Predator-Prey Dynamics in Southern Boreal Forests of Washington State

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Abstract

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Wildlife species, particularly predators with specialized habitat needs and ecological roles, are increasingly vulnerable to range contractions due to human influence, including climate change. This vulnerability to anthropogenic impacts is heightened when behavior-specific habitat requirements are not well understood, hindering informed management decisions. While larger predators often receive more attention and research funding, many smaller mammalian predators (i.e., mesopredators) are also impacted by rapid environmental change. Mesopredator habitat needs remain understudied—most crucially, the habitat required for successful foraging—because observing the foraging behavior of these smaller-sized predators is challenging, particularly in areas and seasons without snow-tracking conditions. Prey-tracking, combined

with advanced forensic techniques such as swabbing for predator saliva on remains, can reveal otherwise undetectable mesopredator kill sites. This approach offers insight into habitat use beyond traditional methods, illuminating where a successful predation event—which depends on a complex sequence of events—occurs on the landscape.

An important mesopredator whose foraging ecology is less understood compared to larger carnivores is the Canada lynx (*Lynx canadensis*). This snow-adapted felid is currently listed as Threatened under the US Endangered Species Act (ESA) within the contiguous United States, where its range has contracted significantly. These remaining southern-range lynx populations face a complex web of threats, including habitat loss, fragmentation, and increased competition with generalist predators. Climate change adds further complexity through altered snowpack conditions—potentially affecting the lynx's competitive edge—and by increasing stand-replacing wildfires, which have jeopardized lynx persistence by eliminating large swaths of remaining usable habitat. Understanding how southern lynx utilize their remaining habitat for successful foraging, especially outside of winter, is crucial for their conservation. However, despite a broad-scale co-occurrence with their preferred prey, the snowshoe hare (*Lepus americanus*), knowledge gaps remain regarding the specific foraging habitat features that support lynx within these areas.

This dissertation explores three dimensions of lynx foraging ecology in the context of a multi-predator southern boreal forest landscape across snow-on and snow-free seasons: where lynx successfully target prey on the landscape, how the habitat at lynx kill sites differentiates them from competing predators, and what factors drive the overall survival of hares—the shared prey species intrinsically linked to lynx persistence. To help address these knowledge gaps, I conducted fieldwork within the Okanogan Lynx Management zone (LMZ) in Washington state, USA, where lynx are listed as state Endangered and identified as a species of greatest conservation need. I trapped, radio-collared, and monitored snowshoe hares, applied forensic techniques to identify predator species at hare kill sites, and measured a variety of habitat data.

In my first dissertation chapter, I establish the need to better understand mesopredator ecology, particularly lynx conservation needs, and highlight the utility of the insights into predators such as lynx that prey-tracking studies such as those in my subsequent chapters can offer. In Chapter 2, I examine lynx foraging behavior by discerning the fine-scale habitat features that predict where lynx successfully capture hares within preferred hare habitat areas. Lynx caught hares primarily in cover, when broadly classified by category type, but I found more evidence for lynx targeting hares where landscape features facilitate capture (accessibility hypothesis) instead of in areas with the maximum-cover features associated with the highest hare abundance, such as regenerating forest or stem density (prey abundance hypothesis). Compared to available nearby habitat, lynx kill sites were most strongly predicted by nearby ambush features behind which a lynx might hide and forest structural complexity, with ambush features consistently being the strongest predictor. Horizontal cover within a height of 0.5-1 m also helped explain where lynx caught hares on the landscape to a lesser extent. These findings underscore the importance of fine-scale, microhabitat features in enabling lynx to forage within areas supporting their main prey, thus promoting a crucial interaction that directly improves lynx fitness.

In Chapter 3, I examine whether lynx differentiate from competing predators in the habitat features at their kill sites. Lynx targeted hares in a narrower range of habitat features compared to generalist predators, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), whose kill sites were more similar to each other and more heterogeneous overall than those of lynx.

Variables that significantly differentiated lynx kill sites from both bobcats and coyotes included forest structural complexity, a high-cover type category, percent horizontal cover within a height of 0.5-1 m, presence of snow, and nearby ambush features. Rather than being distinguished by hunting mode—a hypothesis expecting lynx and bobcats to forage similarly because they are both felids—the three mesopredators aligned with a niche breadth hypothesis (specialists versus generalists). This finding suggests that lynx specialize in where they catch hares compared to these competitors in a southern range population. An important implication of the narrower but overlapping range of habitat features used by lynx is that competition with generalist predators may not be alleviated by niche partitioning. To maintain viable lynx populations in areas with coyotes and bobcats, managers should provide ample hare habitat and promote the habitat features that most strongly differentiate lynx from competitors in where they catch hares.

In Chapter 4, I investigate seasonal, habitat, and demographic patterns of snowshoe hare survival. Seasonal survival baselines revealed the lowest hare survival in spring and summer, suggesting a potential role for generalist predators, which are most active during those seasons. Season-specific Cox proportional hazards models supported this pattern, showing that habitat fragmentation (open matrix habitat) negatively impacted hare survival in summer, especially for female hares. Female hares were particularly vulnerable overall in both summer and autumn, likely due to increased energetic demands for reproduction affecting their movement patterns. This reduced survival of female hares when breeding, particularly at fragmented sites in summer when generalist predator pressure is highest, has important implications for the demographics and management of this prey resource for lynx in the face of climate change.

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CHAPTER 1. General Introduction

1.1 BACKGROUND

Wildlife populations worldwide are increasingly vulnerable to range contractions because of expanding human influence, particularly in the form of habitat loss via direct removal, fragmentation, and altered composition, and impacts of climate change such as increasing frequency and scope of catastrophic wildfires (Venter et al. 2006, Hoffmann et al. 2010, Leadley 2010, Hansen et al. 2013, Segan et al. 2016). Predators are especially vulnerable to anthropogenic impacts because of greater energetic and space requirements (Kleiber 1932, Gittleman and Harvey 1982), with many predators already having reduced geographic distributions compared to their historical ranges (Laliberte and Ripple 2004). Although larger predators often receive the most attention and research funding, many species of smaller mammalian predators (i.e., mesopredators) are also impacted by rapid environmental change (Marneweck et al. 2021), with their roles in ecosystem function remaining understudied (Roemer et al. 2009).

Mitigating the consequences of anthropogenic influence for mesopredators requires an understanding of specific habitat needs, particularly those that will improve fitness and thus long-term persistence of the species. However, forecast models for at-risk species are often unable to address mechanisms for reduced fitness, such as locally occurring interspecific interactions (McMahon et al. 2011, Bellard et al. 2012). Such biotic interactions can shape broader species distributions more than previously realized (Wisz et al. 2013). Successful foraging is a vital biotic interaction for wildlife species because energy intake is the most basic requisite for survival and future reproductive success (Brown et al. 2004). Indeed, successful foraging has a greater influence on survival and fitness than activities such as travelling, unsuccessful foraging attempts, and resting (Stephens and Krebs 1986, Krebs and Davies 2009, Sumpter 2010). For predators, successful foraging entails a multi-stage process in which predator and prey movements result in not only an encounter but also a successful capture (Lima and Dill 1990, Kittle et al. 2022, Suraci et al. 2022). This culmination of a prey capture is crucial for predator fitness (Stephens and Krebs 1986).

Identifying habitat that enables successful foraging behavior is logistically difficult, particularly for smaller and more cryptic predators like many mesopredators. Although the tools available to study elusive predators continue to expand with improvements in tracking methodologies, such as drones, camera traps, lighter GPS collars, and increased noninvasive monitoring using molecular techniques (Waits and Paetkau 2005, Beja-Pereira et al. 2009, Long et al. 2011, Kelly et al. 2012), these methods are usually intended for occupancy modeling and rarely link a specific behavior to a specific location (i.e., fourth-order habitat selection; Johnson 1980). Such models based solely on general habitat-use patterns can miss crucial, finer-scale predictors of a successful prey capture (Trainor et al. 2014). Most of the traditional methods for elucidating predator foraging behavior (e.g., direct observation, GPS cluster analysis for kill sites) are ineffective at revealing where smaller, more cryptic predators are catching prey. For example, GPS collar cluster analyses typically miss small-prey kill sites (Bacon et al. 2011, Cassaigne et al. 2016, Jansen et al. 2019). Intensive snow-tracking surveys can provide detailed behavior-specific habitat-use information (e.g., Maletzke et al. 2008), but these are restricted to certain times of the year and are only possible in regions with adequate tracking conditions (Long et al. 2012). However, an understanding of where smaller predators (mesopredators) of conservation concern are successfully foraging (catching prey) is paramount to understand across all seasons, particularly in the face of climate change with its associated altered ecological interactions and altered snowpack conditions.

As a complement to traditional methods that provide occupancy data, prey-tracking studies can find mesopredators' kill sites that would be otherwise undetectable, thus revealing the fine-scale habitat drivers for foraging success. Although accurately identifying the responsible predator species at kill sites of small prey is challenging in the absence of adequate tracking conditions, advancements in the application of forensics to wildlife ecology have facilitated season-independent predator identification at smaller-prey kill sites using salivary DNA (Mumma et al. 2014, e.g., Wengert et al. 2014, Peelle et al. 2019, Ganz 2022). While this alternative method continues to be underutilized, its broader application could radically improve our understanding of—and ability to manage for—the key habitat drivers that promote foraging success and thus fitness for mesopredators of conservation concern.

An important mesopredator that could benefit from modern forensic techniques is the Canada lynx (*Lynx canadensis*, hereafter referred to as "lynx"). Lynx are among the few extant felids in North America and are unique in being both prey and habitat specialists, with populations only persisting in areas with deep snow in winter. Although historically occurring in at least 24 states (McKelvey 2000) and throughout much of Canada, the range of lynx contracted by 39% across North America in the latter four decades of the 20th century (Laliberte and Ripple 2004), an estimate that does not take into account possible further contraction in the past two decades. Within the contiguous US, lynx today persist only in a few small patches within six geographic areas that currently or recently supported resident lynx distinct population segments (DPS) (U.S. Fish and Wildlife Service [USFWS] 2017) (Fig. 1.1). The core range of the lynx in Canada has also experienced some range contractions (Bayne et al. 2008, Koen et al. 2014; but see Marrotte and Bowman 2021) and is shifting northward due to climate change. Although lynx populations may be recovering in Maine in recent decades (Simons-Legaard et al. 2016), all lynx

DPS populations are considered vulnerable to climate change and other threats and will require continued management of forests for lynx conservation (U.S. Fish and Wildlife Service [USFWS] 2017). Lynx population declines in the US in previous centuries have been largely attributed to fur trapping and loss of habitat due to timber harvest (McKelvey 2000), ultimately leading the U.S. Fish & Wildlife Service to list lynx as Threatened under the Endangered Species Act in 2000 (US Fish and Wildlife Service 2000). Small populations are inherently more vulnerable to extirpation and extinction, and thus, the depleted status of lynx populations in the contiguous US has increased their susceptibility to indirect anthropogenic impacts and stochastic events such as stand-replacing, high-intensity wildfires. At the same time, extreme fire weather (weather conditions enabling extreme fire events) has increased globally (Jain et al. 2022). Climate change further complicates lynx recovery by reducing suitable habitat and increasing overall vulnerability (Carroll 2007, Robbins 2017). Given humanity's long history of fur trapping (Stinson 2001), habitat loss from catastrophic wildfires and timber harvest (Koehler et al. 2008), and the additive impact of northward-shifting boreal forests due to climate change (Leadley 2010), there is need for preemptive measures to manage for suitable lynx habitat in the southern portion of the species' range (Murray et al. 2008).

Broad-scale lynx habitat requirements are better understood than where lynx successfully forage. Across their range, lynx are typically found in areas with deep snow throughout winter (e.g., Peers et al. 2012, King et al. 2020) and that support populations of their preferred prey, snowshoe hares (*Lepus americanus*) (Poole 1994, Ruggiero et al. 1999, Aubry et al. 2000, Mowat et al. 2000, Steury and Murray 2004, Squires and Ruggiero 2007). However, reliable knowledge of where lynx successfully catch hares is primarily limited to snow-on studies (Murray et al. 1994, 1995, O'Donoghue et al. 1997, Fuller et al. 2007, Squires and Ruggiero 2007, Maletzke et al.

2008, Squires et al. 2010, Ivan and Shenk 2016, Peers et al. 2020), and the sparse data on lynx kill site habitat beyond winter conditions are from northern populations and limited by certainty of predator species identification methods (e.g., Feierabend and Kielland 2015). These fine-scale data on where lynx catch their preferred prey are crucial because winter seasons studies already demonstrate that lynx exhibit complex movement patterns based on habitat characteristics (Maletzke et al. 2008), shifting prey availability (Murray et al. 1994) and across seasons (Squires et al. 2010). Indeed, despite a clear specialization on snowshoe hares, lynx do not align their movement patterns as expected based on prey availability alone (Keim et al. 2011, Trainor et al. 2014). Habitat features that enable capture of hares (accessibility hypothesis) may be of greater importance to lynx when foraging than targeting where hares are most abundant (prey abundance hypothesis) (e.g., Fuller et al. 2007). Furthermore, lynx may forage differently from competing predators on the landscape; if true, prioritizing management of habitat features that give lynx a competitive edge across seasons would be crucial in the face of myriad anthropogenic impacts. More broadly, a better understanding of the prey base on which lynx depend—the snowshoe hare—is fundamental for managing for lynx foraging needs, given that hares are intrinsically linked to lynx persistence, and the seasonal survival patterns of hares are particularly understudied in the southern range.

The following chapters of my dissertation help inform these knowledge gaps by exploring multiple dimensions of lynx foraging needs in a southern boreal forest landscape across snow-on and snow-free seasons. I first examined fine-scale habitat features of where lynx engage in their most important fitness-related activity—successful foraging (i.e., killing a hare)—in all seasons and compared to nearby available habitat (Chapter 2). My primary investigation in this chapter aimed to answer the question: do lynx target hares in habitats where they are most abundant, or are other factors, such as those that may facilitate lynx access, more influential in determining successful foraging sites? These findings help clarify whether lynx habitat management should be focused primarily on increasing hare abundance or should consider additional features that facilitate lynx capturing hares. In Chapter 3, I report all predators identified in this study across snow-on and snow-free seasons, further focusing in on the predator species expected to exert high competition with lynx: bobcats (*Lynx rufus*) and coyotes (*Canis latrans*). I tested whether kill site habitat features of these three predators aligned more with expectations based on niche breadth or predator type (hunting mode). Identifying how lynx differentiate from competitors in where they catch prey is crucial for anticipating lynx habitat needs in the face of a likely increasingly necessary coexistence with generalist predators that benefit from habitat fragmentation and reduced snowpack duration. In Chapter 4, I examined survival patterns of the shared prey resource on which lynx depend, the snowshoe hare, including whether overall seasonal hare survival patterns point to increased generalist predator pressure in snow-free seasons. I explored a landscape context for the survival patterns observed by testing an extension of a southern hare refugium model, under which habitat fragmentation (matrix habitat openness) would lower hare survival in seasons with the highest generalist predator presence (summer) because those predators tend to use more edge habitat. I tested these predictions alongside other potentially important drivers of hare survival, including forest stand age, hare sex, and hare body condition. These insights into the drivers of hare survival can help improve management of this prey resource for lynx in the face of climate change. In total, the multiple dimensions of lynx foraging ecology that I assessed in this study aimed to inform lynx conservation needs and more broadly describe predator-prey dynamics in a southern boreal forest ecosystem.

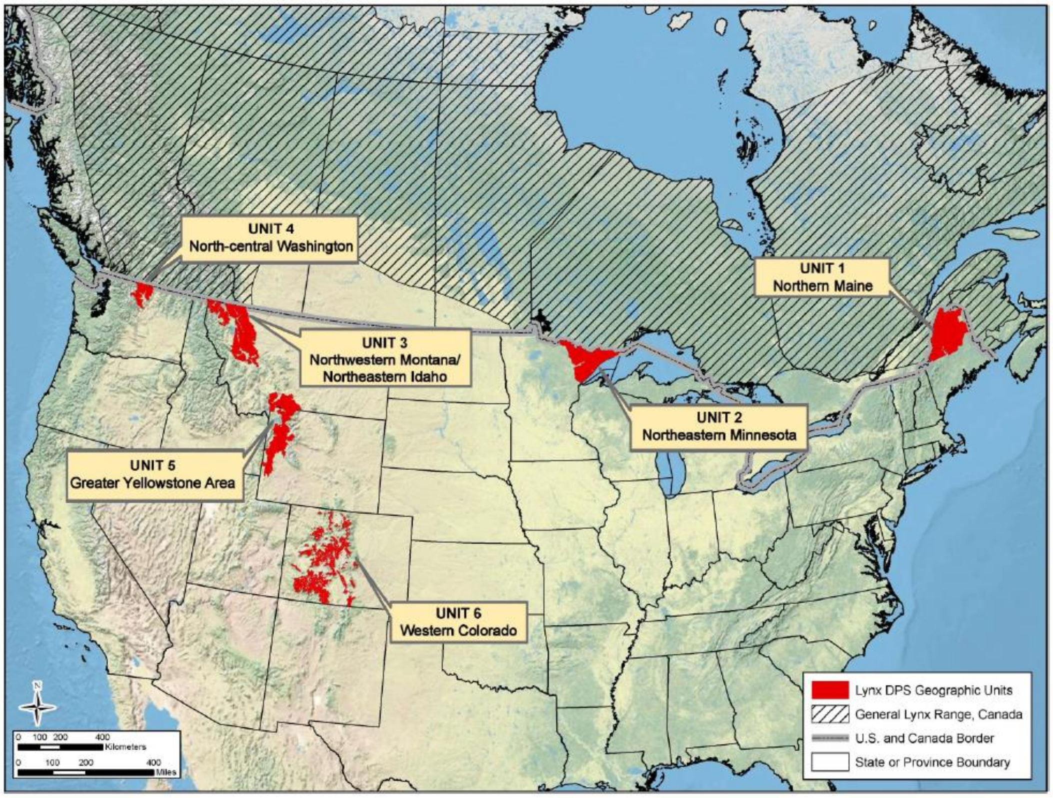

Figure 1.1. Canada lynx distinct population segments in the contiguous United States. Source: (U.S. Fish and Wildlife Service [USFWS] 2017)

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CHAPTER 2. Where the lynx ate the hare: fine-scale drivers of successful foraging habitat for Canada lynx

ABSTRACT

Canada lynx (*Lynx canadensis*) populations are of conservation concern in the southern range (southern Canada and contiguous United States) and are listed as federally threatened due to habitat fragmentation, past hunting, stand-replacing wildfires, and increasing impacts from climate change. Lynx are endangered in Washington state, with one of the only remaining lynx populations in the lower 48 residing within the Okanogan Lynx Management Zone, which has been subject to considerable conservation efforts. A vital aspect of land management for predators is ensuring that fine-scale landscape features which allow a predator to make a successful kill are present. Lynx survival and fitness is heavily dependent on the ability to catch their preferred prey, the snowshoe hare (*Lepus americanus*). However, no studies to date have demonstrated where lynx successfully forage for hares in snow-free seasons, and only a few of the winter studies have examined the fine-scale habitat features characterizing lynx kill sites. Importantly, it is unclear whether successful lynx kills are occurring in areas where hares are most abundant (i.e., dense regenerating stands) or if other habitat features dictate where lynx can access (successfully hunt) hares. To fill this knowledge gap about where lynx successfully forage, and as part of a multi-agency effort to improve forest management recommendations for lynx, I radio-collared and tracked hares to identify lynx kill sites across all four seasons, contrasting habitat data at lynx kill sites and nearby reference plots. Nearby ambush features and greater forest structural complexity were the strongest predictors distinguishing lynx kill sites from the available landscape, rather than the high stem density areas representing the highest hare abundance, which supports the prey accessibility hypothesis for lynx. Additionally, lynx successfully foraged in areas of high overall cover rather than clearings or edge and used relatively higher percentages of horizontal cover at 0.5-1 m height as measured with a

coverboard, but horizontal cover was a weaker predictor than ambush features, forest structural complexity, and cover type category. More lynx kills were found in mature and mixed-age forest than regenerating forest, but this pattern did not differ significantly from available habitat sampled within 100 m. My study supports suggestions that lynx might benefit most from a mosaic of regenerating and mature forest but emphasizes that, unlike in some predator-prey systems, edge habitat and clearings should be minimized when managing for lynx. Creation and retention of ambush features, forest structural complexity, and relatively high horizontal cover in the understory should help promote lynx foraging success within hare habitat.

2.1 INTRODUCTION

As wildlife species worldwide face increasing anthropogenic impacts to habitat, it is crucial to understand the specific habitat needs promoting fitness of animals, especially those of conservation concern. However, not all habitat use is equally beneficial to an animal (Pulliam 1988). Energy intake is the most basic requisite for an animal's survival and future reproductive success (Pyke et al. 1977, Brown et al. 2004), and thus, successful foraging behavior is fundamental for an animal's fitness (Stephens and Krebs 1986, Krebs and Davies 2009, Sumpter 2010). Understanding an animal's habitat requirements warrants knowledge of not only general habitat use but also of where vital resources are accessible to a given species within the available habitat (Matthiopoulos 2003). With this deeper understanding of habitat needs, management actions can be tailored to promote species fitness.

Revealing successful foraging habitat characteristics is particularly important for conservation of predators, which typically have high energetic requirements (Gittleman and Harvey 1982). Indeed, a successful predation event is arguably the most fundamental activity promoting fitness for predators (Stephens and Krebs 1986). Although predators typically follow prey distributions (Carbone and Gittleman 2002, Karanth et al. 2004), the outcome of predator foraging efforts within areas used by both predators and prey relies on a complex sequence of events that may or may not result in successful prey capture (Lima and Dill 1990, Kittle et al. 2022, Suraci et al. 2022). This outcome may be driven more by where prey are easier to capture or "accessible" rather than only where they are most abundant (Hopcraft et al. 2005, Balme et al. 2007, Andruskiw et al. 2008, Borg and Schirokauer 2022), thus requiring knowledge beyond just prey presence to manage appropriately for predator foraging habitat. Yet, this vital interaction is difficult to detect on the landscape, particularly for predators of smaller prey (Bacon et al. 2011, Cassaigne et al. 2016, Jansen et al. 2019). Nonetheless, identifying the key indicators of successful foraging habitat is imperative for predators of conservation concern.

One predator facing an uncertain future across much of its range is the Canada lynx (*Lynx canadensis*), a native North American felid. Although the lynx has historically had a fairly broad latitudinal distribution in North America, its range contracted north significantly in the 20th century (Laliberte and Ripple 2004) primarily because of habitat loss and overharvest for its fur (McKelvey 2000, Stinson 2001, Poole 2003), with further range contractions in recent decades owing to a variety of threats to their habitat (Bayne et al. 2008, Koen et al. 2014). Today, lynx are additionally threatened in the face of climate change and decreasing snowpack (Carroll 2007, Robbins 2017) because they are considered snow specialists. Lynx have specialized morphological adaptations (disproportionately long legs and large paws) that facilitate hunting prey when snow is present (Murray and Boutin 1991), which provides a seasonal competitive edge against co-occurring predators (Buskirk et al. 2000).

Lynx are of particular conservation concern in the southern range of their geographic distribution (Aubry et al. 2000, Steury and Murray 2004, Murray et al. 2008, Koen et al. 2014, Vitense et al. 2016, U.S. Fish and Wildlife Service [USFWS] 2017), especially in the contiguous United States, where they are federally threatened (US Fish and Wildlife Service 2000). Today, lynx persist only in a few limited geographic areas in the contiguous United States (U.S. Fish and Wildlife Service [USFWS] 2017). The Okanogan Lynx Management Zone (LMZ; Fig. 1.1) in Washington state is one of six geographic areas that currently or recently supported resident lynx distinct population segments (DPS) (U.S. Fish and Wildlife Service [USFWS] 2017). Lynx have been listed as Threatened in Washington since 1993 and were upgraded to Endangered in 2016, and their conservation in this state has been the focus of numerous efforts at the federal, state, local non-profit, and tribal levels. Despite these efforts, local lynx populations have not recovered and are at greater stochastic risk in their fragmented remaining habitat after catastrophic wildfires in recent decades significantly reduced available lynx habitat (Lyons et al. 2016). The Washington Department of Fish and Wildlife (WDFW) estimates that roughly 50-100 individuals remain in the state (Lewis 2016). Yet, this location is where lynx are considered to have the best relative chance of long-term persistence under future climate-change scenarios in Washington (King et al. 2020). With lynx populations in the contiguous US facing broad-scale habitat loss due to climate change-induced stand-replacing wildfires compounded with other anthropogenic impacts (Carroll 2007, Gonzalez et al. 2007, Robbins 2017, Vanbianchi et al. 2017*b*), identifying the specific habitat features that promote lynx fitness within their remaining usable habitat is imperative.

Managing the habitat features that enable the persistence of lynx requires knowledge of where they successfully forage. Across its range, lynx fitness is dependent on populations of its preferred prey, the snowshoe hare (*Lepus americanus*) (Saunders 1963, Brand et al. 1976, Parker et al. 1983, O'Donoghue et al. 1997, 1998*a*, Poole 2003, Steury and Murray 2004, Roth et al. 2007, Kosterman et al. 2018, Holbrook et al. 2019), with hares consistently comprising the majority of lynx diet (Roth et al. 2007, Burstahler et al. 2016, Szumski et al. 2023). As such, lynx generally select for areas with high overall hare population densities (Poole 1994, Ruggiero et al. 1999, Aubry et al. 2000, Mowat et al. 2000, Steury and Murray 2004, Squires and Ruggiero 2007). Most studies on lynx, especially those conducted outside of winter, have assessed broader-scale resource selection focusing on their occupancy or general movements on the landscape ("third-order" selection; Johnson 1980) rather than where they capture prey ("fourth-order" selection). While occupancy and habitat-use patterns provide essential and fundamental knowledge, focusing solely on broader-scale habitat use can overlook crucial information about the behavior-specific habitat needs of predators (Bowyer and Kie 2006, Panzacchi et al. 2009), particularly in terms of food procurement. The importance of examining habitat selection at multiple scales has been demonstrated specifically for lynx (Maletzke et al. 2008, Squires et al. 2008, 2010, Farrell et al. 2018, Kosterman et al. 2018).

Evidence is mixed as to whether lynx have greatest foraging success in areas of highest hare abundance (Murray et al. 1994, O'Donoghue et al. 1998*a*, Squires and Ruggiero 2007, Maletzke et al. 2008, Squires et al. 2010) or in areas where hares are more accessible to lynx (Major 1989, Fuller et al. 2007, Ivan and Shenk 2016). This is likely due in part to the use of assumed preferred hare habitat (i.e., high number of trees per hectare, or "stems"). Indeed, some models of lynx resource selection have suggested that lynx target hares directly rather than targeting preferred hare habitat (Keim et al. 2011), suggesting that finer-scale features crucial information is overlooked by using only preferred prey habitat as a proxy for to define the best habitat for predators (Trainor et al. 2014).

Studies of the foraging habitat selection of northern lynx populations cannot necessarily be applied to southern populations, which inhabit more fragmented landscapes with different population dynamics and habitat types (Ruggiero et al. 1999, Buskirk et al. 2000, Koehler et al. 2008, Murray et al. 2008, Vanbianchi et al. 2018). Northern populations of lynx change their hunting strategy and thus their fine-scale, resource-specific (i.e., “fourth-order”; Johnson 1980) habitat selection during different phases of the lynx-hare cycle (Brand et al. 1976, O’Donoghue et al. 1997, 1998*a*), such that lynx increasingly use ambush hunting behavior when hare numbers are low, potentially to conserve energy (Thompson 1977, Menzies et al. 2022). Because preferred hare habitat can also shift depending on the phase of the lynx-hare cycle (Wolff 1980, Mowat et al. 2000), lynx fourth-order habitat selection might shift without any change in whether it is driven by prey availability or accessibility. Lynx populations in the southern range are relatively static and acyclic in comparison, yet these populations still show differences in fourth-order habitat selection for prey abundance or accessibility depending on the management unit, with studies in Maine and Colorado finding evidence for selection based on prey accessibility (Fuller et al. 2007, Ivan and Shenk 2016) and studies in Washington and Montana finding more evidence for selection based on prey abundance (Squires and Ruggiero 2007, Maletzke et al. 2008, Squires et al. 2010). Furthermore, fine-scale habitat features such as horizontal cover, stem density, forest age, or structural complexity may have different outcomes for lynx foraging in different geographical areas of the southern range. Understory vegetation species composition in one area or forest type may present a barrier to lynx in catching hares; conversely, a different forest composition in another area or forest type may provide cover without too much physical obstruction for successful predation. This may also hold true for preferred hare habitat. For example, Siren (2020) found that hares in the northeastern United States have a negative association with high biomass forests (a proxy for age), whereas this association was not significant for lynx. However, forests in the northeastern US are largely deciduous with less understory. By contrast, mature conifer-dominated forests of the western US the Pacific Northwest can provide understory cover for hares through structural complexity in the form of low-hanging boughs and small gaps that encourage dense undergrowth (Koehler et al. 2008, Maletzke et al. 2008, Lewis et al. 2011, Lewis 2016). Thus, recommendations for managing fine-scale habitat features for lynx populations may vary regionally because of differing forest composition, but there has often been a consistent theme of the importance of forest structure in the lynx-hare literature.

Lynx third-order habitat usage may also shift by season (e.g., Squires et al. 2010), but understanding of lynx foraging ecology is limited in snow-free seasons (Buskirk et al. 2000), and few to no studies have addressed lynx fourth-order habitat selection in summer. In one of the few studies on seasonal habitat use for a southern lynx population that also included where lynx successfully forage in winter, Squires et al. (2010) examined third- and fourth-order habitat use in winter and third-order habitat use in summer, finding that lynx in Montana selected for mature spruce and fir stands in winter for both successful foraging (fourth-order habitat use) and travel. That same study found that, in summer, lynx utilized comparatively younger (regenerating) forests for third-order habitat use, which may have reflected changes in seasonal hare abundance in that area (Squires et al. 2010). High understory cover was the most important factor for lynx habitat use for both winter foraging and travel and summer travel, but higher understory cover in the context of mature versus regenerating forests suggested that a mosaic of different cover and structure types was needed to maintain lynx populations in that area (Squires et al. 2010). However, this and other studies that have examined direct evidence for habitat that enables lynx foraging success (kill sites) have been limited to winter (e.g., Murray et al. 1994, 1995, O'Donoghue et al. 1998*a*, Fuller et al. 2007, Squires and Ruggiero 2007, Maletzke et al. 2008, Squires et al. 2010, Ivan and Shenk 2016) because the locations where hares are successfully captured and consumed by lynx are difficult to determine outside of adequate snow-tracking conditions.

Some predictions about year-round lynx foraging habitat may be informed by broader-level (third order) patterns of resource use. For example, Squires et al. (2022) found lynx distributions in Colorado to be driven more by determinants of hare abundance (high stem-density regenerating forest) than forest structure or composition (Squires et al. 2022), whereas the previously mentioned studies in Montana had found horizontal cover to be the most important determinant of lynx habitat use across all seasons (Squires et al. 2010). Although it is reasonable to speculate that lynx kill sites in these two areas were located within the habitat where lynx traveled, such generalizations miss fine-scale landscape features that differentiate a lynx kill site from general lynx habitat and therefore cannot be used to make detailed recommendations to forest managers for increasing lynx foraging success. This type of fine-scale habitat data for lynx is logistically difficult to obtain on the ground but less accurate when obtained by more efficient means such as airborne LiDAR (Fekety et al. 2019). With studies across the range of lynx specifically calling for more information about lynx kill site habitat (e.g., Morin et al. 2020), there is a clear need for further study.

To determine where lynx successfully catch hares on the landscape, I contrasted habitat data at lynx kill sites (a hare mortality attributable to lynx) and available habitat reference areas to test two hypotheses. First, the ‘prey abundance hypothesis’, under which lynx can successfully hunt snowshoe hares in even the highest density forest that hares prefer, predicts that variables such as regenerating forest, high stem density, and high horizontal cover should best explain the site of a successful lynx foraging event because this habitat supports the most hares (Koehler 1990, Walker 2005, Jensen 2020). Alternatively, under the ‘accessibility hypothesis’, a lynx kill site would be predicted by dense-cover features such as low-lying ambush features or forest structural complexity, which allow the predator’s close approach to prey without detection, without physically blocking access to make short chases or leaping to catch the prey. Because lynx are primarily visual hunters (Parker et al. 1983, Murray et al. 1995, O’Donoghue et al. 1998*a*) that limit physical activity when possible (Menzies et al. 2022), these cover features would better enable a lynx to capture a hare than the highest stem-density habitat that might impede physical access to hares (Fuller et al. 2007, Ivan and Shenk 2016).

2.2 METHODS

2.2.1 Study area

I conducted this study in the northeastern Cascades Mountains of Washington state, USA (48˚53’35”N, 119˚49’20”W), approximately 14 miles from the town of Loomis, WA in the Loomis State Forest and Okanogan National Forest (Fig. 2.1). My study area was located in the northern part of the Okanogan Lynx Management Zone (LMZ; Fig. 1.1). This region also hosts a suite of other predators of hares, including bobcats (*Lynx rufus*), coyotes (*Canis latrans*), great-horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*), Pacific martens (*Martes caurina*), and cougars (*Puma concolor*). Elevation ranged from 1,383–1,932 m, and land cover was characterized by mixed southern boreal forest dominated by lodgepole pine (*Pinus* *contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), with occasional Douglas-fir (*Pseudotsuga menziesii*), Sitka alder (*Alnus sinuata*), and western larch (*Larix occidentalis*), along with some meadows and harvested areas, and traversed by logging roads and natural creeks. Within the study area, I live-trapped and tracked hares with radio-telemetry to identify the locations of hare mortalities. I then collected habitat data at hare mortality sites and reference plots to characterize fourth-order resource-selection (locations of successful resource procurement relative to available locations; Johnson 1980). This comparison enabled the identification of habitat drivers for successful lynx foraging within hare-occupied forests.

