistEdge*	3	812.65	2.04	0.19	0.73
Hyp2	Slope + CC3–10* + CC>10*	4	835.47	24.86	0.00	0.74
Hyp3	Slope + CC0–1 + CC1–3 + CC3–10* + CC>10*	6	839.17	28.56	0.00	0.74
Cover	CC0–1 + CC1–3 + CC3–10* + CC>10*	5	840.41	29.81	0.00	0.73
Hyp1	Slope + CC0–1* + CC1–3	4	910.93	100.32	0.00	0.66
2020 – Within-stand Models (n = 700)						
Site	Slope* + DistEdge*	3	858.10	0.00	0.68	0.69
Esc2	Slope* + CC0–1 + DistEdge*	4	860.11	2.01	0.25	0.69
Esc1	CC0_1 + DistEdge*	3	862.81	4.72	0.06	0.68
Hyp3	Slope* + CC0–1 + CC1–3* + CC3–10* + CC>10*	6	883.22	25.12	0.00	0.70
Hyp2	Slope* + CC3–10* + CC>10*	4	885.20	27.10	0.00	0.69

Cover	CC0–1 + CC1–3* + CC3–10* + CC>10*	5	888.32	30.22	0.00	0.69
Hyp1	Slope* + CC0–1* + CC1–3*	4	913.13	55.03	0.00	0.67
2019 - Landscape Models (n = 1000)						
Hyp3	Slope* + CC0–1 + CC1–3* + CC3–10* + CC>10*	6	983.09	0.00	0.83	0.84
Cover	CC0–1 + CC1–3* + CC3–10* + CC>10*	5	986.38	3.29	0.16	0.84
Hyp2	Slope + CC3–10* + CC>10*	4	992.21	9.12	0.01	0.84
Hyp1	Slope* + CC0–1* + CC1–3*	4	1134.64	151.55	0.00	0.77
Esc1	CC0–1* + DistEdge*	3	1316.11	333.02	0.00	0.58
Esc2	Slope + CC0–1* + DistEdge*	4	1318.06	334.97	0.00	0.58
Site	Slope + DistEdge*	3	1320.84	337.75	0.00	0.56
2020 - Landscape Models (n = 1000)						
Hyp3	Slope* + CC0–1 + CC1–3* + CC3–10* + CC>10*	6	981.17	0.00	0.96	0.81
Cover	CC0–1* + CC1–3* + CC3–10* + CC>10*	5	987.43	6.26	0.04	0.81
Hyp2	Slope* + CC3–10* + CC>10*	4	1004.93	23.76	0.00	0.80
Hyp1	Slope* + CC0–1* + CC1–3*	4	1058.77	77.59	0.00	0.77
Esc1	CC0–1* + DistEdge*	3	1224.64	243.47	0.00	0.58
Esc2	Slope + CC0–1*+ DistEdge*	4	1225.81	244.64	0.00	0.58
Site	Slope + DistEdge*	3	1229.61	248.44	0.00	0.56