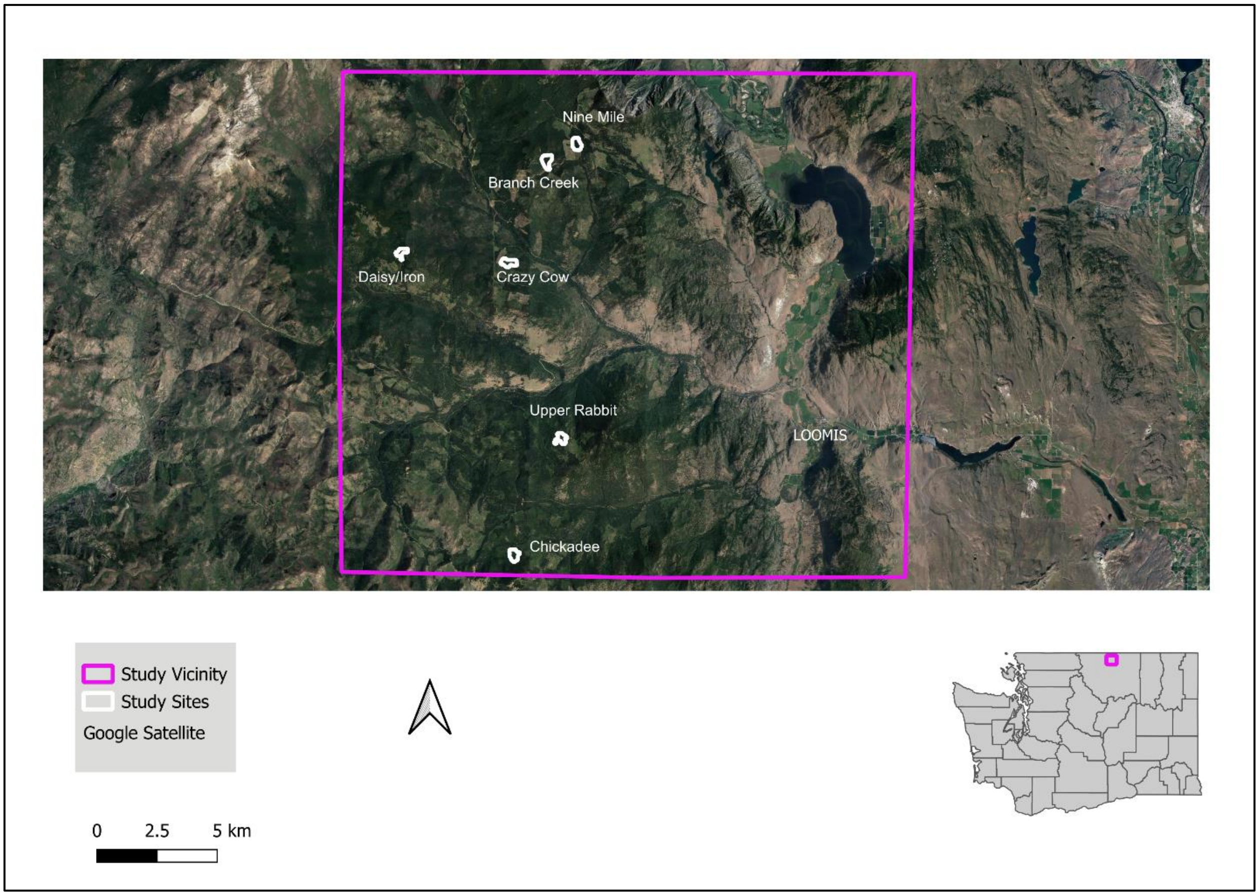

Figure 2.1. Study vicinity in north-central Washington (pink polygon) near the town of Loomis showing the six study sites (white polygons) at which snowshoe hares were trapped and monitored with radiotelemetry from 2010-2013, and where habitat data were collected at hare mortality sites and reference plots from 2011-2015. The study sites were within the northern part of the Okanogan Lynx Management Zone (LMZ) and primarily encompassed by the Loomis State Forest (Nine Mile, Branch Creek, Crazy Cow, Upper Rabbit, and Chickadee sites), with the westernmost site (Daisy Creek/Irongate site) in the adjacent Okanogan National Forest.

2.2.2 Snowshoe hare trapping, collaring, and mortality monitoring

I trapped and monitored hares for mortality events from 2010-2013 at six densely forested sites ("stands") ranging in size from 17-20 ha. All sites were separated by at least 1 km to avoid dispersal from one stand to another (Wirsing et al. 2002*b*). I selected these sites based on minimum area of relatively contiguous habitat and signs of snowshoe hare use such as pellets, hare runways, and browsing evidence, after consideration of many sites, based on a combination of ground-based surveys, aerial mapping, input from local expert state and federal biologists, and definitions for the general thresholds for lynx habitat from prior studies in the region (Koehler and Brittell 1990). Three of the selected sites were regenerating forest stands (estimated 20-40 years) and three were mature (estimated >75 years) boreal forest stands.

I captured hares using Tomahawk live traps (32" × 9" × 9" double-door, Tomahawk Live Trap Co., Tomahawk, WI, USA) baited with alfalfa pellets and covered with tree branches for camouflage and insulation. Stands were trapped on rotation, one at a time, typically at least twice in summer and at least once in winter. Trapping grids consisted of 40–50 traps spaced approximately 50 m apart from each other (Wirsing et al. 2002*b*, Griffin and Mills 2007, 2009, Hodges et al. 2009) and roads (Griffin and Mills 2009, Hodges et al. 2009) and were set in the late afternoon or evening and checked in the morning. Hares were weighed, sexed, identified as adult, subadult, or juvenile, sampled with a 2-mm ear punch to collect a tissue specimen, ear-tagged through the sampling hole and in the other ear (No. 3, National Band and Tag Co., Newport, KT, USA), and measured for right hind foot length (a metric for structural size). I equipped hares weighing at least 550 g with mortality-sensitive VHF radio-collars (Model M1565, 24 g, Advanced Telemetry Systems [ATS], Isanti, MN, USA), keeping collar weight to <5% of total body mass (Cochran 1980). As time allowed, I also trapped partial grids if the number of functional radio-collars at a given stand became appreciably disproportionate compared to other stands. Snowshoe hare capture and handling procedures were approved by the University of Washington Institutional Animal Care and Use Committee (IACUC) under protocol 4226-02 and consistent with standards for capture and handling of mammals (Sikes et al. 2011).

To monitor hares for mortality events and identify hare predators, including lynx, I attempted to detect frequencies from every deployed radio-collar at least 3 times per week, except in spring when snow melt conditions prevented site access. A mortality event was identified when a collar emitted a double pulse (70 beats per minute) signal, which was activated after 8 hours of no movement. Upon detecting a new mortality, I used ground-based radiotelemetry to locate the mortality site the same day of detection or within 24 hours when it was logistically feasible.

2.2.3 Predator species identification

To investigate where lynx caught hares on the landscape in snow-on and snow-free periods, I first determined the specific location and suspected proximate cause of hare mortality using a combination of visible evidence in the field: radio-collar location, signs of a struggle (e.g., a light layer of fur), tracks, a fur trail, amount of carcass or fur remaining (carcass-handling patterns; e.g., Boutin et al. 1986), sub-dermal hemorrhaging, and predator hairs or scat if recently deposited. I limited the predator species identifications used in this study to methods less likely to misclassify a predator (primarily predator saliva, snow tracks where applicable, and occasionally predator hairs if comingled with hare fur), combined with consideration of when the mortality was documented to have occurred. I used microscopy imaging to visually confirm and key out predator identity from hairs, as well as occasional genetic analysis of hairs (Pilgrim et al. 2005). I also sampled for predator saliva from the remains and radio-collars for subsequent mtDNA testing. Predator saliva swabbing and lab analysis for this technique were as described in Peelle et al. (2019), building upon saliva swabbing methods for predation on larger prey like domestic sheep (Williams et al. 2003) and fishers (*Pekania pennanti*) (Wengert et al. 2013) and informed by human forensics for collection of trace genetic material (e.g., Sweet et al. 1997, Ng et al. 2004, Goray et al. 2010). Multiple reliable methods of predator species identification were employed whenever possible.

2.2.4 Habitat data collection and generation

To characterize habitat data that could address hypotheses for whether lynx catch hares where they are more abundant or accessible, and to assess a range of possible predictors for lynx kills with the limited data available, I collected habitat plot data from 2011-2015 at hare mortality sites attributable to any predator and at two points 100 m away in stratified random directions to characterize nearby available habitat (“reference plots”). A number of hare mortalities were deemed to have insufficient evidence of the proximate cause of mortality to warrant further processing or habitat data collection. Outside of instances of adequate snow-on tracking conditions, I limited predator identifications to kills with reliable evidence of the responsible predator (i.e., saliva or hair samples), if also supported by field-based evidence. Because genetic samples were collected and stored for processing at a later date, the responsible predator species was often uncertain at the time of habitat data collection. Thus, the habitat data collection methods I employed were intended to describe and differentiate lynx kill site habitat from both randomly selected reference plots and kill sites ultimately attributed to competing predator species. Plots for which data had been collected in the field but were later determined could not be confidently attributed to predation were excluded from further analysis.

To reduce spatial autocorrelation of the randomly selected points for the reference plots, I employed stratified random sampling. The 360 degrees of a compass were divided into 3 groups of 120 degrees and selected using a random number generator, at which point the number for the degree direction within the selected group was again randomly selected. Two reference plots associated with the same kill site could not fall within the same group of 120 degrees, and the numbers were regenerated if the second plot fell within 90 degrees of the first plot. If a randomly selected plot location was within 30 m of the centerpoint of an existing reference plot for another potential kill site that had already been measured (such that the area of vicinity-plot measures were expected to overlap with each other for the two reference plots), then a new random number was used instead to determine the location of the second plot. In one case, spatially overlapping plots were visually verified as containing the same composition and structure, and the first plot data was re-used instead of collecting a new reference plot. Habitat plots could rarely be sampled within the same day that a kill site was processed. However, I sampled habitat plots within the same seasonal period in which the mortality occurred whenever possible. Spring plots could not be sampled until summer due to snow melt access issues. These plots had minimal deciduous vegetation, but some impacts to measurements of horizontal cover could have occurred.

Habitat variables measured at hare mortality sites and reference points included data measured in a fixed-radius plot (within a 5.64 m fixed-radius plot as measured with rope from plot centroid; 0.1 ha) and visually estimated variables in the plot vicinity (~15 m radius from plot centroid) (Table 2.1). In addition to the standard fixed-radius 0.1 ha plot for more precise measurements, the plot vicinity measures were chosen because a chase may require several bounds, with lynx having more success within <15 m (Murray et al. 1995), and 15 m is a standard distance for horizontal coverboard measurements (Nudds 1977). The 0.1 ha fixed-radius plot habitat variables included count of trees >7.5 cm and ≤7.5 cm DBH (diameter at breast height) in total and by species, basal area, cover type, % downed woody debris, % canopy cover, and the presence and quality of ambush features within the fixed radius plot (Table 2.1). Plot vicinity variables included cover-board cover at four, vertical 0.5-meter intervals (starting from the ground and ending at a height of 2 meters), distance to continuous cover, distance to a clearing, forest age category, structural complexity category (0-9), forest composition, and the presence and quality of ambush features beyond the fixed radius plot (Table 2.1). Habitat variables with infrequent occurrence in the dataset (<25% observations) were dropped from further consideration. Additional habitat measurement details are in Supplemental S1. Predictions generated from competing prey abundance and accessibility hypotheses are summarized in Table 2.2.

Table 2.1. Description of variables measured for habitat plots (fixed-radius plots and broader vicinity plots) at lynx kill site locations and replicate plots. See Supplemental S1 for additional habitat sampling details.

Variable Scale	**Variable**	**Description**
Fixed-radius plot (5.64 m radius; 0.01 ha)	Larger tree count	of trees >7.5 cm DBH, total and by species: lodgepole pine (*Pinus contorta*), Englemann spruce (*Picea sitchensis*), subalpine fir (*Abies lasiocarpa*), and snags
	Basal Area	Basal area of trees >7.5 cm DBH
	Smaller tree count	# Stems (trees ≤7.5 cm DBH), total and by species: lodgepole pine, Englemann spruce, subalpine fir, sitka alder (*Alnus viridis*), Douglas-fir (*Pseudotsuga menziesii*), snags, and "other" (often *Salix* or *Populus* spp.)
	Cover Type	A general categorization of how open the habitat was within the plot, visually approximated in the field and finalized with aerial mapping measurements. Listed from most to least open: 1) Clearing (majority open and centered within a clearing, with a clearing defined as being both >25 m^2 total area and >4 meters minimum width) 2) Edge (edge of clearing >25 m^2 and >4 meters across) 3) Semi-Open (smaller openings [≤25 m^2] dominating ~>50% of plot) 4) Cover (cover dominant with few small openings)
	DWD	% downed woody debris (DWD) >7.5 cm diameter, visually estimated by stratifying the plot into 4 quarters
	Canopy	% canopy cover using a convex densiometer (averaged from 4 cardinal directions)

	Ambush Near	Presence and quality of ambush feature(s) within the plot, rated from 0-6; see text for details
Plot vicinity measures (~15 m radius)	Horizontal Cover (4 variables)	CoverBoard Cover: Horizontal cover (% visual obstruction) measured using a checkered canvas coverboard in 4 cardinal directions (15-m radius) from center of plot, averaged for each 0.5-m increment of height from the ground, up to 2 m
	Distance to Cover	Distance from plot centroid to continuous cover (m); aerial mapping was used if cover was >15 m away
	Distance to Clearing	Distance to a clearing (defined as >25 m^2 total area and >4 meters minimum width) (m); aerial mapping was used to verify these measures
	Age	Forest age category (regenerating, mature, or mixed)
	Structure	Structural complexity represented by the presence and sparsity of combined overstory, mid-canopy, and understory forest layers, rated from 0-3, respectively (0=absent, 3=layer fully present) for a total max score of 9
	Forest Composition	Dominant tree species in the overstory, mid-canopy, and understory forest layers, respectively, recorded in the field and later assigned to a tree community category based on association using hierarchical cluster analysis; see statistical methods for details
	Ambush Far	Presence and quality of ambush feature(s) beyond the fixed-radius plot, rated from 0-6; see methods for details

Table 2.2. Predictions about habitat variables supporting either hare abundance or accessibility hypotheses for where lynx successfully capture hares.

Covariate	Evidence for Hare Abundance	Evidence for Hare Accessibility	Mechanisms for Covariate Classifications
Regenerating Forest	+	~	Regenerating forests have the densest vegetation cover because trees that are still in the photosynthetic competition phase have not yet thinned out, thus providing maximum cover for prey through high stem density (i.e., densely packed tree trunks).
Stem Density	+	~	
Horizontal Cover	+	~	
Ambush Features	~	+	Microhabitat landscape features like logs or boulders that are low to the ground can allow predators to approach prey at close range without detection and with less hindrance for the attack than high stem density.
Structure	–	+	Forests with more structural complexity (more layers present) have often advanced beyond the main photosynthetic competition phase, with new growth in openings and the low-hanging branches of mature spruce providing moderately dense cover without the physical hindrance of even-aged regenerating stands with the highest stem density.

+ predicted to be very high

~ predicted to be moderately high

– predicted to be low

Descriptions for habitat variables requiring more detailed descriptions than in Table 2.1 are as follows.

Cover type category

In addition to comparatively more precise metrics for cover, I also categorized each plot by a coarser measure, “cover type.” The cover type variable fell beyond the purview of hypotheses about hare abundance or accessibility because both lynx and hares are associated with high-cover areas, and predictions about whether lynx select for hare abundance or accessibility are intended to discern drivers within relatively high-cover areas used by both species. Nonetheless, lynx may use a range of habitats, such as in fragmented landscapes (Vanbianchi et al. 2017*a*), and specific foraging habits of lynx across broad habitat types required clarification, particularly if comparing with other studies that have used coarse measures for cover (e.g., Murray et al. 1995, O’Donoghue et al. 1998*a*). Thus, I categorized the amount of openness within the fixed-radius plots using visual estimation during field collection and finalized with aerial mapping measurements and plot photographs. I assigned each plot to 1 of 4 “cover type” categories ranked from most open to least open (clearing, edge, semi-open, or cover. The size threshold for a “clearing” designation was >25 m^2 in size and >4 m across. Roads thus also counted as clearings. “Edge” was a plot at the edge of a clearing. Plots containing smaller openings ≤25 m^2 but with less than around 50% overall cover were “semi-open,” and plots with majority cover were designated as “cover.”

Ambush feature variable

In addition to collecting more standard vegetation and habitat variables, I also documented potential ambush features that could facilitate a successful predation event. Prior studies have shown that lynx employ ambushing behavior when hunting hares (e.g., Murray et al. 1995, O'Donoghue et al. 1998*a*), but these studies were limited to the wintertime when snow allowed for direct observation of the imprint of a lynx hunting bed. By contrast, my study aimed to directly account for localized features that could hide a mesopredator and could be surveyed in all seasons. An explicit metric for ambush features is not standard for studies on Canada lynx, but a similar scale was used in a study on Eurasian lynx (*Lynx lynx*) (Podgórski et al. 2008), albeit with different terminology and for ungulate prey instead of snowshoe hares. See Supplemental S2 for further information.

I evaluated presence and quality of potential ambush features on the landscape (hereafter "ambush features") at two distances: near (within 0.1 ha fixed-radius plot; ≤6 m from plot centroid) and far (beyond fixed-radius plot limits; > 6 m but up to ~15 m) (approximate distance within which lynx are more likely successfully make a kill; Murray et al. 1995, O'Donoghue et al. 1998*a*). I defined ambush features as those that could at least partly conceal a medium-sized terrestrial predator and allow the predator to leap over the feature providing the concealment; that is, provide visual obstruction without hindering access to the prey. Ambush features typically consisted of large, downed logs or boulders, sometimes piles of smaller logs, low-hanging branches of larger trees, and occasionally low, dense shrubs (Fig. 2.2). Vertical tree trunks were not considered in this metric because stem density was already being measured, and cover from continuous, densely packed tree trunks would not facilitate predator access. If no ambush features were located within the specified distances, I assigned a quality value of 0. If an ambush feature was present, I assessed the quality of the feature from 1-6, depending on several characteristics: (1) the degree to which the ambush feature would obscure the predator from prospective prey, (2) distance, (3) slope, and (4) line of sight. For example, an ideal ambush feature would be located on a relatively even slope or upslope of the kill site epicenter (as might be expected of lynx, which are more sedentary than similar-sized predators; Menzies et al. 2022), with enough line of sight through tree trunks to not hinder an ambush and with the feature being low enough to leap over.

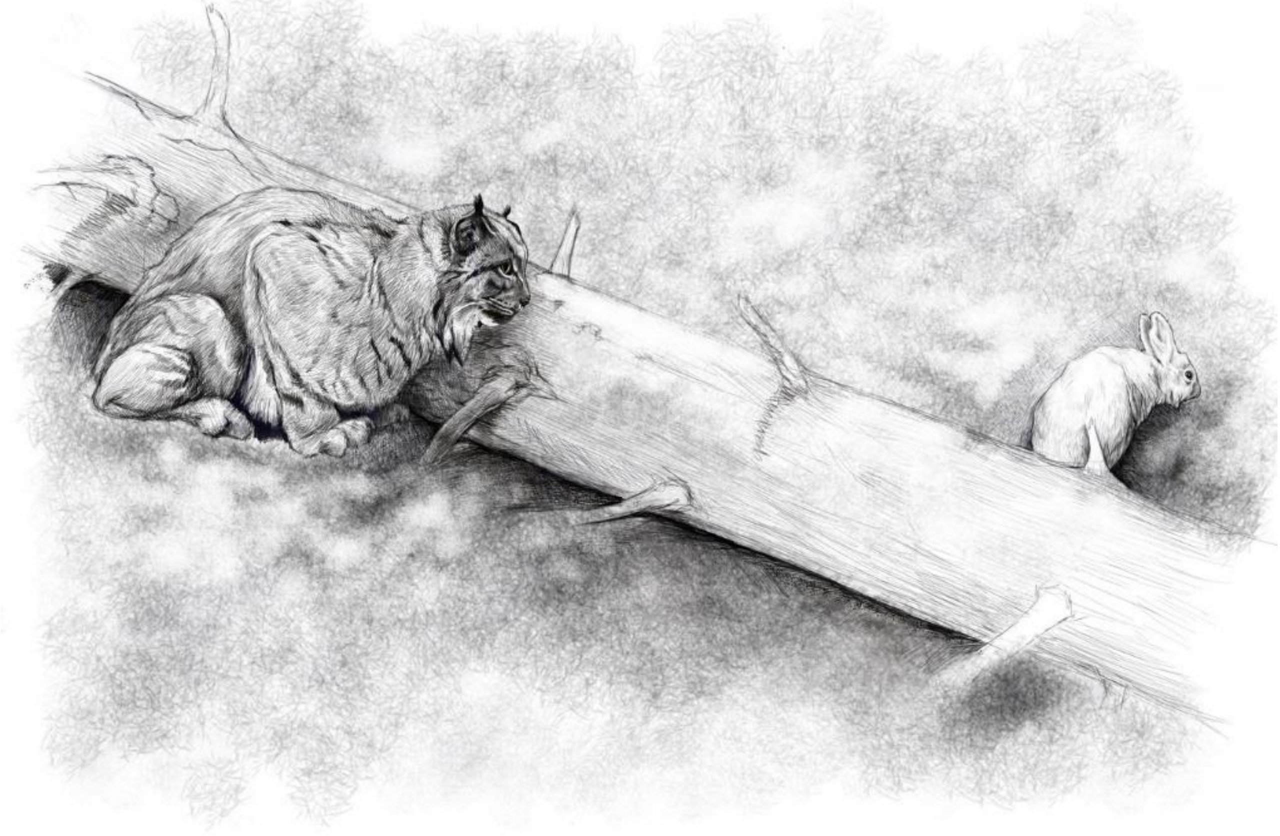

Figure 2.2. Illustration of an example ambush feature on the landscape as characterized in this study. Microhabitat features offering that would obscure high visual obstruction for a medium-sized predator while being relatively low to the ground received a maximum quality rating at hare mortality sites because of providing both cover and access to prey. Winter version of illustration. Credit: Jack DeLap.

Generation of a forest composition variable (tree species dominance by forest structure layer)

Forest type (composition), rather than absolute cover, may better predict where lynx kill hares across seasons (e.g., Feierabend and Kielland 2015). Because broader-scale vegetation composition classifications were unlikely to differentiate between the spatially correlated kill sites and replicate plot habitats, I utilized field-based data on dominant woody vegetation in the plot vicinity to develop a custom forest composition variable. To create this single forest composition variable for inclusion in the main analyses, I performed cluster analyses on a suite of variables representing the dominant woody vegetation type (hereafter "trees") in each forest canopy level (understory, intermediate, and overstory); e.g., subalpine fir in the overstory. I grouped these variables by frequency of co-occurrence into categories using agglomerative hierarchical clustering. To determine which metric should be used to calculate dissimilarity between the tree composition clusters, I evaluated the agglomerative coefficient values of different metrics. I created a dissimilarity matrix using the "vegdist" function in R package *vegan* and the Bray-Curtis metric, which is commonly used in community ecology (M. J. Anderson 2001), to compare species dissimilarities across plots. I then used a flexible beta linkage for the clustering because the tree dominance data had high beta diversity (function "beta.multi" in R package *betapart*). To help determine the appropriate number of clusters, I analyzed dendrograms, elbow plots ("fviz_nbclust" in R package *factoextra*), and cluster visualization on non-metric multidimensional scaling (NMDS) ordination plots ("ordihull" and "metaMDS" in R package *vegan*). Cluster membership information was summarized in a single categorical variable, which I included as three binary predictors for modeling alongside the other variables in the main analysis. The resulting group membership based on this clustering is shown in Fig. 2.3.

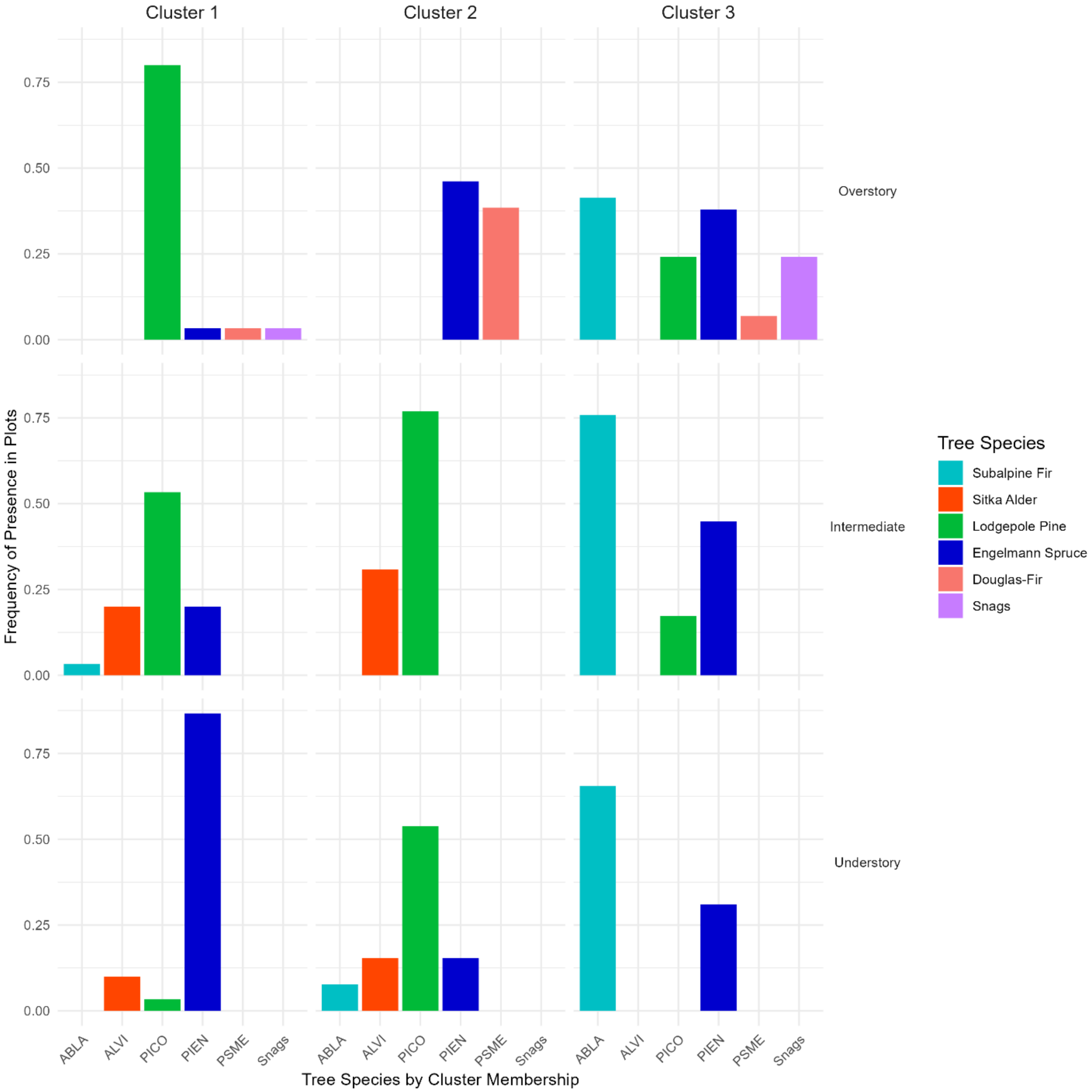

Figure 2.3. Summary figure for the forest composition variable, which I generated from a cluster analysis of dominant trees by structural layer and combined into a single variable for inclusion in the main analysis of this study on lynx kill site habitat. This variable characterized the composition of woody vegetation (tree or woody shrub species, or in some cases snags; hereafter "trees" for simplicity) by dominance (>~50% composition) in each structural level (understory, intermediate, and overstory) across all habitat plots used in this study before inclusion in the analysis of lynx kill sites. I generated this variable by combining presence/absence records of

tree dominance at each forest layer, as measured on the ground during habitat plots in the plot vicinity with ocular estimation. Dominant trees were only recorded if their associated structural levels were not rated as absent (0) or very sparse (1). Two categories could receive a "presence" rating for dominance if they were relatively co-dominant. Vegetation included in this measurement was typically within 15 m distance from the plot center. The understory structural layer in this measure was approximately 1-2 m height. In habitat plots that had all three structural layers present and separated by at least one order of magnitude height per visual estimation, the mid-story was defined by relative height compared to under- and overstory. This combined forest composition variable was generated because broader-scale classifications were unlikely to represent fourth-order habitat use, as measured in my study at kill sites from the perspective of both predator and prey at this finer scale, and which would otherwise have limited the reporting of forest composition details for cross-study comparison. Tree species codes are as follows: subalpine fir (Abies lasiocarpa): ABLA; sitka alder (Alnus viridus: ALVI; lodgepole pine (Pinus contorta): PICO; Englemann spruce (Picea sitchensis): PIEN; Douglas-fir (Pseudotsuga menziesii): PSME.

2.2.5 Modeling of lynx kill site characteristics

To evaluate foraging habitat variables of importance to lynx, particularly those variables indicating whether lynx target areas based on hare abundance or accessibility, I applied regularization techniques that would address high dimensionality and correlation among variables, ultimately identifying those variables that best predicted a lynx kill site on the landscape. Data analyses and visualizations for this main analysis were conducted in RStudio with the following packages: *caret*, *glmnet*, *tidyverse*, *boot*, *and ggplot2*.

To evaluate support for the hare abundance versus accessibility hypotheses, and to generally explore any habitat features that discriminated where lynx caught hares from random points on the landscape across all seasons, I used elastic net logistic regression to identify important features (hereafter referred to as variables or predictors) of a lynx kill site. There is scant direct empirical evidence to guide variable selection for studies of lynx foraging habitat, particularly beyond winter, and elastic net regression is able to handle this complexity (Hastie et al. 2015). In essence, elastic net regression performs variable selection by retaining only the most explanatory variables—akin to keeping only the 'big fish' in the net, thus simplifying an understanding of the dataset. It excels in handling a large number of potential predictors, including correlated ones, by applying penalties to coefficients during the variable selection process. Regularization methods like elastic net aim to enhance the predictive accuracy of models by balancing variance and bias in parameter estimates (Hastie et al. 2009, Friedman et al. 2010). Elastic net can reduce the risks of overfitting and may be more accurate for prediction than other methods such as AIC (Hastie et al. 2009), decision trees (Ashfaq et al. 2001) or generalized linear models (GLMs), classification and regression trees (CARTs), and Random Forest (Lu and Petkova 2014). Elastic net regression combines two regularization (penalizing) methods, ridge regression (Hoerl and Kennard 1970) and LASSO (Least Absolute Shrinkage and Selection Operator) regression (Tibshirani 1996). Both penalties essentially shrink coefficients: the ridge regression penalty reduces the variance inflation associated with multicollinearity but does not reduce model complexity by directly eliminating any variables, whereas LASSO is known for its ability to perform variable selection by shrinking coefficients for weaker predictors to zero, effectively eliminating them from the model. Whereas elastic net and LASSO can both perform well for this variable selection in the face of high dimensionality (i.e., many potential predictors), the combined LASSO and ridge regression penalty used in elastic net is typically superior for handling correlated true variables because a LASSO penalty alone might arbitrarily select only one from a correlated group of variables (Zou and Hastie 2005). The elastic net mathematically balances retention of important predictors while penalizing less relevant ones, as shown in the following formula, where the elastic net logistic regression uses the negative binomial log-likelihood and takes the following form:

$$\min_{\beta_0,\beta)\in\mathbb{R}^{p+1}} -\left[\frac{1}{N}\sum_{i=1}^{N} y_i \,.\, (\beta_0 + x_i^T\beta) - \log\left(1 + e^{(\beta_0 + x_i^T\beta)}\right)\right] + \lambda[(1-\alpha)\parallel \beta \parallel_2^2/2 + \alpha \parallel \beta \parallel_1]$$

in which key components of interest here are the higher level or “hyperparameters” that are adjusted during elastic net implementation: alpha (α), a user-specified hyperparameter bounded between 0 and 1 that determines the relative “mix” of penalty type applied, with $\alpha = 0$ being a full ridge regression and $\alpha = 1$ being a full LASSO regression and $\alpha = 0.5$ being an even mix of the two (Zou and Hastie 2005); and lambda (λ), the hyperparameter controlling overall penalty strength after specifying the mixing parameter (α) level. The elastic net is fit across a grid of λ values using cross-validation, iteratively shrinking standardized coefficients of relatively less-important variables with increasing penalty and then reporting both the λ that minimizes deviance ($\lambda_{\mathbf{min}}$) and a higher-penalty $\lambda_{\mathbf{1se}}$ value that prioritizes a comparatively sparser (more parsimonious) model; essentially, that which retains only the relatively strongest predictors within the proverbial "net." Because the regularization performed by elastic net sets the coefficients of weaker predictors to zero and shrinks the coefficients of the remaining predictors to minimize deviance, the standardized coefficients of the variables selected in the final model reflect their relative strength in explaining the response variable.

To implement elastic net modeling and identify habitat variables that were predictive of a lynx kill site, I first selected an appropriate mixing hyperparameter (α) and then performed the elastic net modeling in R package *glmnet*, which uses cross-validation to identify the optimal regularization penalty strength (λ) that essentially "retains" only the relatively stronger predictors (Hastie et al. 2021). To identify the appropriate values for both of these cross-validation steps, I had to consider my small sample size limitations and the rarity of existing data on where lynx successfully forage outside of winter. Thus, I used leave-one-out cross-validation (LOOCV) (Stone 1977), a special case of cross-validation that utilizes the whole dataset and is more appropriate for small sample sizes (Stone 1977, Wong 2015), to select both the mixing and penalty strength parameters needed for elastic net. To select the α value, I tested a range of λ and α values on the data in R package *caret* with functions "trainControl" and "train," limiting the available α range tested (0.3-1) to ensure that enough LASSO penalty was included to begin to eliminate redundant or unimportant variables; selecting a LASSO-leaning mixing parameter helps ensure sparsity in the face of numerous correlated predictors (Tay et al. 2023). Then, to determine the appropriate penalty strength and identify the strongest predictors of a lynx kill site, I used the selected α to implement elastic net across a range of λ with "cv.glmnet" in R package *glmnet* (Hastie et al. 2021) using LOOCV and including a weights vector to address imbalanced class size (King and Zeng 2001).

To reduce concerns about bias and overstated accuracy of the predictive model (i.e., to reduce overfitting), I assessed final elastic net model performance using pre-validated fits, which are predictions calculated on each held-out fold during cross-validation (Tibshirani and Efron 2002, Hastie et al. 2021, Tay et al. 2023). These predictions are made on "unseen" data prior to model fitting to provide a fairer, more conservative accuracy measure, which may be particularly important when sample sizes limit the more typical splitting of one's data into fully separate training and testing subsets (Tibshirani and Efron 2002, Bates et al. 2023). I report the associated Area Under the Curve (AUC) values for these pre-validated fits at the specific penalty strengths selected in the final *glmnet* model (λ_{min} and λ_{1se}) (Hastie et al. 2021), which measure the overall quality of a binomial model's predictions irrespective of what classification threshold is chosen, and which are often a more appropriate measure for models with imbalanced class sizes (Huang and Ling 2005, Hong and Won 2016), and use Receiver Operating Characteristics (ROC) curves at the specified λ values to report the false positive and true positive classification error rates.

A total of 29 variables (31 with dummy coded unordered categorical variables) were input into the elastic net. Due to the nature of elastic net, traditional measures of statistical significance are not applicable; instead, the strength of selected variables in regularized methods like elastic net is depicted by which are selected as non-zero coefficients after penalties are applied, with relative variable importance demonstrated by consistently larger standardized coefficients. I report the variables retained in the final *glmnet* model at both λ_{min} and λ_{1se} because it is standard practice, and variable selection and regularization at these two penalty levels is conducted simultaneously to offer both the model with least deviance (λ_{min}) and a simpler model (λ_{1se}). However, for the sake of interpretability and given sample size limitations, I focus my results and interpretations on variables retained at the more parsimonious level (λ_{1se}), which contained the core variables that most consistently predict a lynx predation at both $\lambda_{\min}$ and λ_{1se} and provided nearly all of the final model's explanatory power. Finally, I explore more detailed patterns within the strongest variables that predicted a lynx kill site with *post hoc* descriptive analyses.

2.3 RESULTS

2.3.1 Hare captures, habitat data collection, and identification of lynx kill sites

I captured 375 snowshoe hares in 707 trap events. Of these captured hares, I ear-tagged 356 individual hares and affixed radio-collars to 223. Fine-scale habitat variables were measured at 243 plots for locations of kill sites attributable to any predator (*n* = 91) and associated reference habitat plots (*n* = 152). Using a combination of reliable forensic methods, I was able to attribute twenty-four hare mortality events to lynx predation, with lynx kills observed in all seasons and forest age types (Fig. 2.4). Thus, I used data from 72 habitat plots surveyed from 24 lynx-attributed kill sites and 48 associated stratified random points (reference points) to assess whether lynx target hares in habitat representing hare abundance or accessibility.

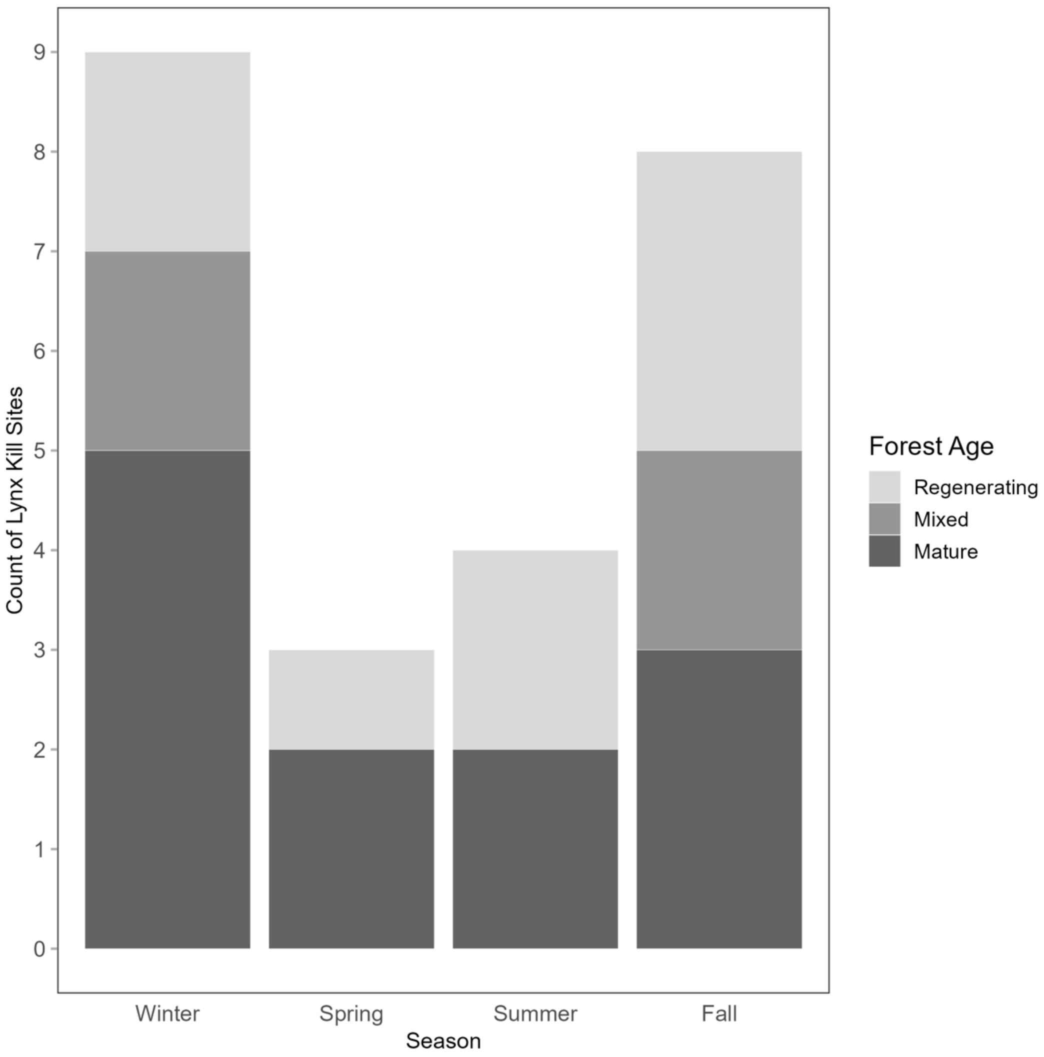

Figure 2.4. Summary of the number of lynx kill sites observed across seasons and forest age types, with season on the x-axis, counts of lynx kill sites by season on the y-axis, and the forest age designation at each kill site represented by the stacks within each bar. Lynx captured hares in all forest age types in this study, with comparatively more in mature and mixed forest, but this pattern was not significantly different from nearby available habitat plots (not shown). Note that the higher frequency of lynx kills in winter and fall is likely due to the improved detection probability in snow-on seasons.

2.3.2 Elastic net modeling results

The final elastic net model for lynx kill site habitat compared to reference plots included 4 variables in the parsimonious model with greater penalty (λ_{1se}: 0.175, SE 0.060), whereas 8 variables were retained at λ_{min} (0.0832, SE 0.0974) with the mixing parameter (α) level set at 0.56. The best predictors of lynx kill sites were nearby ambush features, increased forest structural complexity, high cover as measured by categorical cover type, and percentage horizontal cover measured at 0.5-1 m above ground, as indicated by relatively large and positive β coefficients at $\boldsymbol{\lambda_{1se}}$ and $\boldsymbol{\lambda_{min}}$ (Table 2.3). At λ_{min}, the additional 4 variables with non-zero coefficients that were retained as weaker predictors of a lynx kill were higher horizontal cover at 1.5-2 m above ground, fewer subalpine firs with DBH >7.5 cm, more lodgepole pines ≤7.5 cm, and more Englemann spruce ≤7.5 cm DBH.

I evaluated model fit and report the iterative regularization and model selection process of elastic net on this dataset using a binomial deviance plot (Fig. 2.5). Overall model performance as measured by the final model's pre-validated fits (predictions made on unseen folds during cross-validation to avoid overfitting) gave an AUC at $\boldsymbol{\lambda_{1se}}$ of 0.812 and an AUC at λ_{min} of 0.821, summarizing the final model's overall ability to discriminate a lynx kill from available reference habitat on the landscape (Fig. 2.6). For comparison, a random-guess baseline AUC score would be 0.50 (Fawcett 2006). The additional four variables included at the more libral λ_{min} penalty threshold provided negligible predictive power, as evidenced by the almost identical AUC scores at both thresholds and the small relative coefficients of the lower-ranked covariates at λ_{min}. Thus, interpretation of predictor importance in this study focuses on the more parsimonious penalty threshold (λ_{1se}).

To visually demonstrate patterns in the variables identified by elastic net as most important in predicting lynx kill sites, I plotted the unscaled distribution of the four habitat variables retained at both elastic net penalty thresholds (Fig. 2.7). Lynx kill sites tended to have higher-quality nearby ambush features, more forest structural complexity, more plots within the general category of “cover,” and more horizontal cover at 0.5-1 m height, although not necessarily at the maximum horizontal cover values available (lynx horizontal cover mean: 86% and median: 79%).

Table 2.3. Standardized coefficients of the habitat variables selected from elastic net modeling that predicted a lynx kill site compared to reference plots, listed in order of relative predictive strength. Traditional measures of precision are not typically reported with elastic net because of the bias introduced when selecting the tuning parameters with cross-validation. Furthermore, the shrinkage and variable selection inherent in elastic net complicate the distributional properties of the estimated coefficients, and the primary focus of elastic net is on improving predictive performance and model generalization, not precise coefficient estimation. Instead, the strength of predictors is depicted by which are retained with non-zero coefficients after penalties are applied, with larger values representing relative importance. Coefficients are reported for the model with less penalty applied ($\lambda_{min} = 0.0832$*) and the more parsimonious model (*$\lambda_{1se} = 0.175$*), but the same top 4 variables were retained at both penalty levels. The additional 4 variables retained at the more liberal *λ_{min}* penalty threshold provided minimal additional explanatory value but are reported because modeling at both thresholds occurs simultaneously, and it is standard to report both. Model selection was based on a mixing parameter (α) of 0.56, selected through cross-validation, to apply the relative mix of the ridge and LASSO (Least Absolute Shrinkage and Selection Operator) penalties that comprise the elastic net regression.*

Variables with non-zero coefficients at $\lambda_{\mathbf{min}}$	β	Variables with non-zero coefficients at $\lambda_{\mathbf{1se}}$ (parsimonious model)	β
Nearby Ambush Features	0.731	Nearby Ambush Features	0.463
Forest Structure (↑ structure)	0.510	Forest Structure (↑ structure)	0.274
Cover Type (↑ cover)	0.329	Cover Type (↑ cover)	0.164
Horizontal Cover at 0.5-1 m height	0.254	Horizontal Cover at 0.5-1 m height	0.110
Subalpine Fir >7.5 cm DBH	-0.156		
Lodgepole Pine ≤7.5 cm DBH	0.0718		
Englemann Spruce ≤7.5 cm DBH	0.048		
Horizontal Cover 1-1.5 m	0.0108		

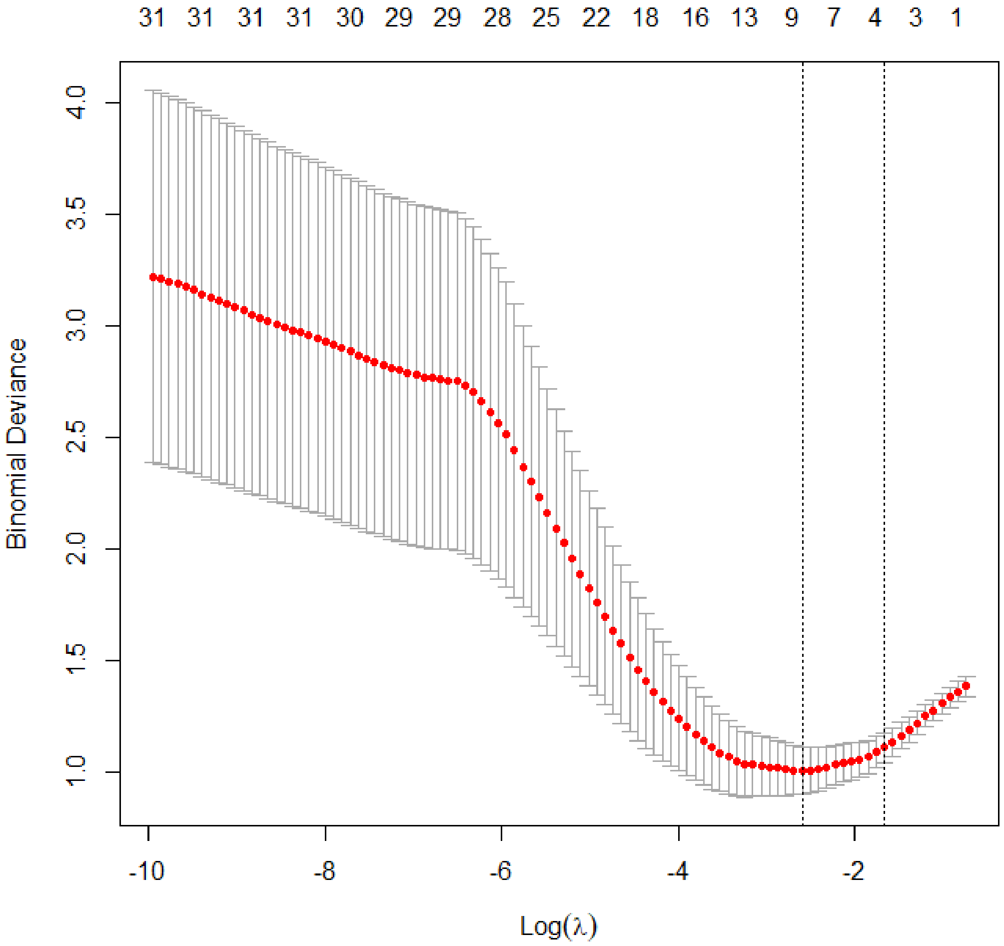

Figure 2.5. Binomial deviance plot for the final elastic net model predicting a lynx kill site compared to reference plots, demonstrating the optimal regularization strengths that balanced accurate model fit with generalizability for prediction. The top axis shows the number of features (variables) first entered into the model (including dummy-coded categorical variable levels) on the left, with increasing penalty strength moving to the right. Penalty strength is indicated by log (λ) on the x-axis. The vertical lines demonstrate the penalty strength at which the variables with non-zero coefficients (stronger predictors) were selected by elastic net (8 at λ_{min} and 4 at λ_{1se}) in the final model to minimize cross-validated error. The mixing parameter for the modeling (α),

which determines the relative degree of coefficient shrinkage and variable elimination penalty for λ to apply, was set at 0.56 after prior training with leave-one-out cross-validation across a *range of λ and α values. The 4 variables selected at* λ_{1se} *(more parsimonious regularization level) as stronger predictors of lynx kill site habitat, all of which were positively associated with a lynx kill, were: nearby ambush features, forest structural complexity, cover type (general category as "cover"), and percent horizontal cover at 0.5-1 m height.*

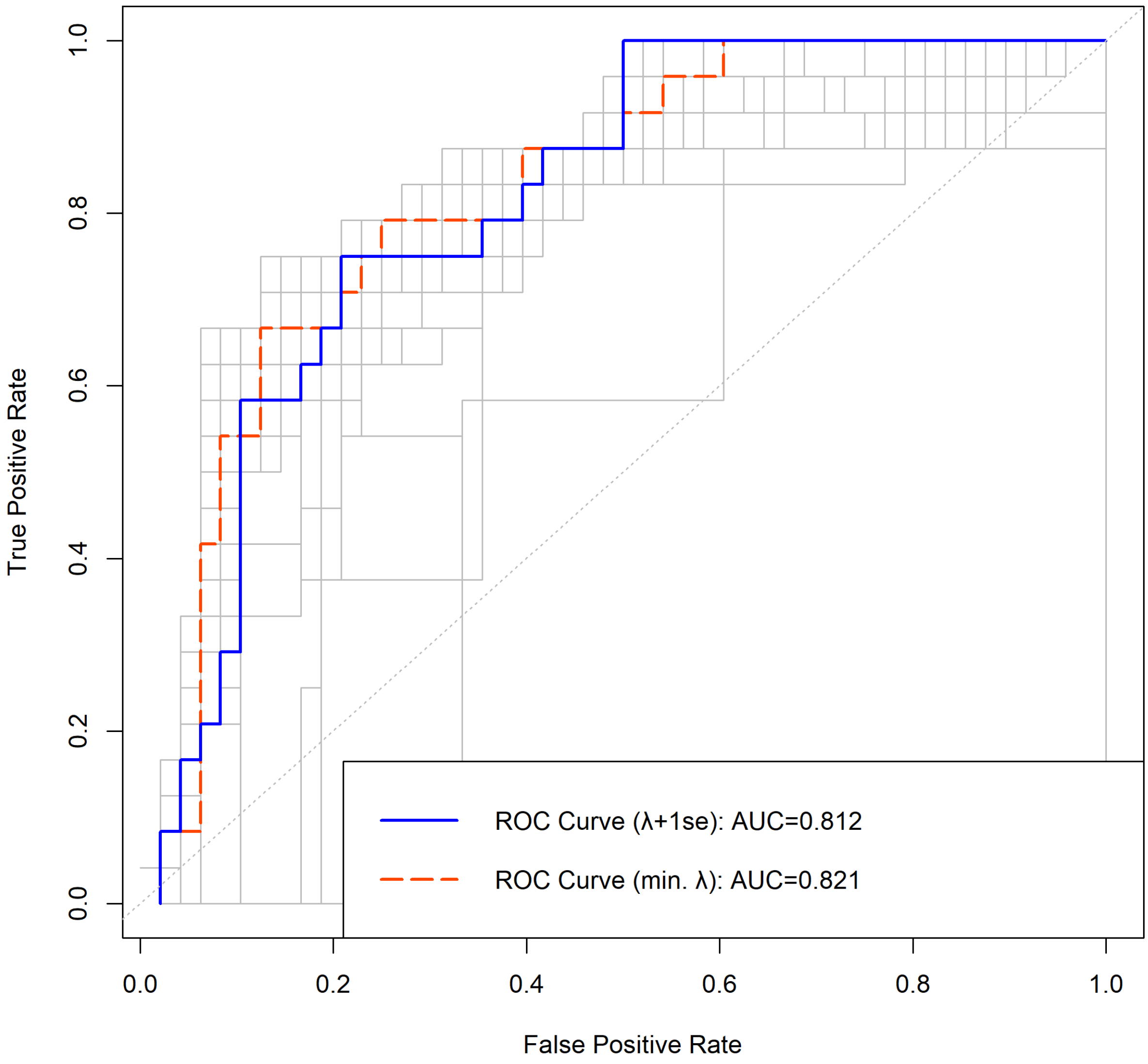

Figure 2.6. Receiver Operating Characteristic (ROC) curves and corresponding Area Under the Curve (AUC) values for the final elastic net model's lynx kill site classification accuracy. The solid blue line represents the ROC curve for the conservative model (λ_{+1se}) with an AUC of 0.812. The dashed red line indicates the ROC curve for the model with the minimal cross-validated error (λ_{min}) with an AUC of 0.821. Each gray line traces the model performance across a spectrum of λ values. The dotted gray line at a diagonal indicates the baseline performance of a non-discriminatory classifier, equivalent to a random guess, with an AUC of 0.5. The plot collectively illustrates the true positive rate against the false positive rate at various classification thresholds, highlighting the discriminative capacity of the final model.

2.3.3 Post hoc exploration of top variables

To provide more context for the key results of the elastic net modeling, I conducted *post hoc* descriptive explorations of the four strongest numeric predictors of a lynx kill site: nearby ambush features, forest structural complexity, and horizontal cover. Specifically, because lynx kill sites have been most often described during the winter season, I assessed whether lynx selection for these habitat features was observed only in winter or throughout the year. Detailed seasonal analyses were beyond the scope of the main study because the reference habitat plots were seasonally tied with kill site habitat plots, and the frequency of kill sites by season was likely influenced by season-specific detection probability. However, visual assessment of data plotting suggests that, whereas lynx kill sites had higher scores for nearby ambush features across most seasons, these nearby ambush features were particularly important in winter (Fig. 2.8). Spring was an exception, although inference was likely hindered by the limited data availability in that season due to site access issues. Structural complexity was also important to lynx throughout the year and higher in all seasons except spring but may have been relatively more important to lynx in summer (Fig. 2.9). Horizontal cover at 0.5-1 m was higher at lynx kill sites in all seasons as well, and perhaps higher in spring and summer (Fig. 2.10), but these seasonal differences were less pronounced for all of the top variables except ambush features. To visually compare values for all three of the top numeric predictor variables identified as most important to lynx (nearby ambush features, forest structural complexity, and horizontal cover from 0.5-1 m height), I scaled relative differences between lynx kill sites and random plots in each of the four seasons (Supplemental Fig. S2.6). These comparisons should be taken as only descriptive measures; that is, they do not reflect relative strength of prediction among these top variables but rather are scaled and thus control for seasonal variation among these top variables, which were already identified as important in the main analysis across seasonal fluctuations.

Pursuant to my finding that lynx were catching hares in both regenerating and mature forest age types, not solely the regenerating forest type predicted by a prey abundance hypothesis, I examined whether forest age in the study area related to forest structural complexity, which was the second strongest predictor of a lynx kill site. Forest structural complexity is generally associated with more mature habitat types (Liira et al. 2011). However, in my study area, lynx appeared to target hares where high structural complexity could be found across all forest age types (Fig. 2.11).

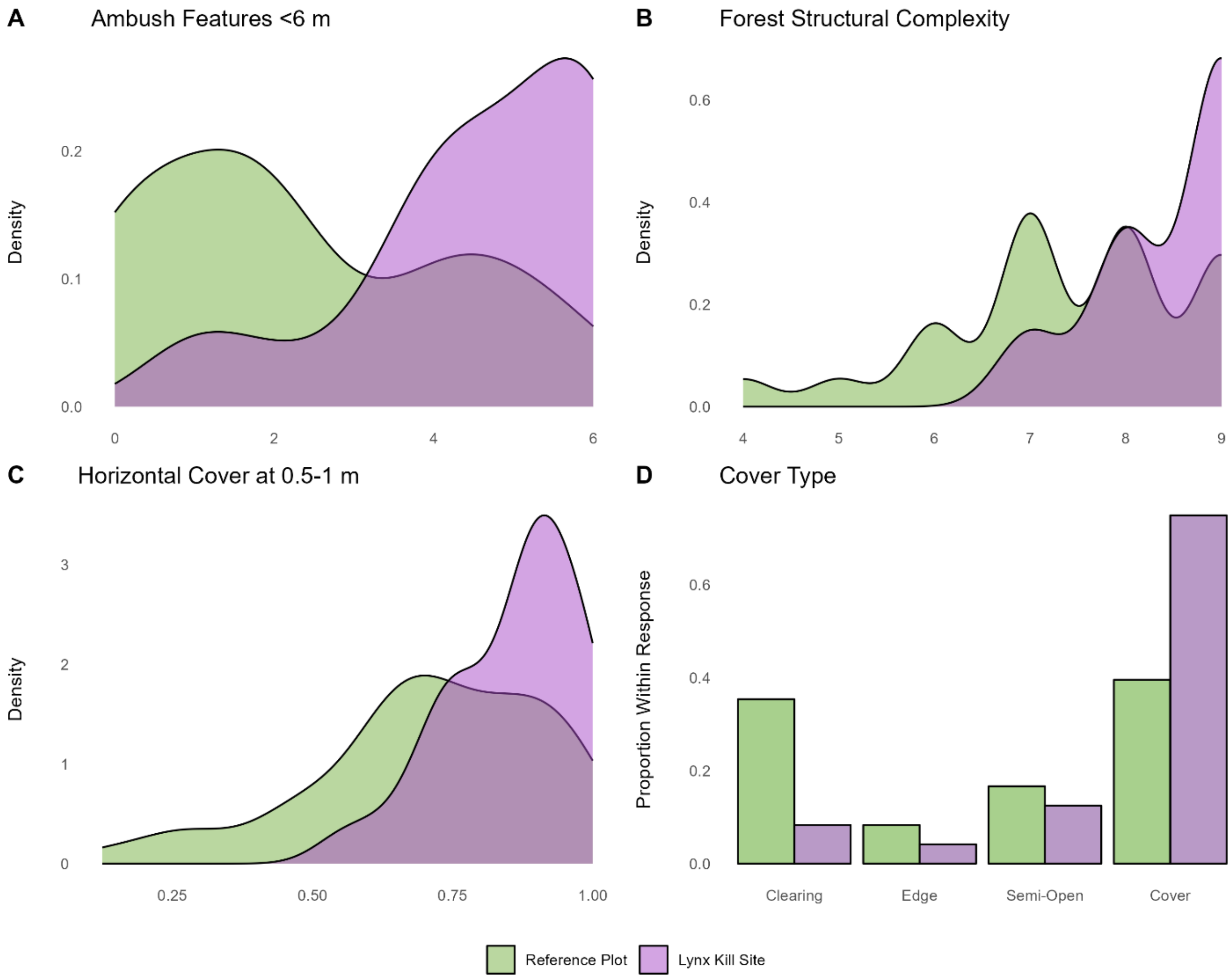

Figure 2.7. Summary of the topmost variables predicting a lynx kill site compared to available habitat in this study, showing the habitat variables that best predicted a lynx kill site compared to reference plots: (A) ambush feature quality within 6 meters at lynx kill sites or reference plots, (B) forest structural complexity, (C) percent horizontal cover at 0.5-1m height above ground, and (D) general cover type category (Clearing, Edge, Semi-Open, and Cover), with each response type (reference or lynx) equaling one. For the probability density plots in A-C, the peaks of the curves (y-axis) indicate where values are more concentrated along the x-axis for that variable. Variables were selected with elastic net regression and are reported for the higher-penalty (simpler) model; these four variables were also the strongest predictors (based on relative standardized coefficient size) in the more complex, lower-penalty model.

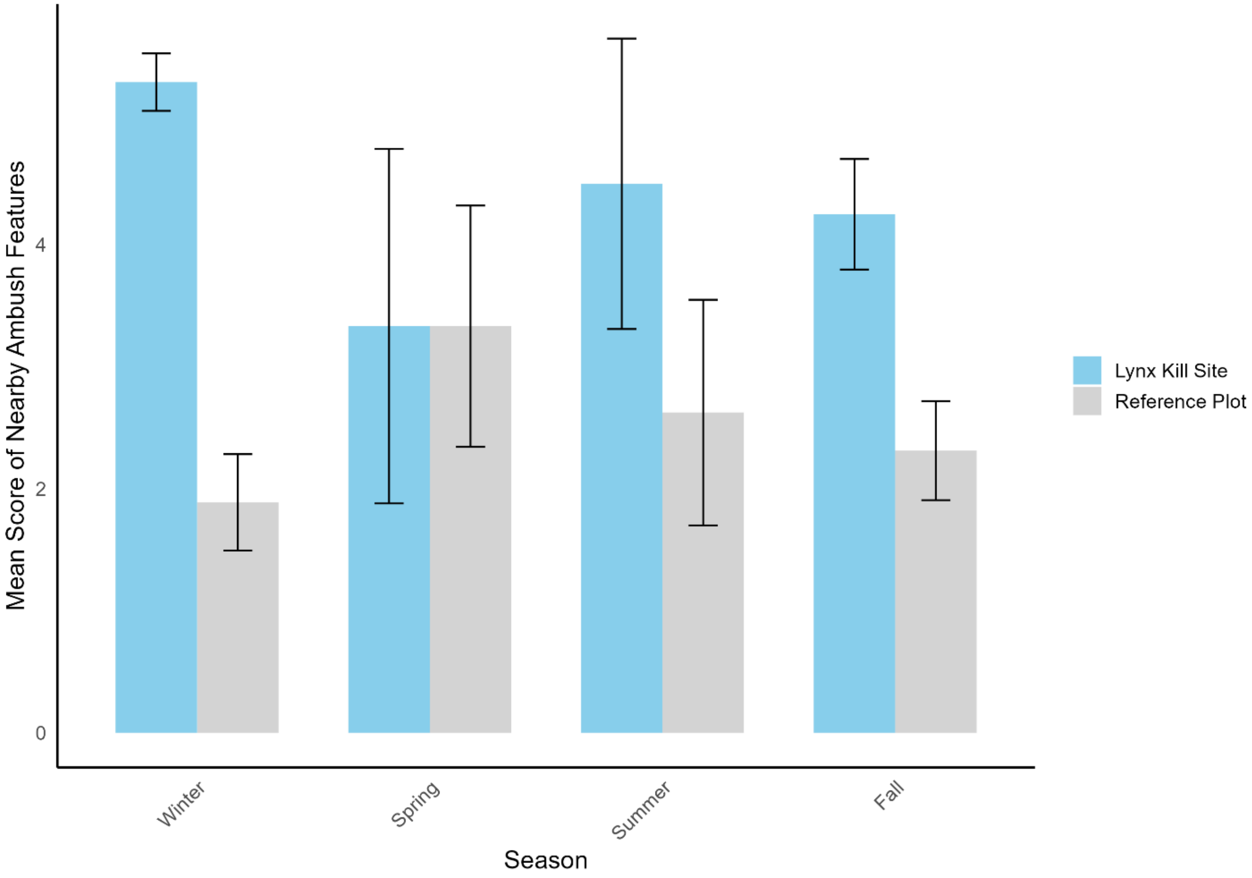

Figure 2.8. Descriptive plot showing seasonal variation in the mean score and standard error of nearby ambush features at lynx kill sites and reference habitat plots. Aside from spring, which had the fewest lynx kill site observations (due to study area access issues), lynx appeared to prioritize ambush features on the landscape across seasons but may have been targeting ambush features more in winter and, to an extent, fall.

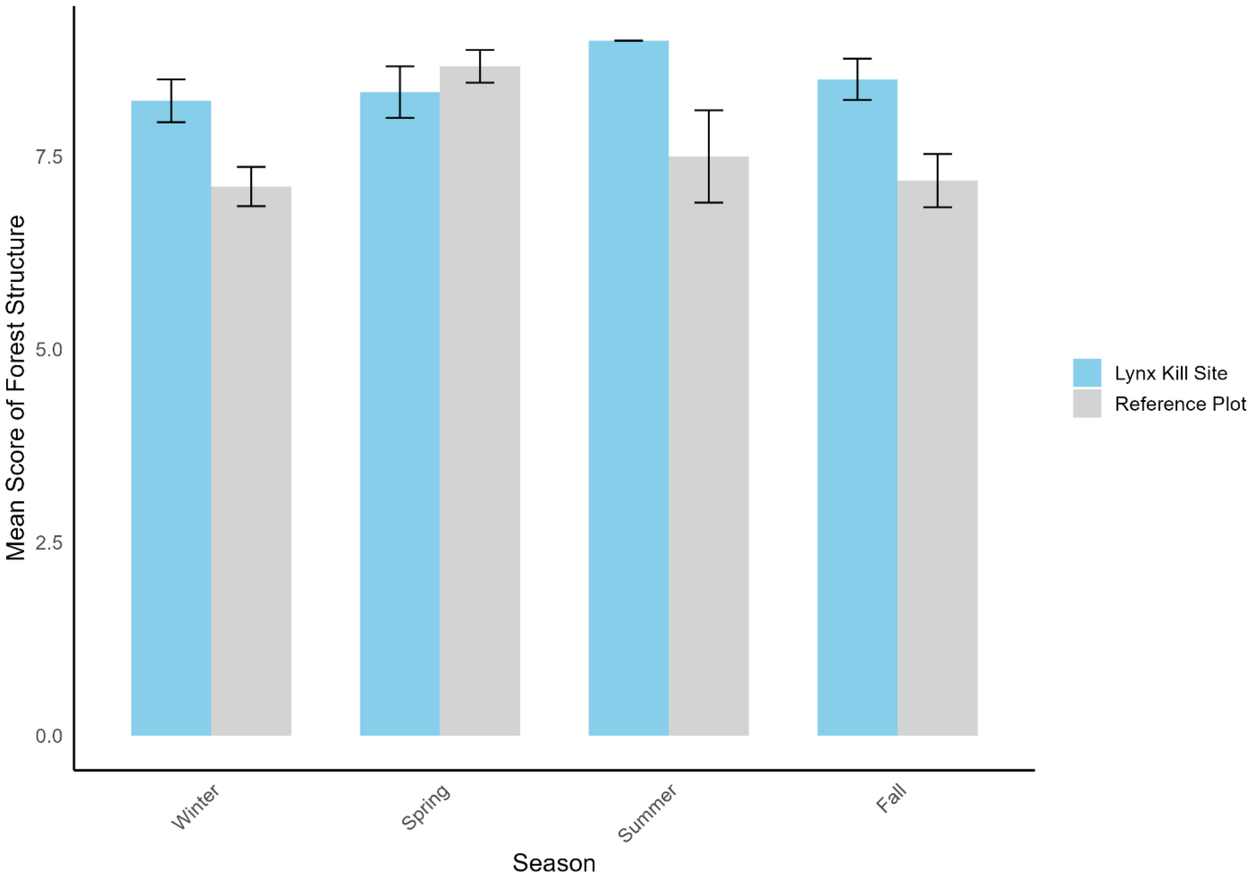

Figure 2.9. Descriptive plot showing seasonal variation in the mean score and standard error of forest structural complexity at lynx kill sites and reference habitat plots. Structural complexity was important across all seasons, and lynx were catching hares at sites with the highest structural complexity in all seasons except spring.

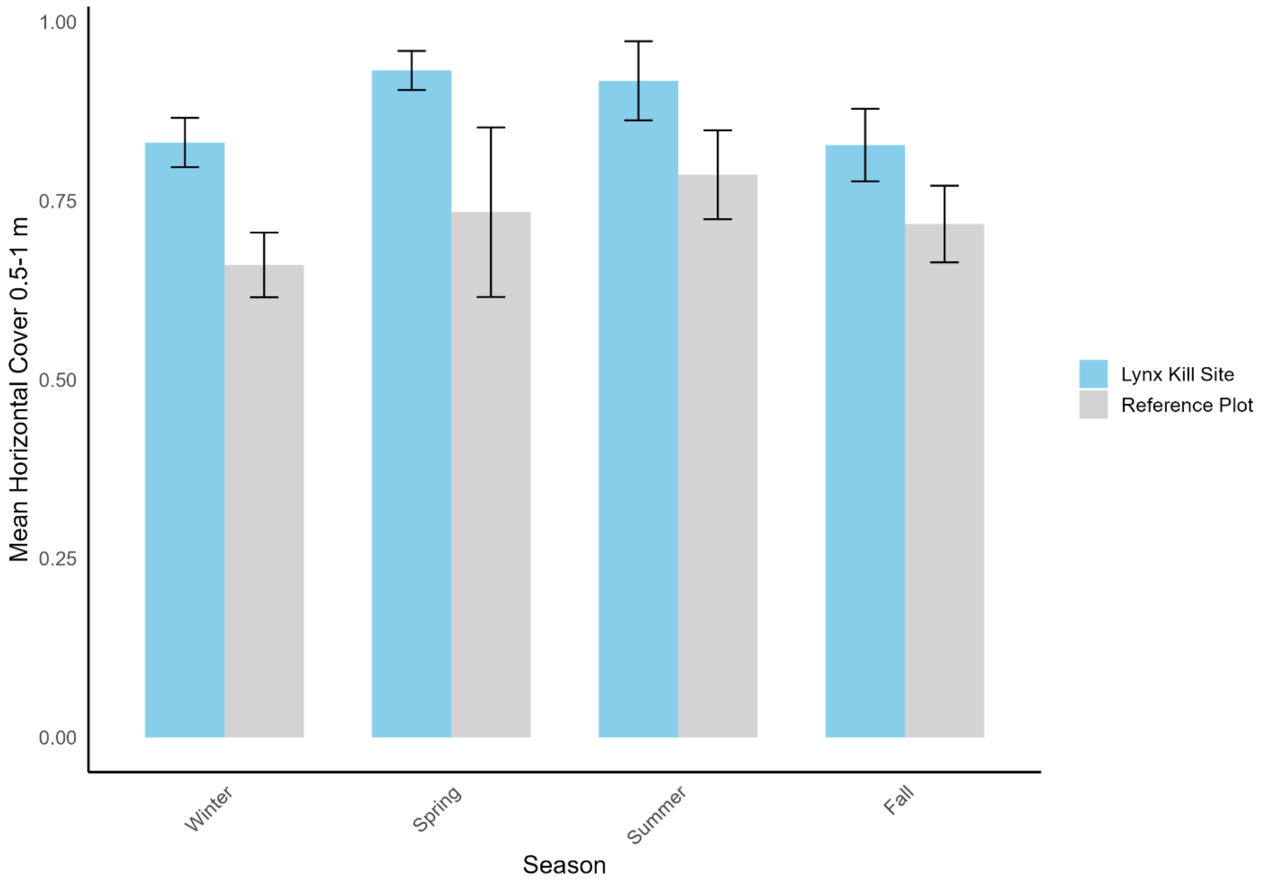

Figure 2.10. Descriptive plot showing seasonal variation in the mean score and standard error of horizontal cover at 0.5-1 m height at lynx kill sites and reference habitat plots. Horizontal cover was important across all seasons.

Figure 2.11. Descriptive plot of forest structural complexity at lynx kill sites and reference habitat plots by forest age category, demonstrating that lynx were capturing hares at sites with relatively high structural complexity across forest ages.

2.4 DISCUSSION

The trophic link between Canada lynx and snowshoe hares is iconic, but knowledge is limited about the habitat features associated with successful lynx predation events on hares, especially outside of winter and in the southern range of this federally threatened felid. My study in Washington utilized forensic tools to overcome limitations of seasonal tracking conditions and modeled lynx kill site habitat characteristics across snow-on and snow-free seasons. The predictors that most strongly differentiated successful lynx predation sites from available habitat plots were nearby ambush features, followed by forest structural complexity, and broadly categorized “cover type.” Horizontal cover in the understory was also an important but lesser predictor. The prominence of ambush features and forest structural complexity at lynx kill sites supports a prey accessibility hypothesis, suggesting that landscape features facilitating capture surpass the influence of hare abundance alone, which in this system would have been represented by high stem density and regenerating forest. These results align with previous studies suggesting that access to hares is a crucial determinant of successful hunting for lynx (Fuller et al. 2007, Ivan and Shenk 2016). However, horizontal cover's retention as a lesser predictor suggests that foraging lynx also utilized areas of high hare abundance afforded by maximum cover, aligning partially with a prey abundance hypothesis (Murray et al. 1995, O’Donoghue et al. 1998*a*, Squires et al. 2010). Additionally, the broad categorization of "cover type" could not definitively support either the prey accessibility or abundance hypothesis because this more coarsely-estimated metric would not have differentiated whether lynx primarily killed hares in high- or moderately high-density cover. Overall, lynx demonstrated a strong pattern of using cover rather than more open habitat when capturing hares, strongly favoring fine-scale landscape attributes such as nearby ambush features and high overall forest structure within areas of relatively high horizontal cover. This study fills an important knowledge gap by characterizing lynx kill site habitat in all four seasons, aided by forensic tools that revealed lynx predation patterns without the limitations of adequate tracking conditions, thus expanding our understanding of lynx foraging ecology in the southern range.

2.4.1 Ambush features

Nearby ambush features were the strongest predictors of lynx kill sites among the array of habitat variables considered in this study. These microhabitat features provided both cover and access, being rated highly when there was relative line of sight and physical access between the ambush feature and the kill site. In contrast, high visual obstruction from continuous, densely packed tree trunks precluded a high ambush feature rating. Lynx could have ambushed in these habitats as well, but trees were already being accounted for with other variables (e.g., stem density), and the ambush feature variable was intended to represent more heterogeneously distributed microhabitat features that were expected to enable close approach and access to prey without detection. Although this study may be the first to examine fine-scale ambush features at lynx kill sites outside of the winter season, multiple winter-based studies have shown lynx using ambushing or a combination of ambushing and stalking behaviors; these studies based on snow-tracking allowed for direct observation of “hunting beds” on the landscape associated with ambushing behavior (i.e., the body imprint in snow and related tracking patterns during a chase) (Saunders 1963, Nellis and Keith 1968, Parker et al. 1983, Murray et al. 1995, O’Donoghue et al. 1998*a*, Von Kienast 2003, Maletzke 2004, Burdett et al. 2007, Squires and Ruggiero 2007). During adequate tracking conditions, I noted both ambush and stalking behaviors at lynx kill sites but did not quantify their relative use because this behavior could not be observed across seasons. Furthermore, although a main finding from my study is the importance of ambush features at lynx kill sites, it does not necessarily follow that ambushing behavior is the sole hunting mode of import for lynx. Reports of lynx having greater success when ambushing vary, perhaps owing in part to differing definitions. For example, Murray et al. (1995) found that lynx were more successful when ambushing, whereas O'Donoghue et al. (1998*a*) found no difference in lynx hunting success between ambushing and stalking. However, O'Donoghue et al. (1998*a*) used a more conservative definition than Murray et al. (1995), such that a lynx kill that started from a hunting bed was not defined as ambushing if the lynx ultimately used a combination of both stalking and ambush. Other studies have similarly defined a kill from an ambush bed with this stricter description (e.g., Von Kienast 2003). Nonetheless, the distinction may be less relevant from the perspective of a lynx foraging at a finer scale (final 30 m—or usually 10-15 m—within which a chase results in a successful kill; Murray et al. 1995, O'Donoghue et al. 1998*b*, 2001). The relative contribution of ambush and stalking behavior within that final stretch of effort may matter little, so long as microhabitats like ambush features contribute to successful hare approach and capture.

Regardless of whether lynx are more successful when ambushing compared to other hunting styles, the importance of ambush features in my study aligns with some others suggesting that ambushing helps lynx conserve energy, particularly when hare numbers are lower (Murray et al. 1995, O'Donoghue et al. 1998*a*), which is more consistently the case in the acyclic southern range of hares (Hodges 1999*a*). Lynx have higher energy needs for their size and appear to compensate to an extent by reducing physical activity, even being called a "lazy cat" because of this tendency (Thompson 1977, Menzies et al. 2022). Furthermore, energy conservation with the use of ambush features on the landscape may be especially important for lynx when hare numbers are more seasonally limited. Although a key takeaway of my study is the importance of ambush features for lynx across all seasons, *post hoc* analyses suggested a comparatively heavier reliance on ambush features at lynx kill sites in winter (Fig. 2.8). This apparent seasonal shift could suggest that lynx are further limiting physical activity to conserve energy when hares are seasonally less abundant. By wintertime, hares are less plentiful on the landscape than during hare breeding season in snow-off months (Hodges 1999*a*). The lack of deciduous vegetation in winter could also increase lynx reliance on ambush cover from other microhabitats such as logs. In general, those studies finding that lynx may shift foraging behavior with temporally fluctuating prey abundance (O'Donoghue et al. 1998*b*) or the amount of cover by various measures (Murray et al. 1995, Maletzke et al. 2008, Squires et al. 2010), suggest some adaptive behavior to prey availability that could have explained the seasonal shifts observed in my study, even if lynx were not focusing only on habitat supporting the highest hare densities on the landscape.

Direct comparisons with prior cross-seasonal lynx-hare studies must include third-order habitat use (movements on the landscape) instead of only where lynx successfully captured hares (i.e., fourth-order habitat use) because lynx kill site studies have previously been limited to winter, but some such evidence points to seasonal shifts in lynx habitat use. For example, studies in Montana suggested that lynx may rely more on older forests during winter and regenerating forests in summer when seeking hares (Squires et al. 2010, 2013), which, in that region, aligns with seasonal patterns of hare abundance (Griffin 2004). Evidence for similar seasonal shifts in Washington is more mixed (Vanbianchi 2015, Glover 2016), but fine-scale differences in foraging habitat use might not have been detectable at the third-order scale used in those studies.

Seasonal patterns in the other top variables were less pronounced than with ambush features and are thus discussed in Supplemental S2.

2.4.2 Forest structure

Lynx kill sites were associated with increasing forest structural complexity, a measure often associated with more mature forests (Liira et al. 2011). However, in this study, while forest age was correlated with greater structural complexity in reference plots, this was not true of lynx kill sites. Instead, lynx appeared to target and successfully capture hares in habitats with high structural complexity across all forest age categories, rather than areas of high-density regenerating forest as would be predicted from a hare abundance hypothesis. The availability of at least some structural complexity within the regenerating forest, not just mature forest, may owe in part to how forest structural complexity was measured in my study, being a more precise measure of heterogeneity in woody vegetation than the categorical forest age variable; see Supplemental S2 for additional discussion on age and structural complexity. Furthermore, the regenerating stands in the study area were not consistently even-aged at a finer scale. Rather, higher structural complexity scores than expected at lynx kill sites in regenerating forest were likely due to fine-scale microhabitat differences (e.g., the occasional interspersion of mature trees retained during the last timber harvest, and/or the development of a separate understory layer, despite the latter being less common in regenerating stands). Studies in nearby Montana have suggested that later-stage regenerating forests in the intermountain west may be old enough to have developed some multistory structure (Squires et al. 2010), which may have been true in my study area as well. The importance of structural complexity but not forest age for predicting lynx kill sites supports some prior evidence that the structural complexity, including understory of mature boreal forests in Washington, may provide enough “accessible” cover to support adequate hare numbers and facilitate lynx foraging (Maletzke et al. 2008).

Forest structural complexity likely affects where lynx successfully forage at a finer scale than would be apparent from studies on their more general habitat use. Indeed, lynx have demonstrated scale-dependent and behavior-specific habitat use patterns in other contexts (Squires et al. 2008, Vashon et al. 2008*a*). Broader-scale studies have suggested that forest structural complexity is less important than I observed at the fine-scale, fourth-order habitat scale in my study. For example, a study in Colorado found that lynx did not alter broad distributions post-fire, despite changes in forest structure and composition after this disturbance (Squires et al. 2022), instead continuing to select for hare distributions that experienced minimal changes because of the high horizontal cover afforded by regenerating high stem density and understory. Broad-scale studies such as these suggest flexibility in lynx habitat use, which provides hope for the persistence of this species in the face of fragmentation (Vanbianchi et al. 2017*a*) and climate change-induced wildfires (Vanbianchi et al. 2017*b*) in these southern systems. However, if catching prey within these habitats requires more effort and results in less frequent kills, despite a continued abundance of hares, then this could reduce lynx fitness in the longer term, highlighting the importance of incorporating data on where lynx are successfully catching hares.

Cross-study comparisons about forest structural complexity at lynx kill sites are complicated by forest structure terminology sometimes being used interchangeably with horizontal cover (visual obstruction) as measured by coverboard cover (e.g., Feierabend and Kielland 2015). Although horizontal cover and forest structure were strongly associated with one another, they are not identical and were both retained in the top model for lynx kill sites, despite the penalties applied to account for highly correlated variables. Horizontal cover in my study at

0.5-1 m was a direct measure for lateral understory cover taken by the observer while kneeling to better approximate the height of a mesopredator like a lynx and then averaged from the 4 cardinal directions, whereas forest structure was an ocular estimation of the sparsity of all three typical forest layers (including an understory). While less precise compared to coverboard measurements, which take substantial time to collect in denser forest, the structural complexity scale was able to summarize multistory forest structure information and was a comparatively stronger predictor of lynx kill sites than horizontal cover in the understory. Nonetheless, it is important to note that understory was a component of the structural complexity variable and has often been shown to be the most important structural component in lynx and hare habitats (Litvaitis et al. 1985, Maletzke et al. 2008, Squires et al. 2022).

2.4.3 Horizontal cover

My finding that horizontal cover (specifically, the percent visual obstruction as measured at 0.5-1 m height) was a comparatively important predictor of a lynx kill site offers some support for the prey abundance hypothesis and aligns with expectations based on prior studies in Montana (Squires and Ruggiero 2007, Squires et al. 2010). Squires et al. (2010) found horizontal cover to be the strongest predictor of a lynx kill site compared to habitat along a lynx’s travel routes, thus comparing two scales of foraging selection for lynx (i.e., third- and fourth-order habitat use). Results from this study in Montana suggest that lynx kill hares in denser horizontal cover than is used along travel routes, and more broadly demonstrate the importance of horizontal cover in all seasons at comparatively broader (third-order) habitat selection, and at kill sites in winter (fourth-order habitat selection).

As with my study, Squires et al. (2010) found horizontal cover to be more strongly associated with lynx kill sites than stem density and regenerating forest. However, that study's inference was more supportive of an abundance hypothesis because hare numbers were somewhat higher in the mature forest in winter (Griffin 2004, Squires and Ruggiero 2007, Griffin and Mills 2009). In those studies, mature forest provided sufficient forest structure and understory cover in winter, perhaps because of low-hanging branches of mature trees in these conifer-dominated forests of the intermountain west, which differ from those in the eastern US with more deciduous cover and may have provided similar cover in my study. The Squires et al. (2010) study was among the few that directly surveyed and modeled a spectrum of detailed metrics for cover at lynx kill sites, including both stem density and horizontal cover as measured by coverboard. Further afield from these intermountain west studies, an extensive investigation in interior Alaska also measured horizontal cover with a coverboard at predation sites of hares, many of which were attributable to lynx, but did not find a clear pattern of horizontal cover driving where predators were catching hares (Feierabend and Kielland 2015). Although Feierabend and Kielland (2015) primarily reported patterns among grouped predator types, lynx were the most common mammalian predator in that system.

Most other studies on understory or horizontal cover at lynx kill sites have used more approximate estimates but provide further evidence that understory horizontal cover is important at lynx kill sites. In Washington, Maletzke et al. (2008) found evidence for lynx targeting hare abundance because lynx killed hares (and occasionally other prey) in stands where hare densities were high. However, this same study found that higher sinuosity of lynx trails (which required more moderate-dense cover) was associated with successful kills. In my study, although horizontal cover was higher at kill sites than at random points for all 4 height increments (not just the at 0.5-1 m as selected in the final model), lynx were not typically capturing hares in 100% horizontal cover (Fig. 2.7, panel C), which aligns with Maletzke et al. (2008) in suggesting that lynx catch hares in high, but perhaps not the maximum understory cover, as might be expected of this primarily visual hunter. Overall, in this study and in many others, relatively high horizontal cover is associated with lynx kill sites and high hare numbers but is not exclusive to the dense regenerating forest often associated with preferred hare habitat.

2.4.4 Cover type

My study's finding of the importance of cover type for lynx when catching hares—specifically, a broad categorization of high vegetation cover—mostly aligns with expectations based on other studies and can be interpreted as inclusive of both the accessibility and abundance hypotheses. Lynx typically prefer cover (Aubry et al. 2000, Mowat et al. 2000, Koehler et al. 2008, Vashon et al. 2008*b*) and, like many other felids, employ vegetation for concealment when hunting prey (Brand et al. 1976, Lavoie et al. 2019), although some studies have suggested that lynx use edge habitat when searching for hares (e.g., Staples 1995). Lynx in my study did not appear to use edge or open habitat at most of their successful kill sites, instead exhibiting a strong selection for cover compared to available habitat, matching existing knowledge about lynx hunting behavior in Washington; Maletzke et al. (2008) found that lynx avoided forest openings when hunting hares in winter. However, it should be noted that the cover type variable used in my study was not characterized to address predictions based on whether lynx were capturing hares in the densest or more moderately dense cover. Rather, the four classes used in the cover type variable, which were ranked from most to least open (clearing, edge, semi-open, and cover), were meant to more holistically categorize the full range of cover openness available on the landscape and thus would not have been fine-scale enough to discern any difference between lynx selection for moderately dense or the densest cover within the relatively high-cover areas already known to be preferred by hares (Koehler 1990, Hodges 1999*a*). Specifically, vegetation cover interspersed with smaller openings was still categorized as "cover" for the purposes of this study. Nonetheless, other measures included in the modeling that were meant to provide further fine-scale information about habitat openness at lynx kill sites, such as the distance to cover or clearing variables, were not retained as important predictors of a lynx kill site relative to the other variables retained in the final model, including overall cover type.

The importance of cover type overall for lynx in where they successfully catch hares has implications in a managed landscape. Although my study generally found more support for lynx targeting comparatively more accessible habitat features rather than proxies for the densest cover on the landscape, lynx were still making kills within the areas of cover preferred by hares (Litvaitis et al. 1985). Accessible habitat for predators must be within areas where prey are sufficiently abundant, as there is little likelihood of a predator-prey encounter otherwise (e.g., Kittle et al. 2022). Hares must be relatively plentiful in the first place to be a resource for lynx (Steury and Murray 2004), and forest management practices like pre-commercial thinning that reduce overall density of cover in hare habitat have been shown in numerous studies to negatively affect hare abundance (Ausband and Baty 2005, Griffin and Mills 2007, Homyack et al. 2007, Abele et al. 2013). As such, inferences about support for an accessibility hypothesis rather than lynx targeting hares in the densest habitat available, as suggested by the other strongest variables predicting a lynx kill sites, must be approached in the context of both lynx and hares still being associated with cover overall.

2.4.5 Support for accessibility hypothesis

The across-season evidence from my study that ambush quality and forest structure strongly predict a lynx kill site supports a prey accessibility hypothesis for lynx. However, horizontal cover was also a predictor of lynx kill sites, if a weaker one. Furthermore, a prey accessibility hypothesis must be interpreted within the context of the well-documented preference of both lynx and hares for areas of higher cover overall. While lynx kills typically occurred in “cover” when categorized as such in coarser categories, the weight of evidence fell on an accessibility hypothesis for lynx not only because of the importance of forest structure and ambush features but also because forest age (regenerating forest) and associated high stem density were not retained as strong predictors of lynx kill site habitat. By design, I attempted to sample (trap and radio-collar) hares relatively evenly in both mature dense stands and regenerating dense stands to control for “availability” of forest ages on the landscape. Thus, a strong pattern for lynx successfully catching hares primarily in the habitat where hares were overall most abundant (i.e., regenerating forest; Walker 2005, Jensen 2020) should have been apparent if lynx were strongly selecting those features. Instead, one-third of lynx kill sites occurred in plots designated as regenerating forest, one-half occurred in mature forest, and the remainder were in “mixed-age” forest. These findings are in agreement with studies from other systems that did not find evidence for a prey abundance hypothesis (Parker et al. 1983, Major 1989, Staples 1995, Fuller et al. 2007, Ivan and Shenk 2016).

Despite the much stronger support for an accessibility hypothesis for lynx in my study, which compared the predictive strength of a suite of fine-scale habitat measures, these findings do not necessarily contradict studies that found more support for a prey abundance hypothesis by coarser measures, instead highlighting the importance of scale in measuring lynx foraging habitat. Many of the studies commonly referred to as supporting an abundance hypothesis for where lynx kill hares primarily used approximate, coarse measures of habitat and cover (e.g., Murray et al. 1995, O'Donoghue et al. 1998*a*), which might not have revealed finer-scale habitat differences that could provide clearer evidence for prey abundance or accessibility hypotheses. For example, studies of northern lynx such as the Kluane studies in the Yukon found that the amount of vegetation cover at lynx kill sites shifted based on where hares were more abundant at that time in the northern lynx-hare cycle, thus supporting a hare abundance hypothesis (Murray et al. 1994, 1995, O'Donoghue et al. 1998*a*). My study results do not necessarily contradict these findings, in part because the acyclic southern hare populations can be considered relatively "fixed" in a low cyclic phase, and I found that lynx made kills in areas of relatively high cover when coarsely categorized by cover type—which aligns with where hares are generally available, similar to the Kluane studies. However, the Kluane studies did not measure finer-scale habitat features at lynx kill sites, such as stem density, that would have more clearly differentiated whether lynx target accessibility versus abundance. Studies of southern hare and lynx populations that have instead supported an accessibility hypothesis have primarily done so by demonstrating that lynx are unable to access prey in regenerating forest areas with the highest stem density, e.g., in Maine (Fuller et al. 2007) and Colorado (Ivan and Shenk 2016). Furthermore, those long-term studies in Kluane were conducted where the habitat was predominantly mature (Murray et al. 1994, 1995). Thus, the denser regenerating forest that appears to sometimes preclude lynx hunting success in other regions may not have been sufficiently available on the landscape in Kluane (O'Donoghue et al. 2010). However, O'Donoghue et al. (1998*a*) also reported in that same long-term study that lynx were using less dense forest than hares based on general movement patterns. Similarly, in interior Alaska, lynx appeared to be targeting hares in more mature spruce forest (Feierabend and Kielland 2015). Much of the lynx-hare literature overall has long speculated that, despite both lynx and hares often selecting for late-stage regenerating (~20-40-year-old) forest at a broader scale, lynx may not be as successful at catching hares in these densest forest stands (Ruggiero et al. 1999, Mowat et al. 2000). A key takeaway of these cross-geographic comparisons is that the highest stem-density regenerating forest does not appear to be a strong predictor of lynx hunting success, even when a hare abundance hypothesis is otherwise supported (e.g., by other metrics for the highest hare abundance such as horizontal cover). However, stem densities averaged higher at lynx kill sites than at reference plots, implying that the highest-density forests that elsewhere act as refugia for hares might not always be barrier to lynx foraging in Washington, even if most kill sites occurred in more moderately high stem density. See Supplemental S2 for further nuances of forest age patterns and stem density.

Some other predator-prey systems support my finding that habitat needs of predators in heterogeneous landscapes cannot be inferred from assumed prey habitat preferences and should also be informed by the accessibility of resources (Matthiopoulos 2003). Studies across a spectrum of terrestrial (W. Ballard, W. 1981, Hopcraft et al. 2005, Miller et al. 2015) and marine (Real et al. 2022) systems have similarly suggested that prey accessibility may be more important for hunting success than mere prey abundance. Such “catchability” of prey within areas where prey are generally available may be particularly important to felids, which tend to shift fine-scale movement patterns based on cover (Sunquist and Sunquist 1989). For example, the Eurasian lynx, which is otherwise not comparable to the Canada lynx because of primarily hunting ungulate prey, has been shown to target prey accessibility (Belotti et al. 2013). Such studies support that predators (and perhaps especially felids) incorporate behavior-specific use of the landscape at a fine scale to successfully forage. As such, management efforts to benefit predators of conservation concern should be informed by the outcome of foraging efforts within available prey areas, rather than solely focused on either the habitats promoting prey abundance or on generalizations based on a predator's broader-scale habitat use when searching for prey.

2.4.6 Caveats, strengths, & limitations

As the first study to reveal lynx foraging habitat in snow-free seasons, this study required overcoming numerous challenges that limited sample size, particularly study area access issues and the relative rarity of detectable predation events identifiable to the responsible predator for the elusive lynx. Some logistical challenges are inherent to a cross-seasonal, field-based study involving trapping and ground-based telemetry in the densely forested hare habitat of the mountainous Cascades. In particular, I was unable to select trapping stands in the most contiguous forest areas (primarily mature spruce) occupied by lynx in the vicinity and thus was unable to fully sample available lynx and hare habitat in relation to fragmentation (further details in Supplemental S1). Nonetheless, much of lynx habitat in the southern range is typified by fragmentation (Buskirk et al. 2000, Koehler et al. 2008, Murray et al. 2008, Vanbianchi et al. 2018), and such access issues are not unique to my study.

Overcoming the challenge of identifying the responsible predator species at hare mortality sites was central to revealing lynx kills in this multi-predator landscape outside of winter. The more conservative forensic approach I used to identify responsible predator species limited the sample size but was intended to limit speculation, considering the similarities in carcass-handling characteristics among mammalian predators of hares (e.g., Feierabend and Kielland 2015). By sampling predator salivary mtDNA to support field evidence (Peelle et al.

2019), I was able to more definitively determine predator identity, and lynx were the most frequent predators of hares identified to species in this study. Although the sample size of lynx kill sites was small, some clear patterns still emerged, supporting prior evidence of lynx exhibiting strong selection of finer-scale features within broader-scale habitat use areas (Maletzke et al. 2008, Squires et al. 2010).

Even small contributions to knowledge gaps of the habitat features that facilitate lynx foraging success are crucial because not all of an animal's time has equal weight on its fitness, with a successful kill having substantially more of a contribution to fitness for predators like lynx. Like many predators, lynx generally have low success when hunting (~30%; Nellis and Keith 1968, Koehler 1990, Murray et al. 1995, O'Donoghue et al. 1998*b*, Ivan and Shenk 2016), and feeding events are rare (<5% of the day for lynx; Studd et al. 2021). My data represent a unique opportunity to evaluate fine-scale behavior-specific habitat needs that support lynx fitness through successful foraging, helping reveal where a lynx's time spent on the landscape is most advantageous, although it should be noted that I could not directly compare with locations of an unsuccessful predation attempt. Furthermore, because my research focused on elusive determinants of lynx kill sites across seasons, there was limited empirical evidence beyond winter to guide *a priori* selection of potentially influential habitat variables. As such, I assessed a suite of habitat variables to identify which measures are better at explaining variation in where lynx are catching hares, which can then be used for targeted management decisions. However, habitat variables in lynx studies tend to be correlated (e.g., Marrotte et al. 2020), which limits comparisons of which metric best predicts lynx use. Thus, my analysis required an approach that deals with rare events, collinearity, and high data dimensionality. The use of elastic net logistic regression helped reduce the risks of model overfitting and was carefully chosen because it is designed to handle such complexity (Hastie et al. 2009).

2.4.7 Management implications

Understanding habitat features of importance to lynx at any scale is important in the face of more heterogeneous and fragmented habitats of their southern range (Buskirk and Beckwith 1999, Koehler et al. 2008, Murray et al. 2008, Vanbianchi et al. 2018), but as a predator whose hunting efforts are often wasted and result in a low success rate (Nellis and Keith 1968, Murray et al. 1994, 1995, O'Donoghue et al. 1998*a*, Ivan and Shenk 2016, Studd et al. 2021, Shiratsuru et al. 2023), and whose use of the landscape cannot be explained only by prey presence or abundance (Fuller et al. 2007, Trainor et al. 2014, Ivan and Shenk 2016), revealing those specific elements that appear to enable lynx to successfully forage is crucial.

Hypotheses and related predictions about lynx targeting hare abundance or accessibility were made because of the precedent of prior studies and because these predictions can help tease out which variables most strongly predicted a lynx kill site within preferred hare habitat areas. However, a focus on the outcome of that prediction could lose sight of the main takeaways that lynx tended to kill hares in cover overall and that an interspersion of dense mid-successional forest and dense mature forest might be best for lynx hunting success, provided there is relatively high cover available that includes ambush features, high structural complexity, and high horizontal cover in the understory. My study supports suggestions that lynx might benefit most from a mosaic of regenerating and mature forest but emphasizes that, unlike in some predator-prey systems, edge habitat and clearings should be minimized when managing for lynx. This would require careful timing and attention to the scale of timber harvesting to limit fragmentation, encouraging enough fine-scale heterogeneity to allow for access in even-aged regenerating stands without enabling competing predators that tend to leverage more fragmented habitats (Buskirk et al. 2000) or decreasing hare survival (Chapter 4 of this dissertation).

High-density regenerating stands are likely important source habitat for hare populations, but if they are not fully accessible to or highly productive for foraging by lynx, then they should not be the sole focus of management efforts, particularly because of their shorter longevity on the landscape as well as the likely importance of mature habitat for lynx when denning (e.g., Kosterman et al. 2018). The ability to tease out the habitat drivers of hare and lynx occupancy, as well as the specific features that impact lynx foraging success, will be key to the improved management of this threatened species. Furthermore, managing for high hare abundance on the landscape as a resource for lynx should not be incompatible with accessibility, particularly if lynx are making use of features that obscure them from the hare and allow a closer approach and can be targeted by management efforts, e.g., retaining large logs on the landscape that are known to be important for both lynx foraging, as found in this study, as well as lynx denning (reproduction), as demonstrated in multiple other studies (Kosterman et al. 2018). Evidence from other areas of the southern range (e.g., Wyoming) suggests that high hare abundance may be predicted by large woody debris (possibly akin to the ambush features found in my study) and increased forest structural complexity more so than even-aged regenerating stands (Berg et al. 2012); thus, a focus on these features could promote both lynx foraging success and relatively high hare abundance, particularly if interspersed with patches of regenerating forest that allow at least some refuge from predation (Chivers et al. 2014).

Forest management approaches that might improve lynx foraging success when seeking hares, such as managing for microhabitat features that provide ambush cover as suggested by my study, might also benefit lynx by facilitating the opportunistic capture of alternative prey. Specifically, lynx sometimes incorporate use ambushing behavior when hunting red squirrels (*Tamiasciurus hudsonicus*) (Squires and Ruggiero 2007, Ivan and Shenk 2016). Although lynx typically only hunt this alternative prey opportunistically when hunting for hares (Maletzke et al. 2008), red squirrels are nonetheless the second-most important prey species for lynx in the southern range (Apps 2000, Aubry et al. 2000, Roth et al. 2007, Ivan and Shenk 2016, Szumski et al. 2023), including in Washington (Koehler 1990, Von Kienast 2003, Maletzke et al. 2008). Northern studies have suggested that hunting red squirrels from ambush beds is important for lynx when hares are scarcer (O'Donoghue et al. 1998*a*). Although direct inference about alternative prey is beyond the scope of my study, this management consideration is relevant in the southern range of lynx because of the persistently fewer hares (Hodges 1999*a*, Murray 2000). Management for lynx should still primarily focus on ample and accessible populations of hares because of their importance for lynx, but encouraging ambush features on the landscape should not be incompatible with providing access to alternative prey if lynx can use these features to hunt both hares and squirrels. Management planning that can provide similar access to alternative prey, specifically red squirrels, could help mitigate the negative effects of climate change on the lynx's dependence on hares (Peers et al. 2014).

2.4.8 Future directions

Forestry and wildlife habitat management practices continue to evolve, and, in light of human forest-harvest needs, novel or underutilized silviculture methods that promote high forest structure and horizontal cover on a shorter timescale than traditional approaches may warrant consideration. For example, a new method called adaptive complexity thinning (ACT) aims to accelerate the development of the multistory forest structure often preferred by hares and lynx as well as retain more short-term cover for hares compared to traditional pre-commercial thinning (Kumar et al. 2018, Larson et al. 2022). Interagency and cross-border cooperation will also be crucial for lynx persistence in the southern range, particularly with reintroduction efforts underway in other parts of the historic range of lynx in Washington (Kettle Range). Although lynx continue to persist and breed in small numbers in Washington, immigration from core lynx populations in BC will be a crucial factor in the resilience and long-term endurance of our local lynx populations (Murray et al. 2008, Interagency Lynx Biology Team (ILBT) 2013, King et al. 2020).

Advancements in measuring or predicting features that are important for lynx foraging on the landscape may also help overcome field collection logistical challenges. For example, obtaining understory structure (e.g., horizontal cover) data is challenging in the density of forests used by lynx and hares, but a combination of machine learning and terrestrial LiDAR shows promise for helping predict horizontal understory cover in lynx habitats from airborne LiDAR data (Batchelor et al. 2023), suggesting hope for better management of this crucial feature for lynx foraging. Perhaps these measures may also be used to help assess ambush features on the landscape, given that many of these features (e.g., often large, downed logs) are structurally denser than understory vegetation and potentially more detectible.

Forensic methods such as the predator identification from saliva used in my study to identify lynx kill sites are gaining traction (Wengert et al. 2014, Peelle et al. 2019, Ganz 2022) but remain underutilized in mesopredator studies. Such techniques continue to improve in their ability to detect trace DNA from predator saliva and could be applied in other systems to evaluate successful foraging behavior year-round for other elusive mesopredators, particularly those of conservation concern.

2.4.9 Conclusion

To my knowledge, this is the first study to evaluate successful foraging habitat for lynx in snow-free seasons and is among the few to provide fine-scale habitat selection data for lynx in the southern range across multiple seasons. Using reliable forensic techniques and prey-tracking, I identified where lynx killed hares on the landscape irrespective of snow conditions. To aid forest managers in prioritizing forest characteristics that support lynx hunting success, I assessed a comprehensive suite of habitat metrics. I used elastic net modeling to address issues of multicollinearity and small sample sizes, allowing for robust comparison of these metrics. This approach identified key variables that best predicted the patterns observed at lynx kill sites relative to available habitat: nearby ambush features, forest structural complexity, and categorical cover type, with horizontal cover in the understory also providing some explanatory power. The particular importance of ambush features underlines the value of considering unique microhabitat features that may enable prey access within areas of cover preferred by hares. More broadly, this study highlights the value of understanding behavior-specific habitat use that promotes fitness because animals do not necessarily utilize the landscape to their maximum benefit (Pulliam 1988), particularly in areas subject to rapid environmental change such as those impacted by human activity (Fahrig 2007, Goodenough et al. 2009, Goad et al. 2014, McConkey and O’Farrill 2015). Furthermore, models that incorporate fine-scale habitat data are more accurate than those at only coarser scales (Randin et al. 2009). Thus, knowledge of an animal’s specific activity patterns (e.g., foraging) in relation to the landscape can yield more detailed insights that can help land managers prioritize specific habitat for conservation and anticipate responses to anthropogenic change (Sutherland 1998). For lynx in the southern range, some next steps for conservation research efforts might explore the specific forest management techniques that would create or retain the fine-scale features facilitating foraging for lynx, particularly ambush features, forest structural complexity, and overall cover. Future studies may reveal important seasonal patterns in lynx foraging strategies.

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CHAPTER 3. Niche breadth predicts divergent patterns of successful foraging among mesopredators targeting snowshoe hares

3.1 INTRODUCTION

Competition is generally predicted to be higher among predators than at other trophic levels because they often compete for a shared prey resource (Hairston et al. 1960, Menge and Sutherland 1976). Intraguild competition among predators also may be on the rise because many generalists are increasing in abundance and geographic range (e.g., Roberts and Crimmins 2010, Hody and Kays 2018), owing at least in part to climate change and other anthropogenic impacts (e.g., Rød-Eriksen 2020). Thus, in areas with rich carnivore guilds, coexistence likely demands niche partitioning (Schuette et al. 2013, Sévêque et al. 2020). Where multiple predators compete for the same prey species, niche segregation can be achieved through variation in how, when, and where prey are targeted (Prugh and Sivy 2020, Rodriguez Curras et al. 2022). These differences in hunting approach may lead to predator-specific impacts on shared prey populations (Harmon and Andow 2004, Toscano et al. 2010, Emery and Mills 2020) and emergent multi-predator effects with implications for both prey and predator fitness and population demography (Sih et al. 1998). Accordingly, studies of intraguild variation in predator foraging behavior can contribute to our understanding of predator ecology and the conservation of both predator and prey populations.

Variation in predator foraging patterns, and thus where they successfully capture prey, may arise from differences in niche breadth, with generalist predators that exploit multiple prey species utilizing a wider range of resources than specialists (Grinnell 1917, Elton 1927, Hutchinson 1957). Alternatively, these foraging patterns might be influenced more strongly by predator traits, particularly hunting mode (hunting mode hypothesis; McLaughlin 1989). Ambushing and stalking predators, which attack prey from a stationary position or after moving undetected into close proximity (Preisser et al. 2007), should be more successful where the landscape provides for concealment (Matthiopoulos 2003, Hopcraft et al. 2005, Miller et al. 2015, Smith et al. 2020). By contrast, the hunting success of active or cursorial predators, which move continuously to find and then chase down prey, should be higher in relatively open environments that facilitate detection and pursuit (e.g. Preisser et al. 2007). Knowing whether predator foraging patterns are driven more by niche breadth or hunting mode can enhance our capacity to predict the outcome of competition for prey in multi-predator systems. Such predictive capacity is particularly important in systems with threatened or endangered predators.

The snowshoe hare (*Lepus americanus*) is a model prey species for examining differences in predation patterns. Throughout their range, this North American leporid is targeted by numerous predators (Litvaitis et al. 1985, Sievert and Keith 1985, Koehler 1990, Hodges 1999*a*, 2000), offering the opportunity to contrast the features of kill sites by varying predator species in a single geographic area. Hares are particularly important prey for Canada lynx (*Lynx canadensis*) (Poole 1994, Roth et al. 2007, Squires and Ruggiero 2007), which are classic specialists with narrow dietary breadth (Buskirk et al. 2000). Lynx are widespread across northern North America but are federally threatened in the contiguous United States (US Fish and Wildlife Service 2000) and have suffered range contractions and reduced genetic diversity along the southern boundary of their range (Bayne et al. 2008, Koen et al. 2014). Along the southern edge of lynx's range, two other similarly-sized mesopredators also target hares: bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) (Murray et al. 2008, Lavoie et al. 2009, Scully et al. 2018). There is limited direct evidence that bobcats and coyotes compete with lynx when foraging (e.g., Guillaumet et al. 2015, Morin et al. 2020). Yet, coyotes are highly dependent on hares where they are abundant (O'Donoghue et al. 1997), and both bobcats (e.g., Peers et al. 2013, King et al. 2021) and coyotes (Bayne et al. 2008) have been implicated in reduced presence of lynx, suggesting some degree of competition within this mesopredator guild. Moreover, natural and anthropogenic fragmentation (Buskirk et al. 2000) and climate impacts on snow quality (Gottlieb and Mankin 2024) are expected to raise the potential for competition between the snow-adapted lynx and the other two predators (Stenseth et al. 2004, Peers et al. 2013, Scully et al. 2018). No study to date, however, has contrasted the fine-scale habitat features these three mesopredators use to capture hares in areas where they co-occur.

These three mesopredators differ in dietary niche and hunting traits. Lynx are dietary specialists whereas bobcats and coyotes are generalists (Bekoff 1977, Azevedo et al. 2006, Marrotte et al. 2020). However, the typical hunting approach used by lynx and bobcats differs from that of coyotes. Namely, lynx and bobcats use both ambush and stalking hunting modes, typically only chasing for short distances; they appear to prefer ambushing at night or when sufficiently dense habitat is available (Murray et al. 1995, O'Donoghue et al. 1998*a*, Anderson and Lovallo 2003, Kolbe and Squires 2007, Squires and Ruggiero 2007, Menzies et al. 2022). In particular, lynx are less active than similarly sized mesopredators (Menzies et al. 2022) and, although lynx appear to adjust hunting modes based on available habitat, ambushing appears to be this felid's preferred hunting mode whenever possible (Murray et al. 1995, Menzies et al. 2022), and they may have greater success when ambushing (Murray et al. 1995; but see O'Donoghue et al. 1998*a*, who found no such difference). Similarly, bobcats are known to use dense understory vegetation to ambush and stalk prey (Anderson and Lovallo 2003). Conversely, coyotes are typically coursing predators (Husseman et al. 2003). By implication, predator-specific foraging patterns may distinguish lynx from the other two mesopredators if they are driven by niche breadth, or coyotes from the two felids if they derive more from hunting modes.

Few studies have been able to compare the habitat attributes of successful foraging sites for these three mesopredators, whose kill sites are difficult to find using methods that are often applied to larger carnivores, such as GPS-collar cluster analysis or direct observation, because of their shorter feeding durations (Vogt et al. 2018). Moreover, existing comparisons have been seasonally specific, having relied on snow tracking in winter (e.g., Maletzke et al. 2008). To address this knowledge gap, I collared and monitored snowshoe hares in an area with sympatric lynx, bobcat, and coyote populations, as well as other opportunistic hare predators in part of the lynx's southern range, the Cascades of north-central Washington, USA. I used forensic techniques to identify the responsible predator at hare kill sites year-round, obtaining the first known data on these predators' kill site habitat in snow-off seasons, and measured an array of habitat variables to allow for comprehensive multi-predator modeling to test two hypotheses explaining how their hunting patterns might group. Under the niche breadth hypothesis, I expected the specialist (lynx) to differ from the generalists (bobcats and coyotes), with lynx exploiting a narrower subset of habitat variables associated with high hare abundance such as high horizontal cover, regenerating forest, high stem density, and forest structural complexity, and bobcats and coyotes utilizing less cover overall and more heterogeneous habitat, including clearing and edge habitat types. Because they have higher footloads than lynx and are thus less able to navigate deep snow efficiently (Parker et al. 1983, Kolbe et al. 2007, Peers et al. 2013), I also expected bobcats and coyotes to make more hare kills during snow-off periods. Alternatively, under the hunting mode hypothesis, I predicted that lynx and bobcats should have better quality ambush features (e.g., a large downed log) at their kill sites than the coursing predator (coyote) because such features should facilitate concealment of the ambusher without hindering a quick transition from crouching into attack. Further evidence for the hunting mode hypothesis would include higher horizontal and understory cover at lynx and bobcat kill sites relative to those of coyotes.

3.2 METHODS

I conducted this study in the northeastern Cascades Mountains of Washington state, USA (48˚53’35”N, 119˚49’20”W), near the town of Loomis in the Loomis State Forest and Okanogan National Forest from 2010-2015. My study area (Chapter 2, Fig. 2.1) is located in the northern part of the Okanogan Lynx Management Zone (LMZ), where lynx are considered to have the best relative chance of long-term persistence in Washington under future climate-change scenarios (King et al. 2020). This region hosts a suite of other predators of hares, including bobcats, coyotes, Pacific martens (*Martes caurina*), cougars (*Puma concolor*), great-horned owls (*Bubo virginianus*), and northern goshawks (*Accipiter gentilis*). Elevation ranged from 1,383–1,932 m and land cover was characterized by mixed southern boreal forest dominated by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), with occasional Douglas-fir (*Pseudotsuga menziesii*), Sitka alder (*Alnus sinuata*), and western larch (*Larix occidentalis*). The region has experienced varying levels of timber harvest over time and is intersected by logging roads; it has also been subject to occasional wildfires, including one a century ago in part of the study area.

I selected three young (estimated 20-40 years) and three mature (estimated >75 years) boreal forest stands 17-20 ha in size for trapping hares. The six sites were selected based on minimum area of relatively contiguous habitat, site accessibility, and signs of hare use such as fecal pellets, hare runways, and browsing evidence. Young sites were typically denser than mature sites and were only chosen if their dominant canopy layer, which was even-aged lodgepole pines in all cases, was tall enough to provide cover for hares when deep snow would be present in winter. Mature sites were more variable but were typically multi-storied, although there was an area of mature, dense, even-aged lodgepole pine at the Daisy Creek site with less understory than was typical elsewhere. All sites were separated by at least one km to avoid dispersal from one stand to another (Wirsing et al. 2002*b*).

I captured hares using Tomahawk live traps (32” × 9” × 9” double-door, Tomahawk Live Trap Co., Tomahawk, WI, USA) baited with alfalfa pellets and covered with tree branches for camouflage and insulation. Sites were trapped on rotation, one at a time, typically at least twice in summer and at least once in winter. Trapping grids consisted of 40–50 traps spaced approximately 50 m apart from each other and roads and were set in the late afternoon or evening and checked in the morning. Trapped hares were weighed, sexed, identified as adult, subadult, or juvenile, sampled with a two-millimeter ear punch to collect a tissue specimen, ear-tagged through the sampling hole and in the other ear (No. 3, National Band and Tag Co., Newport, KT, USA), and measured for right hind foot length (a metric for structural size). I also equipped a subset of individual hares weighing at least 575 g with mortality-sensitive VHF radio-collars (Model M1565, 24 g, Advanced Telemetry Systems [ATS], Isanti, MN, USA) or GPS collars (Telemetry Solutions), keeping collar weight to <5% of total body mass (Cochran 1980); one additional hare weighing 550 g was fitted with a collar weighing 22 g. As time allowed, I also trapped partial grids if the number of functional radio-collars at a given stand became appreciably disproportionate compared to other stands. Hares recaptured within the same season were documented and released without processing. Hare capture and handling procedures were approved by the University of Washington Institutional Animal Care and Use Committee (IACUC) under protocol 4226-02 and consistent with standards for capture and handling of mammals (Sikes et al. 2011).

To monitor hares for mortality events, I attempted to detect frequencies from every deployed radio-collar at least three times per week, except in spring when site access was not possible because of snow melt conditions. A mortality event was identified when a collar emitted a double pulse (70 beats per minute) signal, which was activated after 8 hours of no movement. I typically detected a mortality within 24–72 hours of the last detected “live” signal and then used ground-based radiotelemetry to locate the mortality site. I assessed the specific kill site location and proximate cause of mortality by building upon methods described in Boutin et al. (1986) and based on tracks, a fur trail, amount of carcass or fur remaining, sub-dermal hemorrhaging, predator hairs, signs of a struggle (e.g., a light layer of fur), and mtDNA tests on predator saliva collected from the remains and radio-collar. Predator saliva swabbing and lab analysis for this technique were described in Peelle et al. (2019).

To compare the characteristics of kill sites attributes to different predators, I conducted habitat plots at each kill site. Although habitat plots generally could not be sampled the same day as the kill site was processed due to the time required for finding the kill site and subsequent forensic investigations, I sampled habitat plots within the same seasonal period in which the mortality occurred whenever possible. For a small number of spring kill sites, habitat plots could not be sampled until summer; however, these plots had minimal deciduous vegetation and the different season was therefore less likely to impact the measurements of horizontal cover.

I collected habitat data at kill sites at two scales: within a 5.64-meter radius plot (0.01 ha) and an assessment of overall stand attributes in and within the immediate vicinity of the radius plot (within an approximately 15-m radius of the center of the smaller radius plot). Variables measured included horizontal cover, canopy cover, number of stems and tree diameters within the plot, forest age, ambush quality, percent downed woody debris, structural complexity, dominant tree species by forest layer, and overall cover type (Table 3.1). I measured horizontal cover at half-meter intervals up to 2 m with a cover board and determined cover type by the amount of openness in the stand area containing the plot and ranked into categories from most open to least open (clearing, edge, semi-open, or cover). The minimum size threshold for a clearing was approximately 25 m^2 and at least 4 meters across. Roads also counted as clearings. Edge habitat was determined by whether the plot was at the edge of a clearing. Smaller (<25 m^2) clearings were called openings, and a mix of cover interspersed with openings constituted the semi-open cover type. Denser, relatively closed sites with few small openings were designated as "cover." When necessary, cover type was verified using plot photographs and year-specific aerial imagery. I also assessed if a plot was located at a habitat interface, denoting the presence or absence of a boundary between different-aged forests (e.g., regenerating and mature). The interface variable was assessed at a broader scale than cover type and distinct from the edge category of the "cover type" variable.

Table 3.1. Description of variables measured for habitat plots (fixed-radius plots and broader vicinity plots) at predator kill site locations and replicate plots. Note that perch quality variables were only included in the global (all predator) comparisons for the sake of raptors and were not utilized in the main analysis comparing the three mesopredators.

Variable Scale	**Variable**	**Description**
Fixed-radius plot (5.64 m radius; 0.01 ha)	Larger tree count	Count of trees >7.5 cm DBH, total and by species: lodgepole pine (*Pinus contorta*), Englemann spruce (*Picea sitchensis*), subalpine fir (*Abies lasiocarpa*), and snags
	Mean DBH	Mean diameter at breast height (DBH) of trees >7.5 cm DBH
	Basal Area	Basal area of trees >7.5 cm DBH
	Smaller tree count	# Stems (trees ≤7.5 cm DBH), total and by species: lodgepole pine, Englemann spruce, subalpine fir, sitka alder (*Alnus viridis*), Douglas-fir (*Pseudotsuga menziesii*), snags, and "other" (often *Salix* or *Populus* spp.)
	Cover Type	A general categorization of how open the habitat was within the plot, visually approximated in the field and finalized with aerial mapping measurements. Listed from most to least open: 1) Clearing (majority open and centered within a clearing, with a clearing defined as being both >25 m^2 total area and >4 meters minimum width) 2) Edge (edge of clearing >25 m^2 and >4 meters across) 3) Semi-Open (smaller openings [≤25 m^2] dominating ~>50% of plot) 4) Cover (cover dominant with few small openings)

	DWD	% downed woody debris (DWD) >7.5 cm diameter, visually estimated by stratifying the plot into 4 quarters
	Canopy	% canopy cover using a convex densiometer (averaged from 4 cardinal directions)
	Ambush Near	Presence and quality of ambush feature(s) within the plot, rated from 0-6; see text for details
	Perch Overhead	Presence and quality of raptor perch feature(s) above the plot center, rated from 0-6; see Supplemental S1 for details
	Perch Near	Presence and quality of raptor perch feature(s) within the plot, rated from 0-6; see Supplemental S1 for details
Plot vicinity measures (~15 m radius)	Horizontal Cover (4 variables)	CoverBoard Cover: Horizontal cover (% visual obstruction) measured using a checkered canvas coverboard in 4 cardinal directions (15-m radius) from center of plot, averaged for each 0.5-m increment of height from the ground, up to 2 m
	Distance to Cover	Distance from plot centroid to continuous cover (m); aerial mapping was used if cover was >15 m away
	Distance to Clearing	Distance to a clearing (defined as >25 m^2 total area and >4 meters minimum width) (m); aerial mapping was used to verify these measures
	Age	Forest age category (regenerating, mature, or mixed)
	Structure	Structural complexity represented by the presence and sparsity of combined overstory, mid-canopy, and understory forest layers, rated from 0-3, respectively (0=absent, 3=layer fully present) for a total max score of 9

Overstory	Rating for presence and sparsity of overstory (0-3; 0=absent, 1=very sparse, 2=sparse, 3=layer fully present)
Intermediate (mid-canopy)	Rating for presence and sparsity of intermediate/mid-canopy layer (0-3; 0=absent, 1=very sparse, 2=sparse, 3=layer fully present)
Understory	Rating for presence and sparsity of understory (0-3; 0=absent, 1=very sparse, 2=sparse, 3=layer fully present)
Forest Composition	Dominant tree species in the overstory, mid-canopy, and understory forest layers, respectively, recorded in the field and later assigned to a tree community category based on association using hierarchical cluster analysis; see statistical methods for details
Ambush Far	Presence and quality of ambush feature(s) beyond the plot, rated from 0-6; see methods for details
Perch Far	Presence and quality of raptor perch feature(s) beyond the plot, rated from 0-6; see Supplemental S1 for details
Interface	Whether the plot was situated at or adjacent to a habitat interface, typically between young and mature forest

I determined the ambush quality of a site based on presence of a feature or features that would conceal a medium-sized terrestrial predator such as lynx (both near [<6 m] and far [>6 m], rated by quality) and allow the predator to leap over the feature providing the concealment. Ambush features typically consisted of large, downed logs or boulders, sometimes of piles of smaller logs, and occasionally low, dense shrubs. Trees were not considered in this metric because they were already being measured directly and were deemed to not facilitate predator access as much as features allowing the predator to crouch, peer over the feature with minimal exposure, and quickly jump over it. Ambush quality was rated on a scale of 0-6 based on (1) the degree to which the ambush feature would obscure the predator from prospective prey, (2) distance, (3) slope, and (4) line of sight. For example, an ideal ambush feature would be upslope of the kill site epicenter, with little vegetation obscuring the line of sight, with the crouch spot behind the feature being within a few meters of the kill site, and with the feature being low enough to leap over easily but high enough to hide a crouching lynx. Features that were more spread out were rated less highly. For example, a single large log was often an ideal ambush feature because the steep drop-off on the backside reduced the distance between the crouch spot and potential prey, as illustrated by this examples of typical ambush features in the study area (Fig. 3.1).

Figure 3.1. Illustration of an example ambush feature on the landscape as characterized in this study. Features offering high visual obstruction for a medium-sized predator while being relatively low to the ground received a maximum quality rating at hare mortality sites because of providing both cover and access to prey. Summer version of illustration. Credit: Jack DeLap.

3.2.1 Statistical analyses

To determine whether predator species differed in habitat attributes at sites where they killed hares, I performed a global multivariate test for overall between-group differences among the suite of predators, followed by more targeted comparisons among the three most prevalent predators (lynx, bobcats, and coyotes) to address whether their kill site attributes aligned more with the niche breadth or hunting mode hypotheses. After standardizing the predictor variables (“decostand” in R package *vegan*), I created a dissimilarity matrix (“vegdist” in R package *vegan*; Oksanen 2022) using a Bray-Curtis index, chosen for its ability to handle different data types (e.g., community composition, count, and proportion data) without inflating similarity from tied absences (Faith et al. 1987), its general ability to handle zero values (Jari Oksanen 2022), and its robust ability to detect differences using ANOSIM (M. J. Anderson 2001). To visually assess the combined influence (among all predators) of the habitat variables, many of which are correlated, I used a dimension-reduction method and created unconstrainted ordination plots using non-metric multidimensional scaling (NMDS; “metaMDS” in R package *vegan*). I then plotted 95% confidence interval ellipses for each predator species grouping in this 2-dimensional space using R packages *ggpordiplots* and *ggplot2*. Because a primary purpose of this NMDS ordination was for illustrative purposes, only two dimensions were calculated. I assessed goodness of fit by checking if stress values with this number of dimensions were below acceptable levels (e.g., <0.1; Clarke 1993) before proceeding (“dimcheckMDS” in R package *goeveg*).

I anticipated a substantial amount of overlap in kill site habitat features among the predators of hares because this analysis was restricted spatially to habitat types already selected for by hares (i.e., predation patterns were inferred from investigation of kill sites of hares caught and tagged in areas with resident hare populations). Thus, I selected an omnibus modeling method that could assess differences between groups attributable to not only mean differences but also dispersion, given that differences in dispersion could suggest more support for the niche breadth hypothesis. To test whether a predator’s ecological niche breadth relates to its foraging habitat, I performed an analysis of similarity (ANOSIM) (“anosim” in R package *vegan*) with 9999 permutations on the habitat variables at kill sites attributable to lynx, bobcats, and coyotes.

ANOSIM is a non-parametric multivariate technique that compares the differences between groups (defined *a priori*) and within groups using ranked dissimilarities (Clarke and Green 1988). In concept, ANOSIM is similar to an ANOVA, using a ranked dissimilarity matrix instead of raw data. The test statistic (R) for an ANOSIM is calculated as follows:

$$R = \frac{r_B - r_W}{M/2}$$

where r_B is the average of rank similarities between groups, r_W is the average of rank similarities within groups, and M is $n(n-1)$, with n being the number of samples. The resulting R statistic from an ANOSIM ranges between -1 to 1 and is calculated as the ratio between sites within a group and sites in different groups (with groups being predator species in this study). The significance of the R statistic is attained by permuting the membership of sites in groups. One benefit of this method is that it compares all groups instead of only comparing each group to a reference group (i.e., with a multinomial regression model). An ANOSIM has fewer assumptions than other group-comparison methods such as PERMANOVA because it is rank-based (Paliy and Shankar 2016, Somerfield et al. 2021), which I deemed preferable for my diverse set of habitat variables. After assessing whether there was a significant difference between groups, I then used pairwise ANOSIM to assess whether the two generalist predators (bobcats and coyotes) differed from each other or from the specialist predator, lynx. I then tested the competing hypothesis, that the three mesopredators aligned more by hunting mode, as evidenced by the two felids having more similar kill site habitat to each other than to coyotes. Finally, I used SIMPER (similarity percentages using Bray-Curtis dissimilarities; Clarke 1993) in the R package *vegan* to assess which specific habitat variables resulted in the differences observed among pairwise sets of mesopredators.

SIMPER results are reported based on significance and not by specific percent contribution because that measure is more appropriate for simply comparing species for community composition purposes, in which all species measured would add up to 100%, unlike the diverse habitat variables included in this study. Variables found to differentiate the mesopredators were further explored with probability density plots to visualize the pattern of differentiation across the measurement gradient, or with bar plots for categorical variables.

3.3 RESULTS

A total of 375 snowshoe hares were captured in 707 trap events, of which 356 were ear-tagged and 223 were affixed with radio-collars at least once. A total of 247 habitat plots were surveyed at 91 kill sites attributable to any predator.

Predator species were identified at 66 of the 91 kill sites: lynx (*n* = 24), bobcat (*n* = 13), coyote (*n* = 11), raptors (including great-horned owl and northern goshawk; *n* = 10), Pacific marten (*n* = 5), and cougar (*n* = 3). An additional 25 mortalities were verified as kill sites but had insufficient evidence to definitively attribute the responsible predator. Lynx kills were present at all 6 forest stands in this study. There were both bobcat and coyote kill sites 4 of the stands, and the other two stands had kills attributed to at least one of the generalist mesopredators.

The global comparison of kill site habitat across all predators found them to differ significantly overall (ANOSIM R statistic 0.177, *p* = 0.002; Fig. 3.2), and an NMDS ordination plot revealed some differences among predator centroids as well as dispersion among the predators (Figs. 3.3 & 3.4).

The main analysis to address the study hypotheses, which were the multivariate comparisons among only the three mesopredators, revealed significant differences between lynx and coyotes (*R*= 0.335, *p* = 0.0009) and between lynx and bobcats (*R* = 0.298, *p* = 0.0003) but found no significant differences between bobcats and coyotes (*R* = -0.0616, *p* = 0.919) in overall kill site habitat attributes. The SIMPER analysis found several habitat variables significantly distinguishing lynx from both bobcats and coyotes, with lynx kill sites having more nearby ambush features (Fig. 3.5a), greater forest structural complexity (Fig. 3.5b), more cover (per cover type category) (Fig. 3.6), more snow presence (Fig. 3.7), and horizontal cover at a height of 0.5-1 m (Fig. 3.5g) relative to the generalists. Lynx further differentiated from bobcats in having lower DBH at kill sites. Coyotes had more horizontal cover at 0-0.5 m, canopy closure, and mid-canopy layer presence than lynx kill sites. However, no habitat variables significantly distinguished bobcats and coyotes (Table 3.2).

*Table 3.2. Habitat variables assessed using SIMPER analysis for contributions to dissimilarities between lynx, coyotes, and bobcat kill sites. Variables contributing significantly to dissimilarities between these grouped predators are shown at the top and bolded, those approaching significance are shaded in light gray and italicized, and non-significant variables are shaded in darker gray. The horizontal dotted line below the first five variables denotes which significantly discriminated lynx kill sites from both bobcats and coyotes. "Lynx Use" indicates whether lynx had a positive, negative, or neutral relationship with a variable relative to the other predators; this is only reported for variables significant or approaching significance per SIMPER analysis results with 9999 permutations. P-value significance codes: '**'=<0.01, '*'=<0.05, ' . '=<0.10*

Lynx + Coyote	Lynx Use	Lynx + Bobcat	Lynx Use	Bobcat + Coyote
Forest Structure**	+	**Forest Structure***	+	
Cover Type**	+	**Cover Type***	+	
Snow*	+	**Snow****	+	
Ambush Near*	+	**Ambush Near***	+	
Horiz. Cover 0.5-1m*	+	**Horiz. Cover 0.5-1m***	+	
Horiz. Cover 0-0.5*	+	**Mean DBH***	–	
Canopy Closure*	+			
Mid Canopy Layer*	+			
Mean DBH .	-	*Forest Composition .*	*n/a*	
Trees >7.5cm DBH .	-	*Ambush Far .*	+	
Understory .	+	*Canopy Closure .*	+	
		Overstory .	+	
		Mid Canopy Layer .	+	
		Horiz. Cover 1-1.5m .	+	
Ambush Far		Basal Area		Ambush Qual. Near
Basal Area		Horiz. Cover 0-0.5m		Ambush Qual. Far
Horiz. Cover 1-1.5m		Horiz. Cover 1.5-2m		Basal Area
Horiz. Cover 1.5-2m		Forest Age		Canopy Closure
Forest Age		Habitat Interface		Horiz. Cover 0-0.5m
Forest Composition		Trees >7.5cm.DBH		Horiz. Cover 0.5-1m

Habitat Interface Overstory Trees ≤7.5cm DBH Woody Debris		Trees ≤7.5cm DBH Understory Woody Debris		Horiz. Cover 1-1.5m Horiz. Cover 1.5-2m Cover Type Forest Age Forest Composition Forest Structure Habitat Interface Mean DBH Mid Canopy Layer Overstory Snow Trees >7.5cm DBH Trees ≤7.5cm DBH Understory Woody Debris

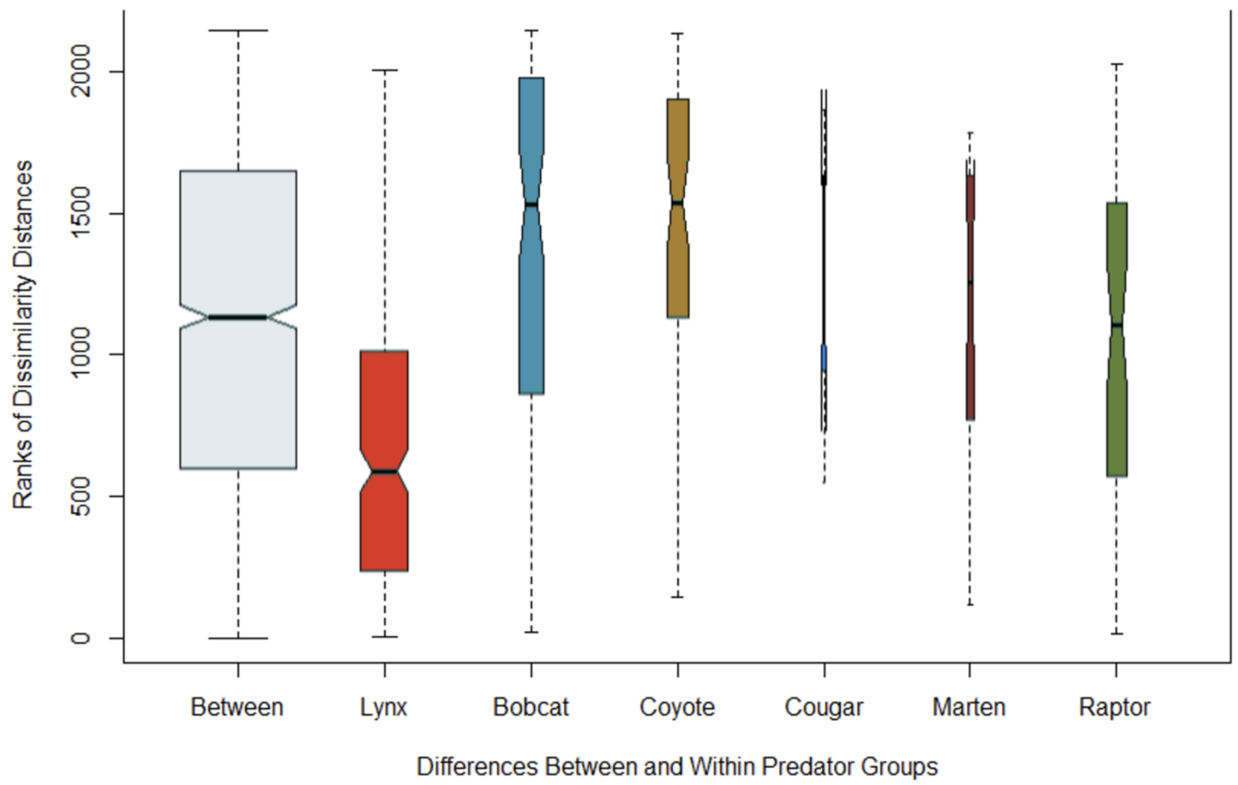

Figure 3.2. ANOSIM (Analysis of Similarities) box and whisker plot showing the relative within-group dissimilarity for each predator species compared to overall between-group dissimilarity. Lynx show the least within-group dissimilarity relative to the other predators, as indicated by the lower dissimilarity rank. Box width indicates per-predator sample size.

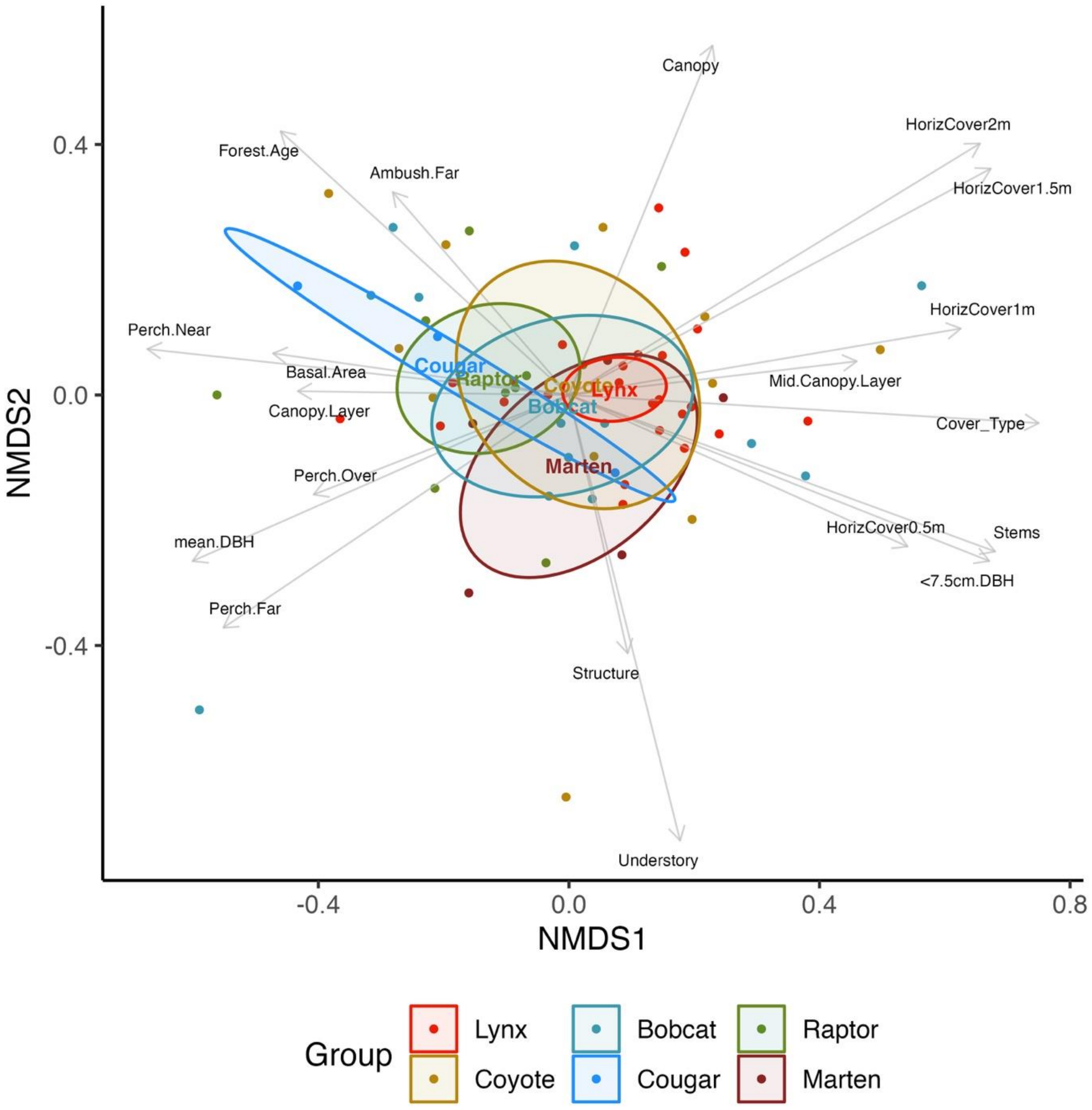

Figure 3.3. Global non-metric multidimensional scaling (NMDS) ordination plot showing the multivariate influence of habitat variables at all predator kill sites. Lynx used a narrower range of habitat features than the other predator species.

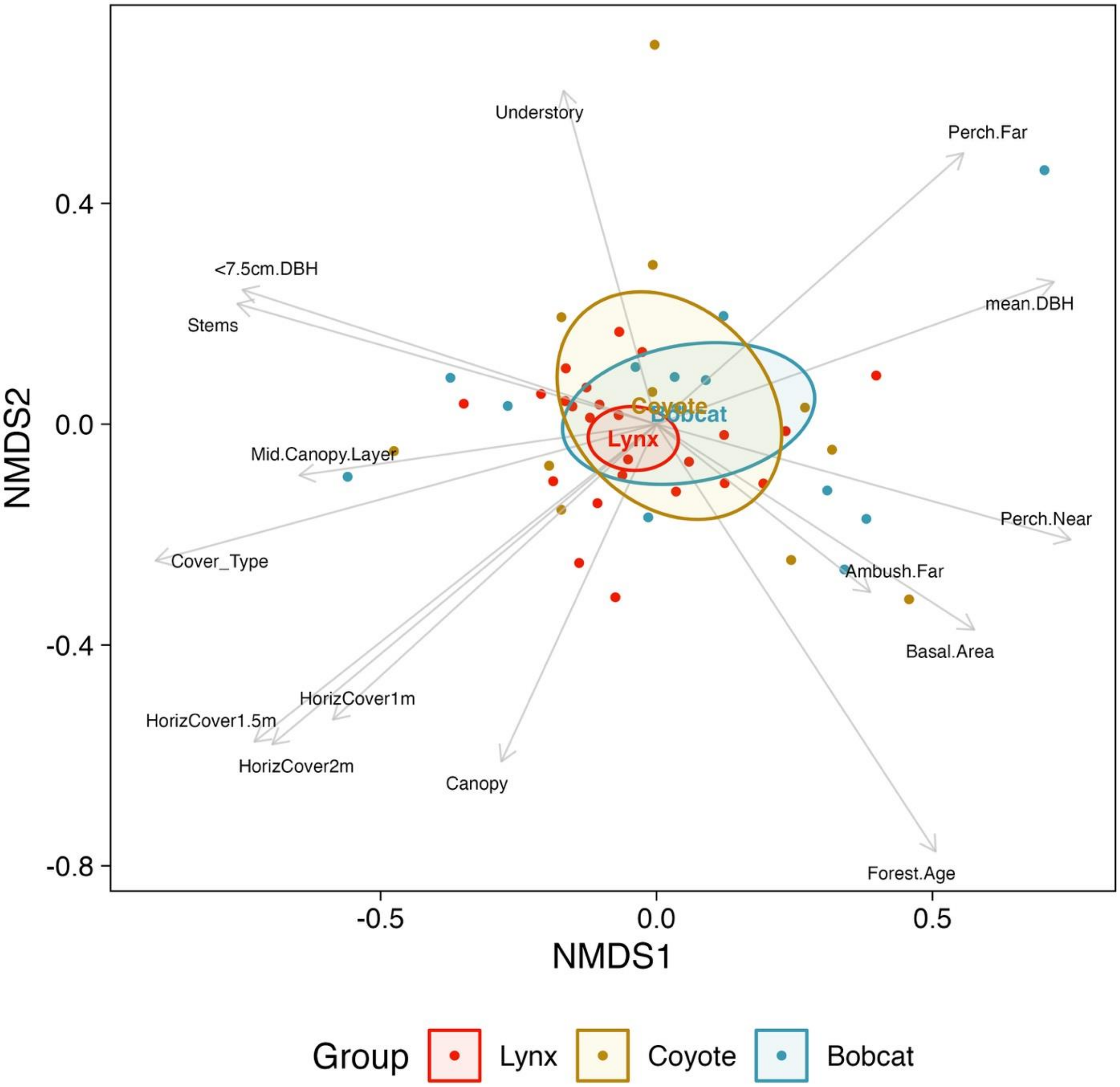

Figure 3.4. Non-metric multidimensional scaling (NMDS) ordination plot showing the multivariate influence of habitat variables at kill sites of the three mesopredators (lynx, coyote, and bobcats).

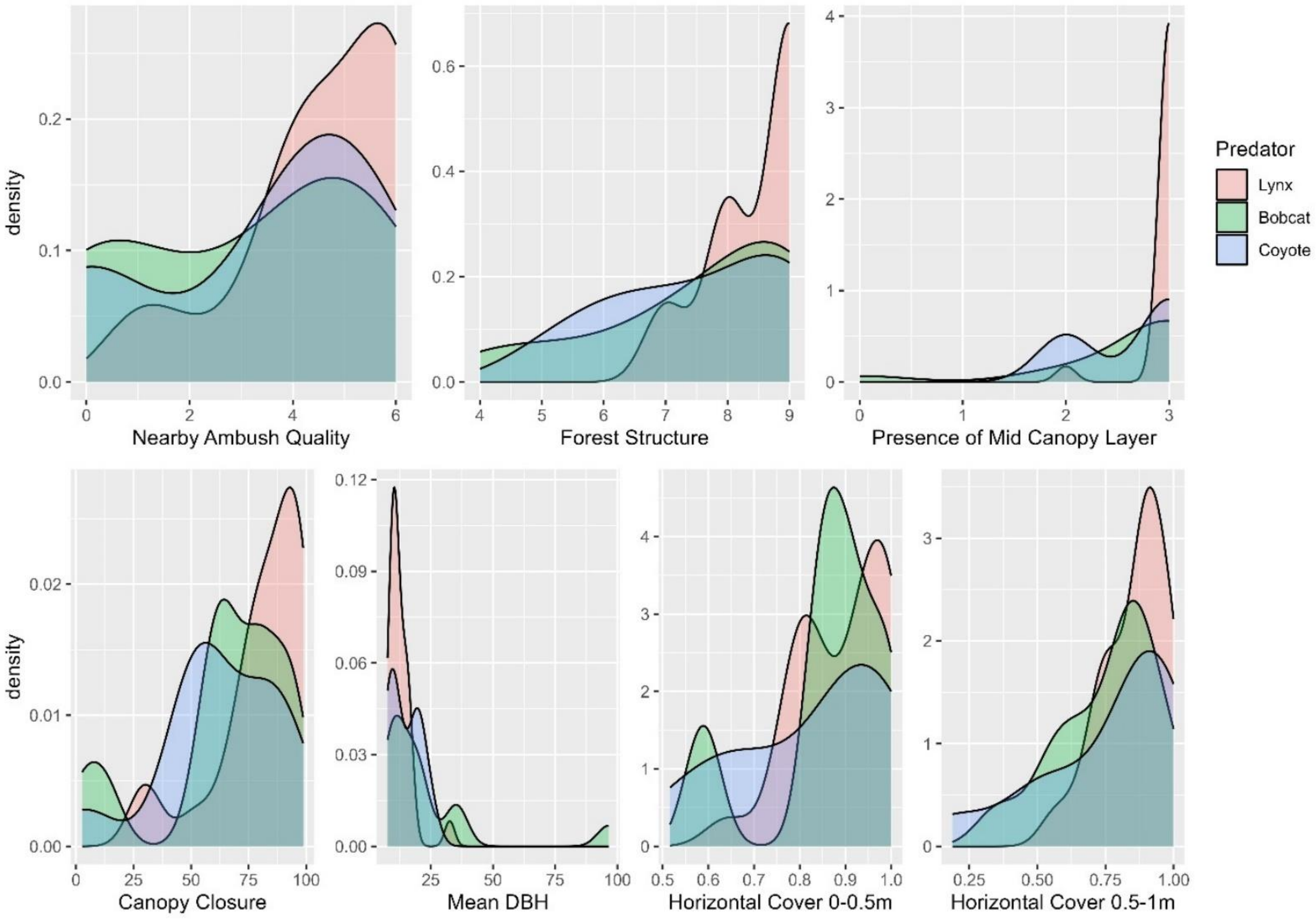

Figure 3.5. Density plots illustrating the distribution of the top numeric habitat variables that distinguished lynx kill sites from those of bobcats, coyotes, or both of these generalist predators. None significantly distinguished bobcats from coyotes. Variables included: (a) nearby ambush feature quality (features that could obscure a mesopredator but were low enough to leap over); (b) amount of forest structure (multilayered canopy); (c) presence of an intermediate (mid) canopy layer; (d) canopy closure; (e) mean diameter at breast height (DBH); (f) horizontal visual obstruction at 0-0.5 m; and (g) horizontal visual obstruction at 0.5-1 m.

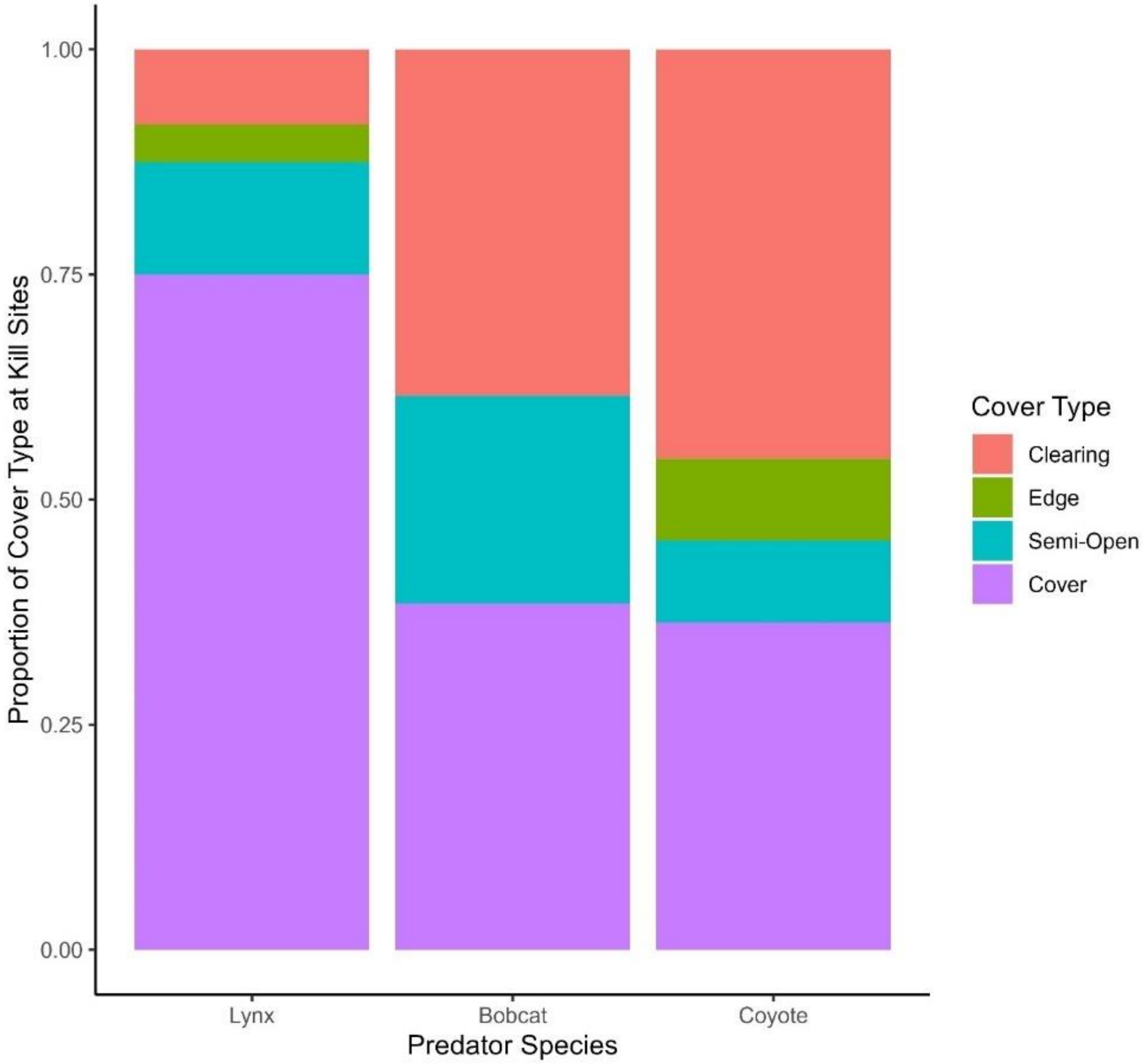

Figure 3.6. Proportion of snowshoe hare kills by cover type for the 3 main predator species predator species (lynx, bobcats, and coyotes).

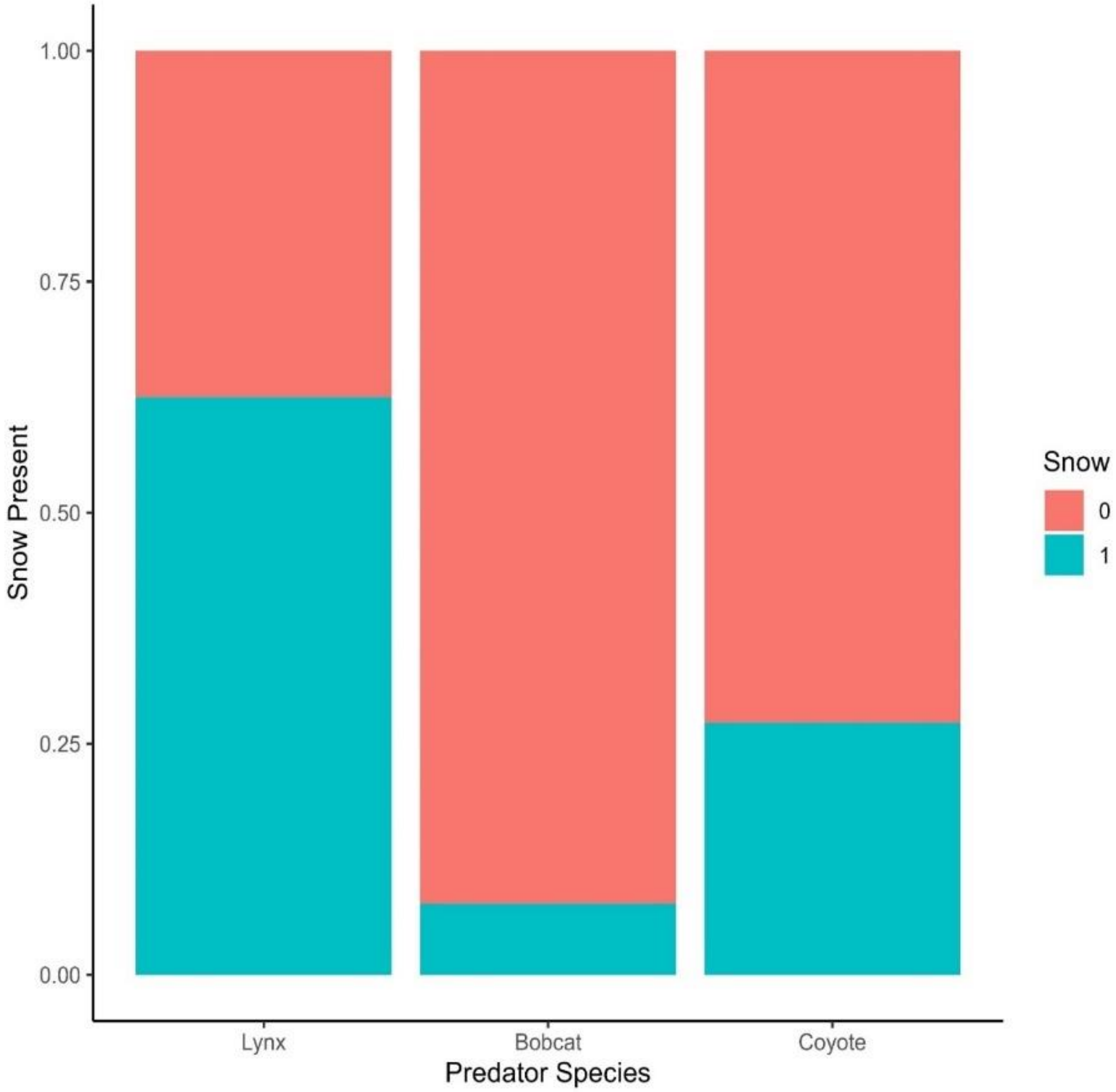

Figure 3.7. Proportion of snowshoe hare kills by snow presence/absence for the three main predator species (lynx, bobcats, and coyotes). Snow presence was defined as measurable snow of a depth ≥ 4cm.

3.4 DISCUSSION

My study found stronger support for the niche breadth hypothesis compared to the hunting mode hypothesis in a mesopredator-snowshoe hare system. Characteristics of lynx kill sites were distinct from those of two generalist predators, bobcats and coyotes, whereas no variables arose as significantly distinguishing coyotes and bobcats. The kill site habitat variables that contributed the most to differences between lynx and the two generalists were forest structure, cover type, snow presence, nearby ambush feature quality, and horizontal cover at 0.5-1 meters, all of which indicated greater structural complexity and cover at lynx kill sites compared to those of bobcats and coyotes. Additional variables that significantly distinguished lynx from coyotes were the presence of a middle (intermediate) canopy layer, percent canopy closure, and horizontal cover at 0-0.5 meters, which were all higher for lynx. A relatively low mean DBH also significantly distinguished lynx from bobcats. Lynx generally made successful snowshoe hare kills at locations with habitat features tending to support higher hare abundance (e.g., sites with more cover), although some variables often associated with the highest hare densities (regenerating forest and higher stem density) were not significant. This trend suggests that lynx are either differentiating themselves from competitors by their specialization more than their hunting mode, or that bobcats in this system have diverged from their traditional role as ambush predators by generalizing and using a wider range of habitats compared to lynx. My findings overall supported a niche breadth hypothesis because the generalists diverged from lynx by having greater habitat heterogeneity at kill sites, which largely aligns with expectations from studies at a coarser habitat-use scale. For example, bobcats have more heterogeneous habitat-use characteristics than lynx (e.g., Farrell et al. 2018, Marrotte et al. 2020).

Studies focusing on single predators in multi-predator systems often inadequately capture the functional roles played by these species, which could provide inaccurate representations of prey vulnerability on the landscape (Kohl et al. 2019). Although the findings of my study align with expectations of lynx as a specialist and bobcats and coyotes as generalists (O'Donoghue et al. 1997, 1998*a*, Mowat and Slough 2003, Roth et al. 2007, Peers et al. 2012) in the southern range, it appears that these three predators are competing for resources rather than avoiding competition through niche differentiation. Lynx were often catching hares in similar habitat to the other two predators, with differences arising primarily from lynx use of a narrower subset of these habitat features. An important implication of this narrower but overlapping range of habitat features used by lynx is that competition may not be alleviated by niche partitioning. Thus, to mitigate this competition and maintain viable lynx populations in areas with coyotes and bobcats, it may be necessary to ensure ample amounts of the habitat that favors successful lynx kills.

The importance of ambush quality for lynx in this study highlights that hypotheses based on roles of generalist/specialist or ambushing/coursing predator can result in overlapping predictions. Ambush predators make fine-scale habitat-use decisions, targeting their habitat use specifically based on the likelihood of encountering prey (Rosenzweig 1966, Husseman et al. 2003). Lynx targeted higher-quality hare habitat (e.g., selecting for cover over more open habitat types, more horizontal cover) compared to the two generalists, demonstrating their specialization on hares, but a clear selection for ambush features suggests the importance of ambushing behavior in lynx, as has been shown in some northern (Murray et al. 1994, 1995, O'Donoghue et al. 1998*a*) and southern (Von Kienast 2003, Maletzke et al. 2008) winter studies on lynx foraging behavior. Coyotes rarely ambush (Murray et al. 1995, O'Donoghue et al. 1998*a*, 2001). However, the low importance of ambush feature quality for bobcats was unexpected. Indeed, bobcats were the “swing player” in this study because the hypotheses that coyotes would be acting more as coursers or as generalists resulted in many overlapping predictions, similar to lynx overlapping their roles as specialists and ambushers. Bobcats differed from typical felid behavior, at least compared to lynx, particularly by using less-dense habitat and not targeting ambush features, which suggests not only a broader niche for bobcats but also niche differentiation between the two felids in this shared system. Possible explanations could include the availability of alternative prey, bobcats having reduced success when hunting in preferred hare habitat or when using ambush features (McCord 1974:197), avoidance of lynx, or some combination thereof.

The difference in cover type among the three mesopredators, though aligning with expectations for niche differentiation, was nonetheless surprising because all of the hare kills must, by definition, occur within hare habitat, and hares predominantly select for cover (Litvaitis et al. 1985, Hodges 1999*a*, Griffin and Mills 2007, Lewis et al. 2011, Jensen 2020). Nonetheless, foraging opportunities or flushing by a predator may cause hares to expose themselves. In either case, most of the features differentiating lynx kill site habitat in this study, including cover type and percentage horizontal cover, were comparatively more similar to preferred hare habitat. Although maximum horizontal cover would likely hinder lynx access to hares (see Chapter 2 of this dissertation), considering that lynx are highly visual hunters (Parker et al. 1983, Murray et al. 1995, O’Donoghue et al. 1998*a*), moderately high cover may offer the best combination of accessibility and hare abundance for lynx (Fuller et al. 2007, Ivan and Shenk 2016). Although more cover might be expected to be similarly beneficial for the congeneric bobcat (Anderson and Lovallo 2003), some evidence suggests otherwise. In a study in Massachusetts, bobcats were shown to target areas of high hare abundance, although they were not particularly successful at making kills in the denser forest supporting more hares, despite frequently making ambush beds there (McCord 1974), thus highlighting the importance of understanding not just where predators attempt to hunt but where they succeed.

The generally higher abundance of hares in dense, regenerating stands of lodgepole pine (Walker 2005) led to expectations that lynx, as the hare specialist, would make significantly more kills in this younger forest type, but this pattern was contrary to my findings that forest age did not differentiate lynx kill sites from those of bobcats and coyotes. Although lynx caught hares in higher cover compared to the generalists, they may still have been hindered from accessing the densest (i.e., regenerating) forest, which would explain why nearly half of lynx kills occurred in mature forest. Indeed, the higher forest structure favored by lynx was a measure of multi-storied forest, which is usually mature forest (Liira et al. 2011) and which may have provided horizontal cover for stalking and ambushing without the hindrance of densely packed tree trunks. Although there was no significant pattern in forest age at the kill sites, it should be noted that the study was set up to sample (trap) hares relatively evenly from both mature and young stands, which could have dampened any forest age effects. Forest age at the kill site was usually the same as the stand age, although there was some disparity in this pattern by stand type. Hares killed by the three mesopredators were sometimes (35%) in adjacent mixed or mature forest, despite the hare originating from a regenerating stand. The reverse was not true; hares originating from mature stands were almost always captured by the mesopredators in mature forest and rarely (14%) in mixed or young. Whereas this disparity might be related to what was available in the surrounding habitat, it could suggest that accessibility in the dense regenerating stands may have reduced the ability of lynx and the other predators to successfully catch hares. Given that hare density in Washington is typically highest in the regenerating stands with the highest stem density (Koehler 1990, Walker 2005, Jensen 2020), lynx should have demonstrated a clear pattern of catching hares in that habitat if accessibility was not an issue. Instead, 67% of lynx kills occurred in mature or mixed forest, with only 33% kills in regenerating forest, which aligns with other studies in the western US that demonstrated lynx use of mature forest when hunting hares (Squires et al. 2010, Ivan and Shenk 2016) but not a strong selection for forest age in either direction (Maletzke et al. 2008). A clearer pattern of lynx killing hares in a different forest age type than competitors would have simplified stand-level management guidance from my study. Nonetheless, mature habitat was more important than expected for lynx, and a mosaic of forest age types might sustain lynx populations in the face of foraging competition, so long as they provide adequate hares and prioritize the fine-scale features that distinguished lynx kill sites from those of bobcats and coyotes.

The seasonal difference between lynx and the two generalists has notable implications. Competition with lynx by bobcats and coyotes was higher in the snow-off season, which constitutes a substantial length of time as the periods of persistent, deep, and fluffy snow—the primary competitive advantage for lynx (Murray and Boutin 1991, Ruggiero et al. 1999, Stenseth et al. 2004)—continue to shorten with climate change (Gottlieb and Mankin 2024). Bobcat kills were particularly infrequent during winters in my study. Few studies have compared bobcat and lynx kill site habitat, which is the finest-scale measure of habitat use because it entails the successful procurement of food (Johnson 1980), and none appear to have done so beyond snow-on seasons. Nevertheless, snow conditions have been shown to influence where these two felids use the landscape (Siren 2020), which includes efforts to forage for prey. Studies of winter habitat selection in Ontario found that lynx and bobcats were segregating at a broader scale but selected for similar fine-scale habitat features (Marrotte et al. 2020, Morin et al. 2020). However, as these studies occurred in winter, the spatial segregation might be expected because of the bobcat's higher footload hindering access in deep, uncompacted snow at higher elevations (Peers et al. 2012, Gooliaff and Hodges 2018, Marrotte et al. 2020, Morin et al. 2020). Indeed, bobcats and lynx exhibit greater spatial overlap in snow-off seasons (Scully et al. 2018), suggesting that competition for prey may be higher during that time. More studies have been done on coyotes in lynx habitat because of greater sympatry, because they are more abundant are less geographically limited by snow

Some of the results of this study align with prior lynx-specific findings in Washington. In an intensive snow-tracking study, Maletzke et al. (2008) found that lynx killed hares less often than expected in openings compared to boreal forest cover, which matches my finding that most lynx kills occurred in cover. Lynx in that study were targeting stands with higher hare abundance, which was in areas with higher understory (Walker 2005). However, Maletzke et al. (2008) also found that lynx exhibited foraging behavior (increased sinuosity) with more intermediate values of understory cover, suggesting that accessibility in the densest habitat may be a hindrance for lynx. Although ocular approximations for understory and overstory cover were only nearing significance in my study, the combined variable of overall forest structural complexity (multi-layer) was highly important for differentiating lynx and the generalists. Furthermore, horizontal cover in the understory, as measured by a coverboard (a more standardized measure), was found to differentiate lynx from both bobcats and coyotes in my study. Maletzke et al. (2008) also found that lynx hunting behavior increased with moderate to high overstory cover, which was not strongly differentiating on its own for lynx kill sites in my study compared to the generalists, although canopy closure was among the measures that significantly differentiated lynx from coyotes in my study. In other regions of the intermountain west, lynx have been shown to catch hares in higher horizontal cover and more forest structure (Squires et al. 2010). This study thus expands on evidence of the importance of forest structure for lynx foraging habitat in WA, contributes several additional habitat metrics that could be used by wildlife managers, and provides novel kill site data for lynx and other predators beyond winter season.

This study faced several limitations, particularly the difficulty in positively identifying the responsible predator at many of the kill sites. My crew and I reduced the risk of erroneous predator identification with frequent monitoring, but I recognize the small possibility that a hare at an older kill site died of another cause and was scavenged, although this is relatively rare for hare kill sites, and when it does occur, it is usually not for several days (Peers et al. 2020). Most kill sites retained in the dataset were forensically surveyed within a few days of the last time a live signal was detected from the hare, and there were no instances of multiple primary predator species being detected from saliva swabs in this study (Peelle et al. 2019). Furthermore, although there is little in the wildlife literature on the topic, human forensics research suggests that the first individual to deposit saliva is typically the primary source of salivary DNA, even after contact with subsequent saliva deposition sources (Warshauer et al. 2012) which makes it unlikely that the only predator detected was a secondary visitor to the kill site. Lastly, the selection of trapping stands for the hares tracked in this study was limited to those that were relatively accessible by logging roads rather than more contiguous swaths of forest. This fragmentation could have increased winter access by coyotes into my study area because of snowmobile trail compaction (Bunnell et al. 2000, Kolbe et al. 2007), and I anecdotally observed coyote use of snowmobile trails on multiple occasions. Nonetheless, coyotes using compacted snow trails to access lynx habitat in snow-on seasons should have increased the similarity of coyote and lynx kill site habitat use as opposed to exaggerating differences. This suggests that my findings may be more conservative than in a study with less-disturbed lynx habitat. I was unable to select trapping stands in the most contiguous forest areas (primarily mature spruce) occupied by lynx in the vicinity (Supplemental S1). However, there are few remaining areas in the southern range of lynx without fragmentation (Buskirk et al. 2000, Koehler et al. 2008, Murray et al. 2008, Vanbianchi et al. 2018), making my study area overall representative of typical landscapes occupied by lynx.

Understanding the differences in how southern boreal forest predators hunt for hares will be important for conservation of the endangered lynx, particularly because lynx are anticipated to have reduced dispersal capacity in the face of climate change compared to coyotes and bobcats (Schloss et al. 2012). Specialist species are predicted to be more sensitive than generalists to climate change and associated changes in biotic interactions (Gilman et al. 2010). Forecasts for the future of the snow-adapted lynx in the southern range in the face of climate change have often been dire (e.g., Robbins 2017), and some studies have found broad-scale evidence that competition with coyotes and bobcats may further limit lynx along the southern range boundary (e.g., Sirén et al. 2021). Increased competition for hares could not only directly reduce hare populations for lynx, but the increased presence of generalist predators on the landscape could also have non-consumptive effects on hares because these generalists may hunt more diffusely on the landscape, and the constant exposure risk could increase stress levels in hares (Hik 1995, Boonstra et al. 1998, Sheriff et al. 2009*a*, Lavergne et al. 2021), thus reducing fecundity and population growth and impacting the food source for lynx. However, despite these challenges, it may be possible to give this federally threatened species more of a comparative advantage by managing for the key habitat features that differentiate where lynx are successfully capturing hares. It is likely that the two generalists are less adept at catching hares in the narrower range of habitat features I observed lynx using, particularly in winter. Understanding how these predators differ in where they catch prey can facilitate better habitat management for lynx, enabling them to leverage their full competitive advantage when hunting hares, in the face of climate change and other anthropogenic impacts. More research would be needed to address some of these potential implications of competition with generalists, but identifying explicit habitat differences in where these competing predators are catching hares is an important step in understanding the ecological roles and niche breadths of these predators.

Lynx experienced resource competition with other predators in my study area as well. The hypotheses of this chapter are focused primarily on bobcats and coyotes as they compared with lynx in part because other predators were expected to have more complex or fluctuating roles as hare predators in the southern range, particularly in their relative niche breadth. However, the importance of the other predators should not be disregarded, given potential implications for lynx from competition with this entire cohort of hare predators in the southern range (Hodges 1999*a*, Buskirk et al. 2000) and given the general paucity of reliable data on predator species-specific kill sites in southern lynx ecosystems. While only possible to explore descriptively, raptors were the most common hare predators implicated in this study aside from the three focal mesopredators (lynx, bobcats, and coyotes), with great horned owls often deemed the likely raptor species from suggestive evidence (e.g., relative size of raptor wing marks, anecdotally being the most commonly observed raptor in the study area, being photographed with hare remains on a local trail cam [S. Fisher, pers. comm.], etc.), as well as an incident with clear evidence for lethal interference competition between a great horned owl and lynx. Specifically, a lynx with kittens confiscated a hare from a great horned owl in winter, killing the owl and leaving it uneaten after the lynx family consumed the hare (see Supplemental S3 for forensic details). While anecdotal, such unique interactions are rarely observable, and this instance is worth mentioning in light of collective evidence for raptors, particularly great horned owls, being major predators of hares in both northern and southern hare populations (Hodges 1999*a*, 2000, Krebs et al. 2001) and potentially contributing to the stabilizing effects of generalist predators on southern hare populations. Evidence for great horned owl niche breadth is mixed, with great horned owls in more northern populations periodically specializing on hares as they become more abundant (Houston 1987, Boutin et al. 1995, Rohner 1995, 1997), with delayed density dependence (Boutin et al. 1995, Rohner 1997). The functional role of great horned owls in southern range areas is murkier, with great horned owls exhibiting highly variable niche breadth across geographic regions and seasonally (Donázar et al. 1989), making their contributions to multi-predator effects in the southern range difficult to predict. Nonetheless, this unique observation captured a rarely observable instance of interference and resource competition between lynx and great horned owls, although it is unlikely that the owls would exert negative impacts by reversing this interference competition on (i.e., by initiating an attack on) an adult lynx (Buskirk et al. 2000), considering their size difference. Rather, the potential for great horned owls or other raptors to be competing with lynx cannot be ruled out, particularly given the difficulty of reliably identifying raptors to species at hare kill sites in this study.

3.5 CONCLUSION

This study found stronger support for the niche breadth hypothesis compared to the hunting mode hypothesis in a mesopredator-hare system, wherein characteristics of lynx kill sites were distinct from those of generalist predators, suggesting that lynx are more successful than both bobcats and coyotes at hunting hares in areas with greater structural complexity, cover, ambush features, and when snow is present. My results suggest that lynx are either differentiating themselves from competitors by their specialization more than their hunting mode, or that bobcats are diverging from a traditional felid role as an ambush predator by generalizing and using a wider range of habitats compared to lynx. However, the narrower range of habitat features at lynx kill sites compared to the generalist predators was not exclusive, which suggests that intraguild competition in this system is not fully alleviated by niche partitioning, particularly in snow-free seasons.

Beyond the lynx-hare system, an improved understanding of how habitat differences and prey availability benefit particular predators would allow for better predictions into the broad-scale ecosystem impacts of climate change. Predators are often keystone players in the trophic web (Paine 1966). Insights into the habitat features that provide one predator a competitive edge may enable land managers to better support a healthy and functioning ecosystem as the climate and landscape evolves. This study utilized forensic techniques to identify the predator species associated with kill sites, a common challenge, particularly in studies of mesopredators too small for GPS cluster analysis. Future studies on any species of mesopredator would similarly benefit from saliva-swabbing and other methods made possible by continuing technological advancements, such as the use of acoustic recorders and accelerometer logging on GPS collars to assess kill rates and even prey species in the case of a specialist like the lynx (Studd et al. 2021).

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CHAPTER 4. Drivers of snowshoe hare survival in a southern boreal forest

4.1 INTRODUCTION

Survival and demographic patterns at the boundary of a species' geographic distribution may have unique traits not seen in core populations, owing to myriad factors such as differing species assemblages and fragmentation of suitable habitat (Risser 1995, Chuang and Peterson 2016). Understanding the drivers of survival near species’ range boundaries is particularly imperative in the face of climate change, as many species’ distributions shift poleward (Gibson et al. 2009, Sultaire et al. 2016, Oldfather et al. 2020). These climate-induced shifts may convert core populations into range edges, with southern range margins in the Northern hemisphere and northern range margins in the Southern hemisphere expected to be particularly vulnerable to negative population effects (Anderson et al. 2009). Furthermore, for many species, these distribution shifts will require much of the core population to adjust to conditions that may be similar to those at previous range boundaries (Hill et al. 2011, Rehm et al. 2015, Zettlemoyer and Peterson 2021). Thus, understanding survival and other aspects of demography will be crucial not only for vulnerable range-edge populations but also for predicting how central populations will likely respond to climate change in the future.

An exemplary species for investigating range-edge dynamics in the face of climate change is the snowshoe hare (*Lepus americanus*), which is the preferred prey species of the specialist predator Canada lynx (*Lynx canadensis*). This snow-adapted lagomorph has a broad latitudinal distribution in North America that is already experiencing some declines in southern range-edge populations (e.g., Sultaire et al. 2016). By contrast to hares in northern core populations in Canada and Alaska, renowned for their 10-year predator-prey cycles in conjunction with lynx populations (Krebs et al. 1995, 2018), southern hare populations in the contiguous USA appear to be kept at dampened or acyclic population levels by some combination of generalist hare predators, discontinuous coniferous forest, a higher number of alternative prey species, and inferior diet quality (Wolff 1980, Hodges 1999*a*, Wirsing et al. 2002*a*). Climate change-induced delayed snowfall and earlier snowmelt are expected to further exacerbate such population-limiting effects. Snow-adapted hares change coat color to white in autumn/winter and back to brown in spring/summer to match with snow-on and snow-free conditions. The shifting seasons will likely result in camouflage mismatch (Mills et al. 2013, Zimova et al. 2014), which can result in decreased survival and unsustainable predation rates (Zimova et al. 2016, Wilson et al. 2019), suggesting that increased seasonal vulnerability to predation is a possible mechanism for observed northward range shifts.

In North America, hares face a unique predator composition in their southern range that likely contributes to different demographic patterns from their northern counterparts. In recent years, southern populations face an increased presence of generalist predators like bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), with the coyote having considerably expanded beyond its original native range into forested habitats of North America (Hody and Kays 2018). These generalist predators likely exert different seasonal predation patterns on hares than lynx have historically. Southern hare populations, typified by this increased generalist predator presence, should show lower survival in transitional and snow-free seasons (hereafter "snow-free"), which is when all predators, not just lynx, can easily access them. As accelerating climate change results in a shorter snowy season (Diffenbaugh et al. 2013) and more compacted snow, generalist predators historically limited by snow conditions will impact hare survival more heavily (e.g., Peers et al. 2020), thus further altering southern range dynamics and potentially foreshadowing the future of northern core populations.

Current understanding of key habitat drivers suggests that forest density and continuity (fragmentation) may play a role in survival of southern hares, differentiating these populations from northern hares (Buskirk et al. 2000). Hares across their geographic range exhibit a strong affinity for dense understory cover (e.g., Parker et al. 1983, Griffin and Mills 2009) and may increase their survival by utilizing cover that conceals them from predators (Sievert and Keith 1985). In the southern range of hares, habitat is more fragmented both naturally and through forest management practices (Buskirk et al. 2000, Koehler et al. 2008). Given advancing climate change, and with hares being prey to nearly all capable predators within their North American range (Hodges 2000), it is crucial to understand these drivers of hare survival in a landscape context, as they will likely contribute to differences observed in southern hare population demography.

Explanations of how habitat and predator cohort characteristics might drive northern hare cycles (and fail to drive similar cycles in the south) have typically fallen under the "refugium model," which posits that northern hares use dense cover to reduce their vulnerability to predation during population declines and that hare dispersal into suboptimal habitat can drive the increase phase of population cycles observed (Wolff 1980). By contrast, southern hares might remain at more dampened, acyclic numbers because of the more fragmented landscape, combined with an unrelenting presence of generalist predators that capture hares dispersing between the more isolated patches of preferred habitat (Keith et al. 1993). Wirsing et al. (2002*b*) found low hare survival even within the patches of preferred habitat on a fragmented landscape, suggesting a revised refugium model whereby open (suboptimal) habitat surrounding a patch of preferred habitat can facilitate predator access into the patch. Because generalist predators such as coyotes are more effective hunters both in open areas and during the snow-free season (as opposed to specialist lynx, which select for denser cover and are more effective hunters in snow) (Parker et al. 1983, Murray and Boutin 1991, Buskirk et al. 2000, Kolbe et al. 2007, Peers et al. 2013, Pozzanghera et al. 2016), there is likely a seasonal component to this model where open matrix and seasonality have a compounding effect on hare mortality.

Although the quality of this so-called “matrix” habitat that surrounds a patch of preferred habitat is known to strongly influence occupancy in many wildlife species (Prugh et al. 2008), including southern hares (Walker 2005), the majority of hare studies examining matrix and other habitat attributes have addressed occupancy rather than survival. Survival information can reveal complex dynamics and help forecast population trends and persistence, which is particularly crucial in the context of climate change if indeed southern hares are experiencing seasonal increases in predation pressure that cannot be buffered by suitable habitat refuge. Identifying potential habitat drivers for southern hare demography, such as seasonality and habitat context, is crucial for interpreting not only southern periphery dynamics but also forecasting future shifts in northern populations that might eventually follow suit.

To address these knowledge gaps about season-specific drivers of hare survival in the context of a fragmented southern range, I tested the southern hare refugium model by trapping and monitoring hares to track hare survival in the Cascades of north-central Washington, USA, within an area known to support a resident lynx population as well as generalist predators. I hypothesized that hare survival would fit within a seasonal southern refugium model, in which hares are preyed upon most heavily in seasons with increased generalist predator presence and at sites with more open surrounding matrix habitat. Under this model, survival will be lowest under those conditions with no evidence of refugia (i.e., openness of matrix surrounding patches of hare habitat will allow access to predators despite dense cover). Specifically, this model predicts

(1) lower hare survival in summer and, to an extent, shoulder seasons because generalist predators are better able to access hare habitat in snow-free seasons and thus exert greater predation pressure during those seasons, and (2) reduced hare survival at open-matrix sites in summer, and potentially also in shoulder seasons, when generalist predators such as coyotes and bobcats known to leverage edge and open habitat for hunting are more active. Alternatively, if predator access by generalist predators does not vary seasonally or is unaffected by matrix habitat openness, then hares should have higher survival in summer due to the increased nutrition and cover provided by deciduous vegetation.

4.2 METHODS

4.2.1 Study area

I conducted this study in the northeastern Cascades Mountains of Washington state, USA (48˚53’35”N, 119˚49’20”W), near the town of Loomis in the Loomis State Forest and Okanogan National Forest from 2010-2013. The study area (Chapter 2, Fig. 2.1) is located in the northern part of the Okanogan Lynx Management Zone (LMZ), where lynx are considered to have the best relative chance of long-term persistence under future climate-change scenarios in Washington (King et al. 2020). This region hosts a suite of other predators of hares, including bobcats, coyotes, American martens (*Martes americana*), great-horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*), and cougars (*Puma concolor*). Elevation ranged from 1,383–1,932 m, and land cover was characterized by mixed southern boreal forest dominated by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), with occasional Douglas-fir (*Pseudotsuga menziesii*), sitka alder (*Alnus* *sinuata*), and western larch (*Larix occidentalis*), along with some meadows and harvested areas and traversed by logging roads and natural creeks.

4.2.2 Field methods

Trapping sites were selected based on signs of hare activity and minimum patch size. I considered habitat variables for stand age (whether the forest stand in which hares were captured was mature or young [“regenerating”]) and openness of surrounding “matrix” habitat. To assess whether the habitat surrounding the primary trapping grids (surrounding “matrix” habitat) was affecting survival, the percentage of open perimeter for each of the six sites was measured using aerial imagery and the Google Earth Pro distance measuring tool.

To assess seasonal habitat and other variables potentially affecting hare survival, I selected 3 young (estimated 20-40 years) and 3 mature (estimated >75 years) boreal forest stands 17-20 ha in size for trapping hares. The 6 sites were selected based on minimum area of relatively contiguous habitat, site accessibility, and signs of hare use such as pellets, hare runways, and browsing evidence. Young sites were typically denser than mature sites and were only chosen if their dominant canopy layer, which was even-aged lodgepole pines in all cases, was tall enough to provide cover for hares when <1 meter of snow would be present in winter. All sites were separated by at least 1 km to avoid dispersal from one stand to another (Wirsing et al. 2002*b*).

I captured hares using Tomahawk live traps (32” × 9” × 9” double-door, Tomahawk Live Trap Co., Tomahawk, WI, USA) baited with alfalfa pellets and covered with tree branches for camouflage and insulation. Sites were trapped on rotation, one at a time, typically at least twice in summer and at least once in winter. Trapping grids consisted of 40–50 traps spaced approximately 50 m apart from each other and roads and were set in the late afternoon or evening and checked in the morning. Captured hares were weighed in grams, sexed, identified as adult, subadult, or juvenile, sampled with a 2-mm ear punch to collect a tissue specimen, ear-tagged through the sampling hole and in the other ear (No. 3, National Band and Tag Co., Newport, KT, USA), and measured for right hind foot length (a metric for structural size that would be used for a body condition index) in centimeters. I also equipped a subset of individual hares weighing at least 575 g with mortality-sensitive VHF radio-collars (Model M1565, 24 g, Advanced Telemetry Systems [ATS], Isanti, MN, USA), keeping collar weight to <5% of total body mass (Cochran 1980); one additional hare weighing 550 g was fitted with a collar weighing 22 g. As time allowed, I also trapped partial grids if the number of functional radio-collars at a given stand became appreciably disproportionate compared to other stands. When hares were recaptured, new measurements were taken unless the hare had already been measured in the same season or if the animal seemed stressed or injured. Hare capture and handling procedures were approved by the University of Washington Institutional Animal Care and Use Committee (IACUC) under protocol 4226-02 and consistent with standards for capture and handling of mammals (Sikes et al. 2011).

To monitor hares for mortality events, radio-collars were checked at least 3 times per week, except in spring when site access was less frequent because of snowmelt and subsequent muddy conditions that restricted access by either snowmobile or truck. A mortality event was identified when a collar emitted a signal at twice the baseline rate (70 beats per minute), which was activated after 8 hours of no movement. Survival monitoring also ceased if radio-collars stopped emitting signals, such as when batteries stopped working. I typically detected a mortality within 24–72 hours of the last detected “live” signal and then used ground-based radiotelemetry to locate the mortality site. I assessed the proximate cause of mortality by building upon methods such as those described in Boutin et al. (1986) and based on tracks, a fur trail, amount of carcass or fur remaining, sub-dermal hemorrhaging, predator hairs, signs of a struggle (e.g., a light layer of fur), and mtDNA tests on predator saliva (Peelle et al. 2019), which I collected from the remains and radio-collar.

4.2.3 Study covariates

Along with testing the overarching hypothesis that hares lack seasonal refuge from generalist predators in the fragmented habitat of the southern range, as measured by seasonal differences in hare survival combined with the openness of the surrounding matrix habitat, I also considered key variables that prior studies suggest may influence hare survival, including forest stand age, sex, and body condition. The primary cause of hare mortality across the species' range is predation (Keith et al. 1984, 1993, Sievert and Keith 1985, Murray et al. 1997, Hodges et al. 2001, Wirsing et al. 2002*b*, Griffin et al. 2005), but differences in survival may relate to an individual hare's characteristics, including sex (Hodges 1999*b*, Murray 2002) and body condition (Keith et al. 1984), and may also be linked to other habitat characteristics (Sievert and Keith 1985), stand age (Lewis et al. 2011) or some combination of these variables (Feierabend and Kielland 2015, Majchrzak et al. 2022).

To include hare body condition (a proxy for stored body fat) in the survival modeling, I calculated a Scaled Mass Index (SMI). The SMI uses the regression coefficient for body mass and body size (for hares, represented by hind foot length) to adjust the observed body mass to a standardized size (Peig and Green 2009, 2010, Nip et al. 2018, Rizzuto et al. 2019). This method corrects for biases associated with traditional residual-based approaches, providing a more accurate reflection of body condition (Peig and Green 2010). I calculated the mean SMI separately for juveniles as well as adult male and female hares to obtain age- and sex-specific condition indices (Murray 2002, Green 2001).

4.2.4 Statistical analyses

I used Kaplan-Meier estimates and Cox proportional hazards (CPH) models to assess seasonal patterns of hare survival. Preliminary tests showed that season violated CPH assumptions, even when added as a time-varying interaction term, because season was not proportional to the other variables' (matrix openness, stand age, sex, and body condition) hazards over time and therefore could not be modeled directly with the other covariates. To address this violation, I adopted a two-stage approach to analyses. I first implemented simpler Kaplan-Meier analyses to estimate hare survival across seasons (Kleinbaum and Klein 2005). I then performed CPH modeling separately for spring, summer, autumn and winter, which controlled for seasonal influence while also evaluating the effects of other covariates within each season. This stratification approach aligns with standard practices in survival analysis when encountering such violations (Therneau et al. 2023) and is commonly required with CPH (e.g., Murray 2006, Allison 2010).

In the first stage of analysis, Kaplan-Meier survival curves were generated for all hares by season. I then estimated 90-day survival probabilities after the first day a hare was known to be alive, conditional on survival at the start of a season. After summarizing broad seasonal patterns of hare survival, I then explored the role of other covariates expected to affect hare survival through Cox regression analyses. CPH is a robust semiparametric regression that can identify variables affecting survival without needing to specify the baseline hazard (i.e., factors contributing to death that cannot be known). CPH quantifies the risk (hazard ratios) associated with specified variables, which are assumed to be constant relative to each other over time (Cox 1972, Cox and Oakes 1984, Kleinbaum and Klein 2005).

The CPH model form is:

$$h(t) = h_0(t)\exp(X\beta)$$

where $h(t)$ is the hazard at time t, $h_0(t)$ is the unspecified baseline hazard function (the instantaneous potential for death to occur, given survival up to that point) evaluated at time t, X is a vector of covariates, and β is a vector of regression coefficients.

For building the CPH models, I used time in days since a hare's first capture for the timescale, t. Thus, hazard ratios represented average comparisons of risk for hares collared for the same amount of time. I selected time since capture over calendar day (e.g., time since the start of study) for my timescale because using a calendar day timescale would have precluded consideration of season as a covariate; i.e., the baseline hazard would absorb seasonal variability on the calendar timescale. Then, to account for risk factors that change over time (time-varying covariates), I split a hare's follow-up time (total number of days until an event, i.e., mortality or last day of contact while known to be alive) into multiple records (time intervals) (Therneau et al. 2023). Time-varying covariates considered for this study included external covariates that did not require access to the animal to know that they changed over time (season, hare age) and internal covariates that could not be known except when a hare is captured and measured (condition, based on weight and hind foot length). Thus, I created time interval splits by seasonal transitions (defined as starting on January 1, April 1, July 1, and October 1) for the overall dataset.

Interval censoring was implemented in the CPH modeling to allow inclusion of the time-varying condition variable, given that future re-measurements cannot justifiably be interpolated (e.g., Murray and Sandercock 2019, Therneau et al. 2023). This additional data manipulation was required to account for (1) approximately when hares changed age status (juvenile to adult) because the condition variable metric relied on age status, and the associated relationship between HFL and body mass will vary between these age groups, and (2) censoring individuals that had not yet reached a minimum adult weight as of their last measurement. My data indicated that adult hare weight could remain stable below 1000 g (e.g., as indicated a year later), but adult weight measurements below 900 grams were not as stable and thus considered unreliable approximations of stabilized adult weight, if not remeasured again within a few months. Thus, in addition to seasonal time interval splits, a time split was also applied if a hare was recaptured and remeasured, which updated a hare's demographic information at that moment in time without losing information about accumulated risk (i.e., the count of days since first capture continued into the next time interval).

To apply these demographic time-varying splits appropriately, I applied the SMI condition variable calculations by age status to allow for consistent censoring based on expected growth rates. The following censoring ultimately precluded hare age as an explanatory covariate but is nonetheless reported because it defined both the final dataset used and the age-specific SMI calculations. Hares were classified as either juvenile or adult using a weight cutoff of 800 grams (Keith et al. 1968, Jensen et al. 2022). Hares that were juveniles at first capture were labeled as such for 60 days after capture, at which point their record was split and the remaining follow-up time was assigned to the adult age group. The 60-day cutoff is based on the maximum duration of the juvenile period (Keith et al. 1968). Furthermore, hare weight can change substantially between the juvenile period and the adult period, and even during a post-juvenile period when hares are above 800 grams but still growing. After confirming that all adult hares stabilized at a weight above 900 g, any records with weight measurements below 900 grams were censored at 100 days after that measurement was taken because the projection of future values in time-varying covariates should be avoided in survival analyses (Therneau et al. 2023), and the future weight of these growing hares was too uncertain. Hare age status as adult or juvenile was ultimately discarded as a direct covariate in the CPH modeling because the number of juvenile mortalities after censoring (n = 8) was insufficient for meaningful inference, but a future analysis could be conducted on the juvenile dataset if measurement data are removed.

I performed the hare survival analyses using packages "survival" and "survminer" in R (Kassambara et al. 2021, Therneau et al. 2023) and tested if matrix openness varied by season and if survival varied by season overall, both of which would suggest a seasonal increase in generalist predator activity in the study area. Stand age (with regenerating stands as a proxy for dense cover) and demographic variables of sex and condition were additionally posited if the relationship was theoretically justifiable per earlier sections of this chapter. I assessed whether the candidate CPH regression models adequately described the data by testing the proportional hazards assumption (scaled Schoenfeld residuals). If a model violated proportional hazards, I tried adding either of the time-varying covariates as a time-varying interaction term to resolve the issue (Therneau et al. 2023).

Within each stratified season, I built 8 candidate global models to test whether the additive or interacting effects of these habitat and demographic variables influenced survival patterns based on *a priori* expectations. I ranked candidate models using AIC_c for small sample size and considered those with $\Delta AIC_c < 2$ as competitive (Akaike 1974, Burnham 2004). Kaplan-Meier survival curves are presented for the top-ranking models' significant covariate terms because these allow for clearer interpretations than those requiring CPH assumptions, and hazard ratio plots are presented for the overall top model for each season to demonstrate which terms had non-overlapping confidence intervals. Null models are also presented for each season.

4.3 RESULTS

A total of 375 hares were captured in 707 trap events, of which 356 individual hares were ear-tagged and 223 were equipped with radio-collars. Among the hares affixed with radio-collars, 2 were subsequently excluded for trapping-related mortalities and 1 was excluded because its follow-up time was <1 day before a possible collar failure, yielding a final tally of 220 hares for inclusion in Kaplan-Meier survival analyses. A total of 131 mortality events were detected prior to censoring. Approximately 75% of captured/monitored hares were adults, and the sex ratio of captured hares was roughly equal (Table 4.1). Proportions and numbers of hares monitored by day since first capture are shown in Fig. 4.1 to visualize the interspersion of monitoring time across seasons. Specific follow-up times and mortality events for each forest stand where hares were trapped are displayed in Supplemental Figures S4.2-7.

Table 4.1. Raw summaries at first capture of the 220 snowshoe hares (Lepus americanus) included in this study by status (hare age and sex), measurements (weight in grams and hind foot length in centimeters), and whether a hare was subsequently recaptured.

Hare Metric	Mean/Count (SD/ %)
Age	
adult	167 (75.9%)
juvenile	53 (24.1%)
Sex	
female	113 (51.4%)
male	102 (46.4%)
unknown	5 (2.3%)
Weight (g)	
	969.3 (257.3)
Hind foot length (cm)	
	12.4 (1.3)
Recaptured	
no	111 (50.5%)
yes	109 (49.5%)

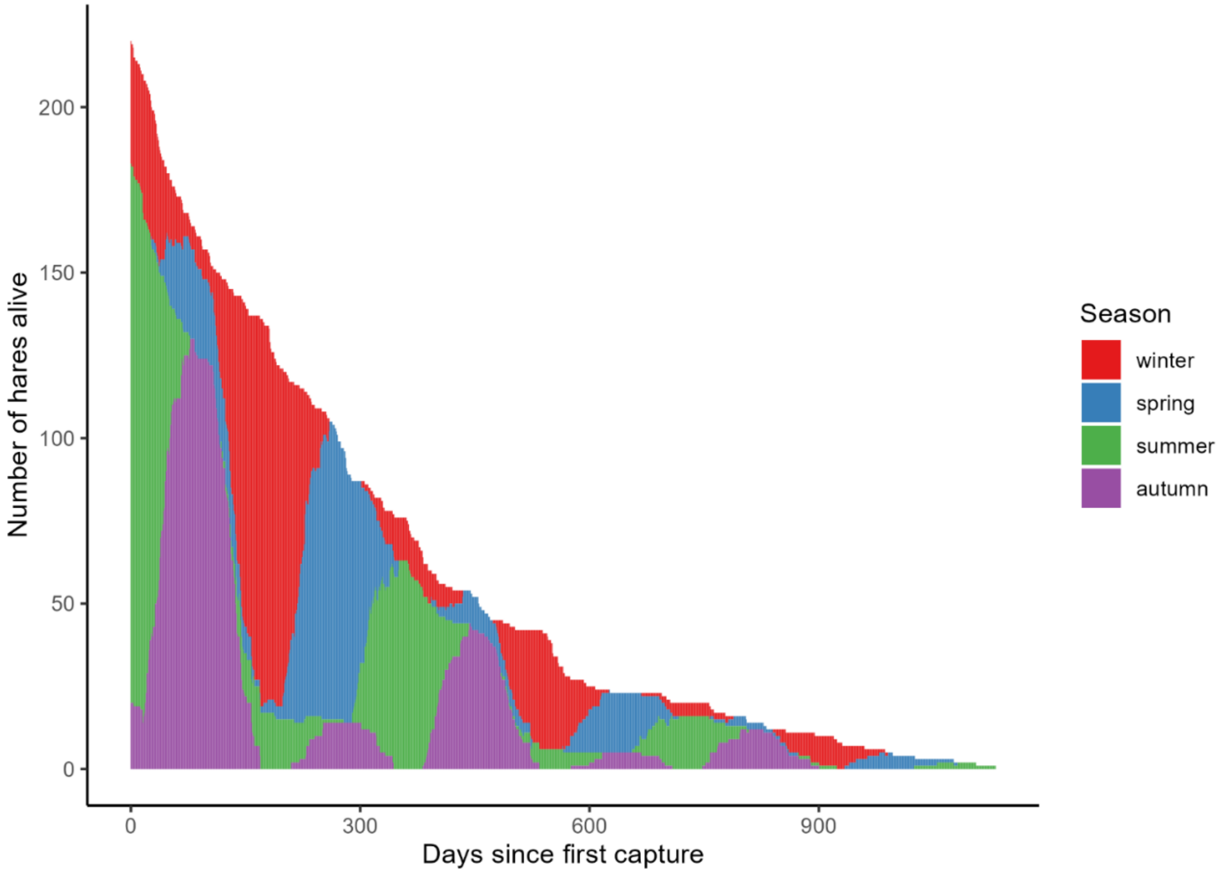

Figure 4.1. Overview illustration of monitoring duration patterns for hares post-capture, with a breakdown by seasonal proportions.

4.3.1 Kaplan-Meier analysis

Kaplan-Meier survival estimates revealed that 90-day survival rates were highest in winter (0.91) and lower in spring (0.73) and summer (0.80) (Table 4.2). Spring and summer survival were significantly lower compared to winter survival, and spring survival was significantly lower compared to autumn and winter survival (Table 4.2, Fig. 4.2).

Table 4.2: Kaplan Meier estimates and 95% confidence intervals for seasonal hare survival after the first day a hare was known to be alive, conditional on survival at the start of a season.

Season	Survival Probability 90d	Lower CI 90d	Upper CI 90d
Winter	0.910	0.871	0.951
Spring	0.733	0.668	0.803
Summer	0.797	0.737	0.863
Autumn	0.868	0.825	0.913

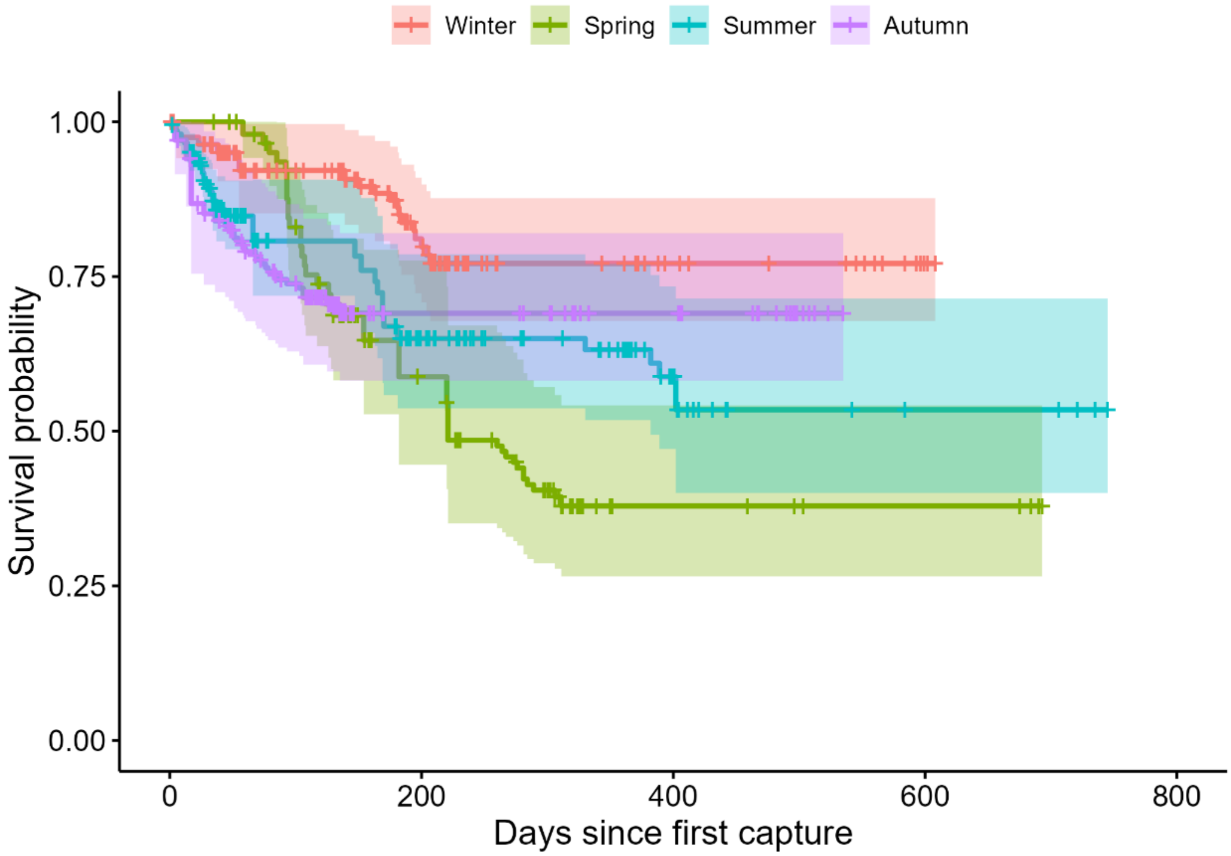

Figure 4.2. Overall survival probability of hares in days since first capture by season. Seasonal strata represent hypothetical cohorts of hares that live their entire lives in one season. Colored areas surrounding each line represent 95% CIs.

A summary Kaplan-Meier figure was generated to illustrate survival in male versus female sex, mature versus regenerating (young) forest stand age, and open versus moderate matrix habitat, shown in Fig. 4.3. Overall survival was highest in winter and lowest in spring, followed by summer, but some within-season differences emerged, such as the notably higher male survival in summer and autumn. More precise estimates based on 1000-day mortality rates are in Supplemental S1; the overall pattern of these estimates aligned with the 90-day Kaplan-Meier survival estimates, albeit in a reverse pattern because mortality and survival are opposites.

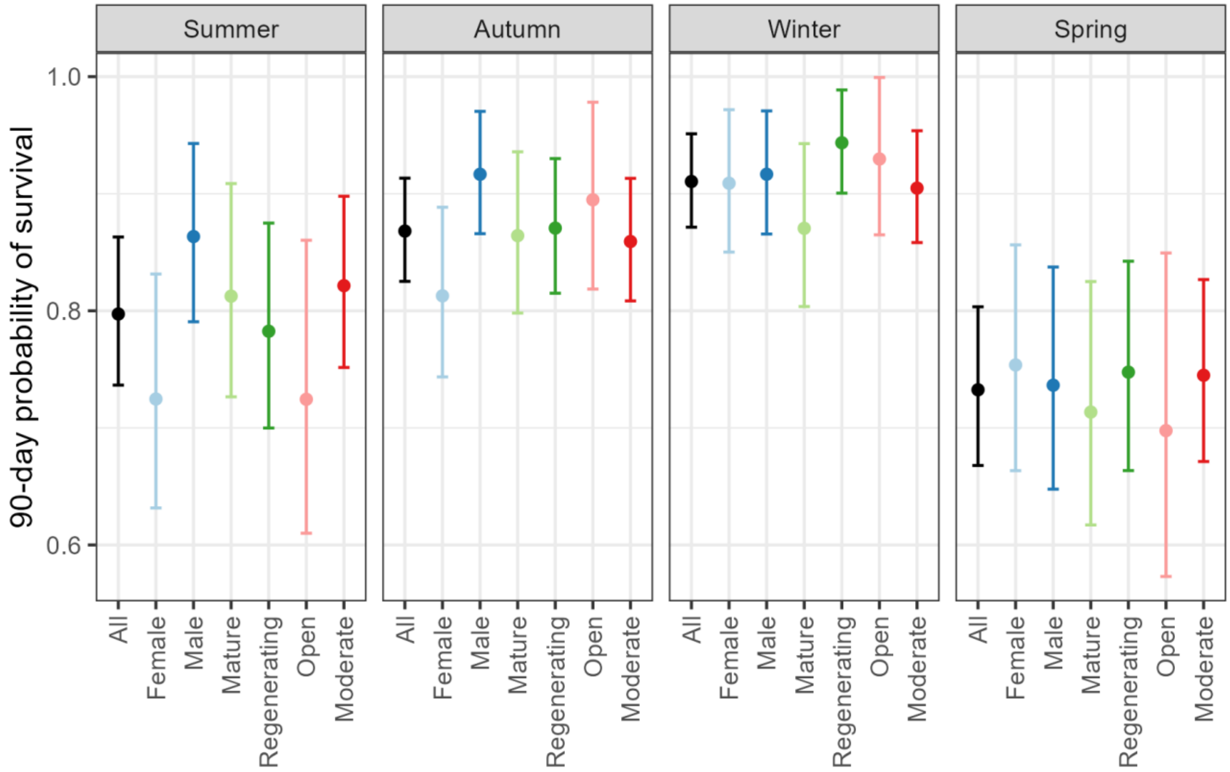

Figure 4.3. Kaplan-Meier-based 90-day survival probabilities after the first day a hare was known to be alive, conditional on survival at the start of a season. Summaries with 95% confidence intervals are included for all hares by season and categorical variables of sex (male or female), forest stand age (mature or regenerating), and matrix habitat (open or moderate).

4.3.2 Cox proportional hazards analysis

In the season-specific modeling, which stratified by season and allowed comparison of the explanatory variables' relative influence on hare survival, I found differences in the year-round drivers of hare survival (Table 4.3). All top models passed tests for Cox proportional hazards assumptions. CPH models estimate the hazard ratio (HR) for each model term, where an HR>1 indicates that the model term increases risk/lowers survival, and an HR<1 indicates that the model term decreases risk/increases survival. Two models originally considered (matrix*sex and matrix + site.age) were discarded from AICc model selection due to violating proportional hazards in at least one season, despite the stratification approach. Neither of these models had arisen as the top explanatory model prior to elimination, although the model for a matrix*sex interaction was occasionally within delta 2 AICc.

The top model for summer included significant terms for both matrix openness (HR 2.96, 95% CI 1.51-5.78) and sex (HR 0.36, 95% CI 0.18-0.71), revealing lower survival at open-matrix sites (Fig. 4.4A), particularly for female hares (Fig. 4.4B). Stand age was not retained as a covariate in the summer models. Summer models within <2 delta AICc suggested that hares with higher SMI (body condition) values had lower survival, but condition was not a significant term when including the sex and matrix covariates in these summer models. The top model for autumn included terms for sex, matrix, and SMI; only the term for sex was significant, with a HR for of 0.31 (95% CI 0.12-0.77) (Fig. 4.4C) indicating females had lower survival, whereas matrix openness and SMI were not significantly associated with survival. In the winter the HR for SMI was 0.62 (95% CI 0.42-0.91), indicating poor body condition was associated with lower survival (Fig. 4.4D). Matrix and sex were not significantly associated with survival in the winter. In the spring, there was no significant difference in survival by matrix, sex, or SMI, and the null model was the top model.

In summary, significant explanatory variables for hare survival based on hazard ratios included decreased survival for female hares in summer and autumn, decreased survival for hares at sites with open matrix in summer, and increased survival for hares with better body condition in winter. Although an interaction term between matrix openness and sex could not be modeled due to violation of Cox proportional hazards, a potential interactive effect was observed wherein female hares had disproportionately lower survival in plots with open matrix in the summer months (Fig. 4.4B). Hazard ratios and their CIs are visualized in Fig. 4.5.

Table 4.3. Season-specific model results for hare survival using Cox proportional hazards and AICc corrected for small sample sizes. For each season, models within ΔAICc <2 and null models are presented. In spring, the null model emerged as the top model; thus, the highest-ranking model with covariates is also showcased for comparison.

SUMMER

Top Model: matrix_cat + sex, Δ AICc: 0

Terms	β	*p*-value
Open matrix habitat	1.08	0.00156
Sex (male, relative to female)	-1.03	0.00318

matrix_cat + sex + SMI100, Δ AICc: 0.208

Terms	β	*p*-value
Open matrix habitat	1.1400	0.000931
Sex (male, relative to female)	-0.9550	0.006550
Condition (SMI)	0.0948	0.152000

matrix_cat + SMI100 * sex, Δ AICc: 1.360

Terms	β	*p*-value
Open matrix habitat	1.100	0.00165
Condition (SMI)	0.137	0.07520
Sex (male, relative to female)	0.774	0.60100
Male sex by condition (interaction)	-0.165	0.23400

Null Model: Δ AICc: 12.056

AUTUMN

Top Model: matrix_cat + sex, Δ AICc: 0

Terms	β	*p*-value
Open matrix habitat	-0.523	0.3140
Sex (male, relative to female)	-1.180	0.0115

Null Model: Δ AICc: 4.316

WINTER

Top Model: matrix_cat + SMI100, Δ AICc: 0

Terms	β	*p*-value
Open matrix habitat	-0.626	0.414
Condition (SMI)	-0.497	0.013

matrix_cat + SMI100 + stand.age, Δ AICc: 0.833

Terms	β	*p*-value
Open matrix habitat	-0.432	0.5780
Condition (SMI)	-0.421	0.0283
Stand age	0.835	0.1450

Null Model: Δ AICc: 2.771

SPRING

Top Model: Null Model, Δ AICc: 0

Highest-ranked model with Covariates: matrix_cat + sex, Δ AICc: 4.2

Terms	β	*p*-value
Open matrix habitat	0.0836	0.829
Sex (male, relative to female)	-0.1050	0.756

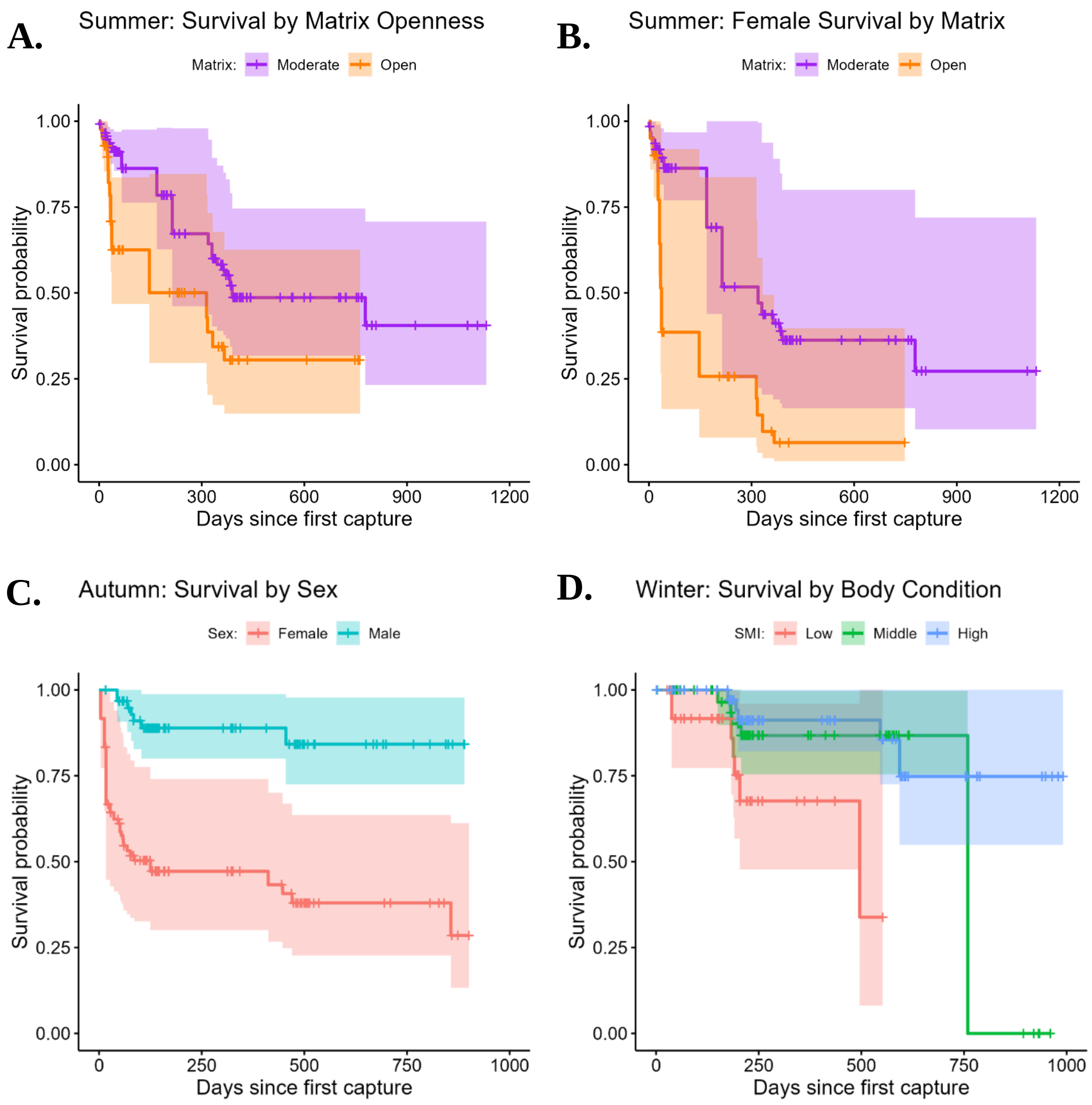

Figure 4.4. Kaplan-Meier survival curves showing A) overall hare survival by matrix habitat openness in summer, B) female hare survival by matrix habitat openness in summer, C) overall hare survival by sex in autumn, and D) overall hare survival by body condition in winter.

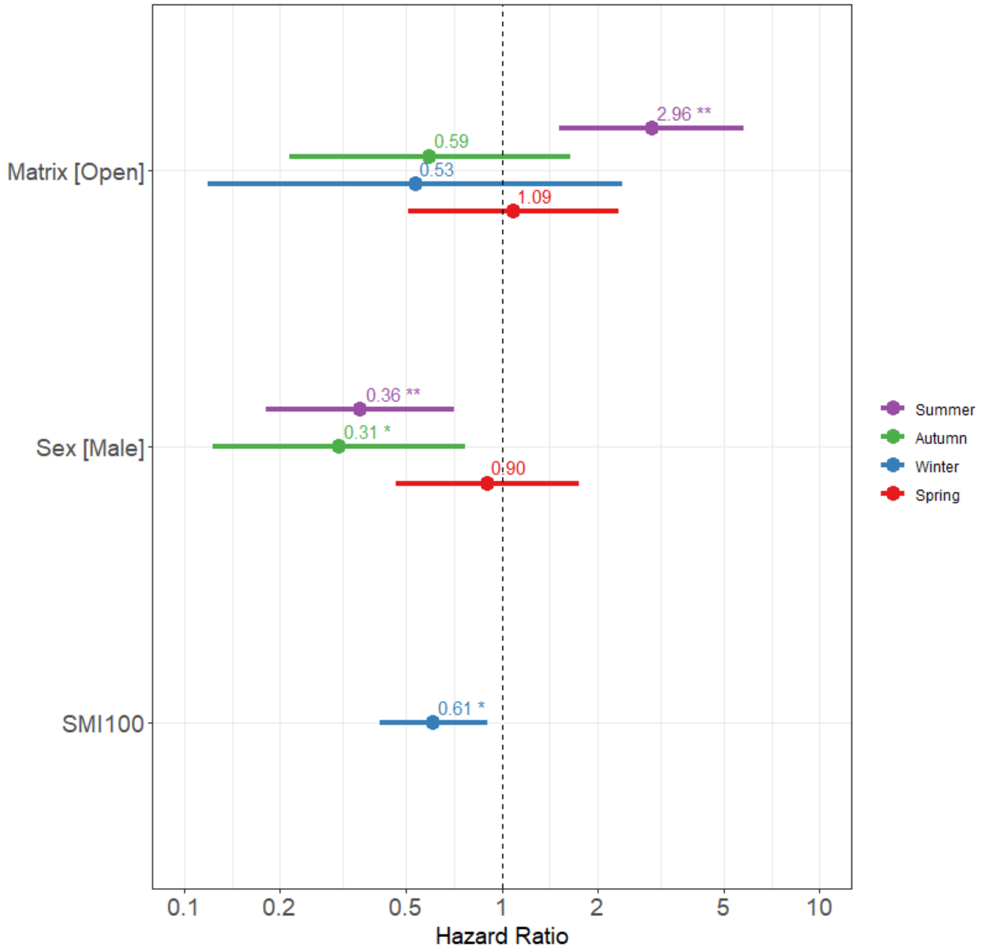

Figure 4.5. Hazard ratio plot of the covariates from the top models for each season-specific Cox proportional hazards model. The plot displays hazard ratios with 95% confidence intervals for the covariates: Matrix [Open], Sex [Male], and hare body condition (SMI100) across four seasons (Summer, Autumn, Winter, Spring). Note that the baseline hazard is not the same for all seasons, as the models were stratified by season. Asterisks represent statistically significant hazards, including decreased survival with open matrix in summer, increased survival for male vs female hares in summer and autumn, and increased survival with better body condition in winter.

4.4 DISCUSSION

Identifying factors affecting survival of hares in the species' southern distribution is critical for anticipating range boundary dynamics, particularly in light of the vulnerability of southern boreal forest ecosystems to climate change (Stralberg et al. 2020). Understanding seasonal variation in survival for these populations is also vital in the context of climate change, as conditions currently facing southern populations may soon be experienced by their northern counterparts. The southern refugium model (Hodges 1999*a*, Wirsing et al. 2002*b*) posits that preferred hare habitat, which in the hare's southern range is in general fragmented both naturally and because of forest management, does not provide adequate protection from predation compared to northern preferred habitat patches. This is in part because preferred habitat is often surrounded by open matrix that allows predators greater access to hares (i.e., true "refugia" for southern hares may be rare or non-existent; Wirsing et al. 2002*b*). This study addresses knowledge gaps regarding season-specific drivers of hare survival in the context of a fragmented southern range. I found evidence for a seasonal southern refugium model, whereby decreased hare survival is linked to habitat access by generalist predators that are seasonally restricted by snowpack, a situation that appears to be exacerbated in summer by the openness of surrounding matrix habitat (i.e., increased fragmentation). I also found evidence for female hares having lower survival during breeding season at more fragmented sites. Other less-significant factors influencing survival included hare body condition (SMI), which was linked to survival only in the winter months. With increasingly long snow-free seasons due to climate change (Gottlieb and Mankin 2024), these findings have important implications for forest management targeted at sustaining hare populations as a prey resource for lynx.

As predicted from a seasonal hare survival model, my study found hare survival to vary dramatically by season, with survival lowest in spring, followed by summer, and highest in winter (Table 4.2, Fig. 4.2). Lower hare survival in snow-free seasons could be due to increased predation pressure from generalist predator species (e.g., Scully et al. 2018; also see Chapter 4 of this dissertation). Namely, summer should be when generalist predator (e.g., coyote and bobcat) activity in high-latitude mountainous environments is strongest overall, as snow cover impedes these species' access in winter months (e.g., Murray and Boutin 1991). This trend is consistent with a seasonal refugium model, where generalist predator access in the absence of deep or soft snowpack is a stronger driver of survival than the availability of denser horizontal cover, better quality forage, and greater abundance of alternative prey species that are attributed to higher summer survival in northern hare populations (Hodges 2000, Feierabend and Kielland 2015).

Hares exhibiting the highest survival in winter in this study also lends support to a seasonal refugium model in the southern range. If decreased hare survival is linked to greater numbers of generalist predators, then hare survival should be higher in winter months, when predation is mainly limited to specialist predators such as lynx due to the presence of heavy snowpack. Higher winter survival in this study is in opposition to the lower winter survival observed in many studies of northern hare populations (Hodges 2000, Feierabend and Kielland 2015, Oli et al. 2020). Higher winter survival of hares in the southern range cannot be attributed to decreased generalist predator pressure alone, however; in the southern range, winter temperatures tend to not drop as low as in the northern range, and thus southern hares movements in winter are more likely to be driven by predator avoidance than seeking warmer resting spots (Gigliotti et al. 2017). Regardless, the warmer temperatures/shallower snowpack of the southern ranges are directly linked to survival of generalist non-snow-adapted predators, and so these two factors affecting winter survival of southern hares cannot be disentangled (Peers et al. 2020, Butler et al. 2023). Other possible factors increasing winter survival for hares in southern regions might include more active alternative prey animals and better quality of winter browse compared to their northern counterparts, which would both also correlate with warmer temperatures.

To the extent to which winter hare survival is predominantly driven by restricted generalist access, increased winter hare survival in southern ranges may serve as a bastion against population extinction so long as substantial winter snowpack is present. This advantage may disappear as climate change causes earlier snowmelt and later snowfall, leading not only to increased generalist predator access but to hare coat color camouflage mismatch with the environment in spring and autumn, increasing hare visibility to predators and decreasing hare survival. Mismatched or transitioning hares tend to use denser understory cover than hares with pelage that is in sync with the season (Litvaitis 1991), which may lead to further stress on hares that are making foraging risk tradeoffs to mitigate an increased predator presence (Hik 1995).

While hare survival was lowest in spring in this study, it was second-highest in autumn, suggesting that the risks of camouflage mismatch and generalist predator access may not be equal between spring and autumn, depending on the geographical location. For example, spring snow cover in my study area was much more variable and patchier compared to autumn because thaw-freeze cycles resulted in dense or crusted snow, and in many places resulted in patchy loss of snow completely. These inconsistent snow conditions are why hare mortality monitoring in spring was conducted less frequently; patchy snow and muddy conditions frequently prevented access. By contrast, in autumn, there was a fairly rapid transition from no or negligible snow cover to a state of more consistent and fluffy snow. Given hare vulnerability to a camouflage mismatch with snow conditions (e.g., Mills et al. 2013, Zimova et al. 2014, Wilson et al. 2019), this patchiness of spring snow conditions relative to autumn suggests that hare mismatch, and thus increased visibility to predators, may have played a role in seasonal hare survival.

Snow compaction or "hardness" caused by periods of greater temperature fluctuations may further influence hare survival by facilitating generalist predators, which are limited by snow density and sink depths (Sullender et al. 2023). These contrasting snowpack conditions for spring versus autumn would likely also alter predator communities at the study site; generalist hare predators like coyotes are known to utilize harder (more compacted) and shallower snow than lynx and would therefore likely be more successful predators in the spring than in the fall (Murray and Boutin 1991, Bunnell et al. 2000, Pozzanghera et al. 2016). Thus, a lower hare survival rate in seasons with no snow (summer) or when snow is only patchily distributed or compacted (spring) could be explained by their coinciding with generalist predator access, consistent with the seasonal refugium model.

This study's finding of the importance of season in hare survival has major implications in the context of climate change. For example, a climate change meta-analysis on numerous plant and animal species found that local extinctions were associated with larger, more rapid changes in maximum temperatures (Román-Palacios and Wiens 2020). If springtime temperatures in southern hare habitat are higher and characterized by more extreme fluctuations compared to historical baselines, this disparity would provide a mechanism for springtime changes in the persistence, continuity, and hardness of snow cover that would likely continue to increase spring access for generalist predator to this region and thus lower survival for hares.

My finding that stand age was not a strong driver of hare survival supports a southern hare refugium model in which hares are vulnerable to predation regardless of vegetation density, at least within preferred habitat. I did observe somewhat lower survival over time in regenerating sites in autumn and slightly higher survival in winter when compared to mature sites (e.g., Supplemental Fig. 8), but the stand age variable was not retained in the top model and was not a significant covariate. This differs from expectations based on some prior hare abundance studies in Washington, which suggested higher abundance in regenerating boreal forests stands (e.g., Koehler 1990, Lewis et al. 2011, Jensen 2020, Parsons et al. 2020). Abundance studies such as these can provide context for my study results, given the limited number of southern hare survival studies that examined stand age, and the relationship between hares and preferred habitat is not always clear. Hodges (2009) found hares in Yellowstone National Park, USA to be more likely to use mature stands over regenerating stands, although overall hare densities were fairly low in that study area. Other abundance studies in southern hare populations have suggested that hares might not be most abundant in regenerating stands like they appear to be in Washington. In Wyoming, USA, Berg et al. (2012) examined the influence of forest structure and age on hares with more precision than most prior studies, breaking stands down into seven categories using a combination of the two metrics considered most important to hares within boreal forest ecosystems: horizontal cover and stand age. Contrary to expectations, they found that hares were more likely to use more mature habitats with higher amounts of forest structure compared to even-aged regenerating (30-70 year old) stands, although hares were strongly associated with both. In Montana, hares may have higher abundance in mature forests in winter (Griffin 2004). Like some other studies on other hare predators, a patchwork of stand ages may ultimately provide the best combination of foraging and denning features for prey (Parsons et al. 2020).

Small patch size may also have contributed to a lack of clear differences in hare survival between mature and regenerating stands. Other studies indicate that hares do not fare well in small patch sizes (Wirsing et al. 2002*b*) and are more likely to be found and to persist within relatively large forest patches (Buehler and Keith, 1982; Keith et al., 1993; Thomas et al. 1998). My study area in north-central Washington is heavily fragmented; most early and mid-successional patches recovering from timber harvest in the area are >15 ha and often >10 ha (L. Peelle, unpublished data collected during site-selection process), far below general recommendations for hares or their predators (review in Washington DNR, 2006). Too much edge habitat because of small patches, or too much open habitat (e.g., pre-commercially thinned), could potentially intensify hare vulnerability to predators such that hares decline to dangerously low numbers or disperse in search of safer habitat (Abele et al. 2013, Litvaitis et al. 1985). Thus, the small patch sizes characterizing my study area could have dampened potentially protective effects of denser, regenerating habitat on hare survival.

Although stand age was not supported as a strong driver of hare survival, the openness of surrounding matrix habitat was important. Matrix openness, a proxy for fragmentation, is a particular concern for southern hare populations because generalist predators often utilize edge habitat and disturbed areas when hunting (Buskirk et al. 2000). Preference of hares for dense cover is well-documented for northern hare populations in general (Wolff 1980, Hodges 2000). This preference has also been demonstrated in north-central Washington, where hare abundance was positively correlated with cover in the surrounding matrix containing shrubs/trees/understory cover within 300m of hare habitat patches (Lewis et al. 2011), highlighting the importance of the surrounding between-stand matrix habitat for hare selection and, likely, survival. The potential negative impacts of open matrix quality on hare survival may be compounded when the habitat patch size is so small that it cannot provide refuge for hares, as has been found in some studies in the southern range (e.g., 5-10 ha; Keith et al. 1993, Wirsing et al. 2002*b*). In most studies that have found hare survival risk to be unaffected by cover, the suggested likely mechanism has been small patch size that facilitates incursion by the various predators of hares (Keith et al. 1993, Wirsing et al. 2002*b*, Feierabend and Kielland 2015).

An implication of the original refugium model, which posits that dense habitat can exclude predators, could theoretically be that a landscape comprised primarily of extremely dense, contiguous forest might not allow sufficient access for predators, potentially even lynx, which favor increased cover for hunting. This scenario, if true, would be problematic for lynx conservation. Because my study area is quite fragmented, as is common with many southern boreal forest habitats (Agee 2000), I was unable to trap in fully contiguous forest with no edge habitat for comparison to directly test whether matrix habitat containing dense cover inhibited predation of hares to the detriment of important predators. Nonetheless, there were notable differences in the percentage open matrix habitat surrounding the study sites, ranging from 10-50% matrix openness, which allowed for testing of hare survival in fully open vs semi-closed matrix habitat.

Data from this study indicate that open matrix does indeed influence hare survival, but the effect is not consistent throughout the year. Matrix openness was a significant predictor of hare survival during the summer months, during which it correlated with lower survival, but was not a significant driver of survival in any other season. This pattern supports the seasonal southern refugium model, which predicted that generalist predators, which have greater access to hare habitat during the snow-free seasons, would have better hunting success in habitats with open edges (Hornseth et al. 2014). By contrast, specialist lynx prefer moderately high dense cover for hunting and experience relaxed competition with generalist predators during winter. Under a seasonal refugium model, I would therefore expect no change or even an increase in hare survival with open matrix in winter months, since lynx would be less likely to hunt in open areas; this is supported by this study's finding that open matrix had no effect on hare survival in winter.

Sex was also a significant predictor for hare survival, but as with matrix quality, this effect was not consistent across seasons. In summer and autumn, female hares manifested lower survival compared to males, with no sex differences in survival observed in winter and spring. Few studies examine sex differences in hare survival, either seasonally or in general, making it difficult to put these findings into context with northern or southern populations. Male hares tend to have higher movement rates than females (Hodges et al. 1999), which may suggest that males would be more vulnerable to predation and therefore have lower survival. However, this pattern is contradicted by multiple studies (e.g., Sievert and Keith 1985, Hodges 1999*b*) where no sex-biased differences in mortality were observed. One possible explanation for this discrepancy is seasonality in sex-based mortality. In support of this scenario, Murray (2002) found that male and female hares had similar activity patterns, but that they differed seasonally, with males being more active in March–April, whereas females were more active in May–June. Further, Murray (2002) found that non-scrotal males, heavier males, and recently pregnant (within 60 days) females had the highest survival within their sex cohorts, but the sexes were not directly compared. However, if the sex-based seasonal differences in activity levels observed by Murray (2002) were the sole driver, I would also expect to see higher mortality for male hares in spring, which I do not.

Unexpectedly, I observed increased female summer mortality at sites with open-matrix habitat compared to those at sites with moderate-closed matrix habitat (Fig. 4.4B), which could suggest that female hares are using the landscape differently than males and thus exposing themselves to greater predation risk from generalist predators. Because my study did not directly evaluate hare behavior, explaining this complex interactive effect of sex, season, and habitat type on survival requires some conjecture. One potential explanation may be that the increased nutritional requirements of pregnancy and lactation drive female hares to forage farther away from preferred habitat/cover than male hares do during breeding season, as suggested by Litvaitis (1990). At sites with more open matrix consisting of clearcuts or sparse/open areas resulting from forest management decisions, this disparity would leave females more vulnerable to generalist predators (coyote, bobcat, etc) that leverage open areas for hunting (Buskirk et al. 2000).

Research linking northern hare population cycles to maternal stress and predator awareness (Boonstra et al. 1998, Sheriff et al. 2009*b*, 2010, 2011, Lavergne et al. 2014) suggests that the conditions that female hares experience during pregnancy may potentially provide vital information for predicting hare demographics that may have implications for predicting southern hare demographics as well. However, few studies have directly compared survival of male and female hares in the months of breeding and pregnancy, particularly in interaction with predator type, habitat type, and season. Litvaitis (1990) found that male habitat use was associated with areas of greater cover, whereas females were associated with areas of greater forage. This difference may further support a proposed explanation that females have lower survival in the southern range because of increased susceptibility to predation by a suite of generalists while seeking to fulfill their higher energetic needs during breeding season. My study reveals a significant research gap on how sex-based differences in behavior influence hare survival during the snow-free months in the southern range, particularly in the face of mounting pressure from generalist predators.

Body condition of hares was a significant driver of hare survival only in the winter season, which was the season during which hares had the highest survival. Although this finding does not directly support a seasonal southern refugium model for hare survival, the absence of matrix openness as a driver of survival in winter, in conjunction with higher survival in winter overall, fits with a scenario in which generalist predators, which use more open and fragmented habitat than lynx (Buskirk et al. 2000), partially or wholly excluded by winter snowpack. The seasonal impact of body condition on hare survival offers further evidence of differences from northern hare populations. An extensive hare survival study in Alaska by Feierabend and Kielland (2015) found body condition to have little importance during periods when hare survival estimates were higher overall (July in the case of that study) and for condition to exert more influence when survival estimates were low overall (in the winter months). This seasonal pattern is the reverse of my findings in a southern population, in which survival was highest in winter. Nonetheless, these disparate seasonal survival patterns across northern and southern hare populations share a commonality of body condition only being important in winter, which is likely linked to food availability (Hodges et al. 2001). Feierabend and Kielland (2015) also found a strong link between better hare condition and ability to escape predators. Other studies have demonstrated sublethal effects of predator presence on hare body condition (e.g., Hik 1995), which would further exacerbate predation risk. Because hares die almost exclusively from predation (Keith 1990), which was also the case in my study, there does appear to be a relationship between body condition and predation risk at my sites, one that is not linked to predator use of different types of matrix. It may be that this effect exists at other times of year as well but is masked by the strong generalist predator pressure in areas with more open matrix during snow-free months. Other hare survival studies in the southern range, such as those by Wirsing et al. (2002*b*, *c*), have found little evidence that body condition affects hare survival. My study aligns with these findings in that, while body condition was significant in winter, its effect on the hazard ratio was smaller compared to the key drivers of survival in other seasons (i.e., sex and matrix openness; Fig. 4.5)

Elucidating seasonal mechanisms that regulate hare survival may allow for more targeted population management approaches, helping prevent the extirpation of regional hare populations in the face of climate change and continued habitat fragmentation. Even before the more recent threats from climate change concerns, hare populations were known to have attenuated in their southern range over time (Aubry et al. 2000, Murray 2000). Loss of southern hare populations is of particular conservation concern from a broad-scale metapopulation perspective because southern hare populations contribute genetically unique alleles, thus increasing future evolutionary potential for the species as a whole (Cheng et al. 2014). In addition, the dynamics of southern hare populations provide a model for the potential future of central and northern populations as temperatures rise and snowpack becomes scarcer.

Further and larger-scale investigations of the interaction between season and matrix quality in southern hares are therefore warranted. This study was limited in its ability to explicitly model interactions between explanatory variables because season alone violated CPH assumptions, even when added as a time-varying interaction term. However, summary measures clearly indicated seasonal hare survival patterns, and it was still possible to make inferences about habitat and demographic drivers of hare survival in each season with CPH modeling through a common solution of stratification (Therneau et al. 2023), which allowed the baseline hazard function to absorb seasonal variation, thus controlling for its influence while also evaluating the effects of other covariates. Although the season-only component of the analysis provides insights into seasonal effects, it does not account for effects of other covariates that were explored in the subsequent Cox regression analysis. I was also limited in addressing drivers of spring survival influencing hare survival due to less frequent telemetry monitoring during spring, where mud from snow-melt limited access, which reduced the between-individual variation needed for robust survival estimates.

4.5 CONCLUSION

In this study of hare survival in north-central Washington, part of the southern range of lynx and hares, I found evidence for season-specific drivers of hare mortality related to habitat quality, sex, and body condition. A key finding of this study was the association of lower hare survival in summer (but not other seasons) with open matrix/fragmented habitat. My data support a seasonal southern refugium model with a “seasonal predator access as a primary driver of hare survival” scenario. In this model, matrix quality is a main driver of hare seasonal survival and increased predation in summer months, likely due to combined pressure of both year-round specialist and mostly snow-avoidant generalist predators, further exacerbated at sites with open matrix.

Most studies of hare survival, foraging behavior, and predation avoidance have been conducted in the context of the 10-year lynx-hare cycle in northern boreal forests (Hik 1994, Murray 2002, Majchrzak et al. 2022). The lynx-hare cycle is dampened or non-existent in the southernmost range of both species (northwestern U.S. – Washington, Idaho, Montana) (Stinson 2001), suggesting a different behavioral dynamic between lynx and hare populations that may owe to the increased presence of generalist predators (Guillaumet et al. 2015) and decreased snowpack. These results suggest that southern winters are a time of preservation and protection for hares, as the presence of heavy snowpack reduces access to hare habitat by generalist predators, while warmer southern temperatures in winter allow for hares to prioritize predator avoidance behavior over maintaining body temperature. Climate change-induced earlier snowmelt and later snowfall would in this case allow increasing seasonal access to generalist predators, decreasing hare populations overall. Additionally, the lower summer survival of female hares at sites with more open matrix observed in this study present intriguing directions for follow-up research, particularly given new theories linking the 10-year hare/lynx cycle to the effect of maternal stress hormones. Recent studies suggest that through physiological changes to new hare generations caused by *in-utero* maternal stress hormones after pregnant hare exposure to predators, risk of predation may exert dampening pressure on hare demography even when the predators are no longer present (Sheriff et al. 2009*b*, 2011, Lavergne et al. 2014). Increased exposure of female hares to generalist predators in summer months may be having profound effects on long-term southern hare population stability, which could potentially contribute to the acyclic patterns observed among southern hares.

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SUPPLEMENTAL

S1 – Chapter 1 and General Field Methods Supplemental

Additional Field Data Collection Information

S1.1 Study area fragmentation and sampling of predator kill site habitat (Chapters 2 and 3)

My findings in Chapters 2 (lynx kill site features) and 3 (multi-predator analysis) should be noted with the caveat that I was unable to select the least-fragmented forest stands for hare trapping because of logistical limitations, namely the inability to access the area for repeated trapping sessions on rotation. Although this is a standard study limitation, it could bring into question whether (1) I was able to adequately represent available lynx and other predator kill site habitat under less-fragmented conditions, and (2) whether other factors such as human presence were influencing the behaviors observed in where predators killed hares. In particular, I believe I was unable to adequately sample and thus represent lynx use of the most contiguous forest available in the study area, e.g., the large swath to the northeast of my Daisy Creek/Irongate trapping stand. I initially surveyed some of these more contiguous lynx habitat (primarily mature spruce) in the region as potential study sites, and although these areas met the study site criteria otherwise in terms of the forest attributes and evidence of both lynx and hare use, they could not be included in the study because of the difficulty of repeatedly trapping and monitoring these areas; even the final six trapping stands were too spread out to be accessed within the same day, and the sites needed to be relatively near an accessible dirt road because my crew and I were hauling 40-50 9-lb traps in and out of each site individually for the trapping sessions. This is a common limitation in wildlife studies that require trapping, but it is important to note because I was unable to sample sites with minimal recent human disturbance/fragmentation. Other studies in the dense forest associated with hare and lynx habitat have also commented on logistical constraints because of distance to roads (e.g., Berg et al. 2012, Ivan and Shenk 2016). This common problem of convenience sampling (D. R. Anderson 2001) could lead to spatial correlation and nonrandom heterogeneity among subjects. In particular, some of the metrics for fragmentation that I surveyed at kill sites and reference plots, particularly distance to contiguous cover or clearing, may not have varied sufficiently to detect differences within the sampling area.

Regarding human use, all but one of the roads was closed to public access, and traffic disruption was minimal, especially in snow-off seasons. But the forest at all sites would have been affected by edge effects, particularly the three sites that were more heavily fragmented, and this could not be compared to fully contiguous forest. Additionally, snowmobilers were able to access the roads adjacent to the sites during winter and could have contributed not only noise pollution but also facilitated access into lynx habitat by coyotes by compacting snow (Bunnell et al. 2000); coyote use of snowmobile trails was often anecdotally observed in my study area. These effects are unlikely to have influenced the results of the Competition chapter because they represent common conditions in the fragmented southern range of lynx, including edge habitat used more by the generalist predators.

Habitat plots could rarely be sampled within the same day that a kill site was processed due to (a) an inability to obtain frequencies for all radio-collared hares from any single location in the study area (due to area topography), particularly once radio-collar batteries became weaker over time and took longer to clearly hear; (b) the time required for locating the kill site on the landscape with radio-telemetry, and (c) the amount of time required for detailed subsequent forensic investigations at hare mortality sites. However, I sampled habitat plots within the same season type in which the mortality occurred whenever possible. Spring plots could not be sampled until summer due to snow melt access issues. These plots had minimal deciduous vegetation, but some impacts to measurements of horizontal cover could have occurred. Spring also had the fewest hare mortalities at which a responsible predator species could be attributed as the proximate cause of mortality in general because of site access issues during that season requiring less-frequent telemetry monitoring.

S1.2 Precedence for ambush features as a measure in studies on other predators

The ambush feature scale for this study was created specifically for use in the absence of tracks because little is known about the use of ambush features by Canada lynx outside of snowy periods. However, some studies have documented structures on the landscape similar to this study's "ambush feature" measure and found them to be important to other *Lynx* spp. beyond the winter season (Podgórski et al. 2008). For example, the Eurasian lynx (*Lynx lynx*) is much larger than the Canada lynx and targets ungulate prey, making it easier to discern kill site locations outside of winter. As such, Podgórski et al. (2008) were able to measure habitat at kill sites of Eurasian lynx in both summer and winter and rated "complexity" at kill sites, which in their study was a measure for structures that would facilitate stalking and approaching prey undetected (e.g., root plates, fallen logs and branches, shrub patches). Eurasian lynx did indeed select for these features that facilitate access to prey year-round (Podgórski et al. 2008), akin to the ambush features measured in my study. However, while features that facilitate an ambush or accessibility strategy should not vary through time or space, the features that support prey abundance do vary by prey species. Ungulates and hares differ broadly in their seasonal habitat needs and life-history strategies in general; the takeaway of this comparison is that there is some precedence for creating an ambush feature metric, which may be useful in any study on predators that leverage stealth to approach prey.

S1.3 Ambush feature quality and perch quality scales

The following scale was used to quantify the quality and number of nearby ambush features (within 6 m of plot center) and far ambush features (6-15 m) in Chapters 2 and 3. The same scale was used to score potential perches for raptors in Chapter 3, specifically: perch quality directly overhead, nearby (within 6 m of plot center), and far (6-15 m).

6 ==> 2+ Good

5 ==> 1+ Good

4 ==> 3+ Possible

3 ==> 2 Possible

2 ==> 1 Possible

1 ==> Poor (any number)

0 ==> None

S1.4 Further notes on habitat plot data collection

I collected information on horizontal cover using a 2m x 0.5m checkered coverboard in 4 cardinal directions at 15m from plot center, recording coverage separately for each vertical 0.5m increment. I recorded canopy closure using a densiometer at plot center in 4 cardinal directions, averaging the measurements. Within a 5.64m-radius plot (1/100th of a hectare), I counted the number of stems of woody perennials capable of growing to tree-like height (>2m) because these species could feasibly provide year-round cover; the majority of species encountered were coniferous trees. I tallied stems >0.5m tall by species and measured the diameter at breast height (DBH) for all non-sapling trees (Griffin and Mills 2007, Hodges et al. 2009). I ocularly estimated the percentage cover of downed woody debris (DWD) >7.5cm in diameter by visually splitting the circular plot into 4 sections, estimating the DWD cover, and averaging the 4 estimates. I measured forest structure by documenting the presence, absence, or sparsity of 3 canopy layers: overstory, intermediate, and understory, noting the dominant and subdominant tree species in each canopy layer.

Habitat plots were not collected for the remaining 27 possible kills if there was not enough evidence to determine the proximate cause of mortality, or a mortality had most likely not occurred, although 4 habitat plots (2 kills and 2 replicates) had been collected before I determined they could not be included, resulting in 91 kill sites and 243 habitat plots. The lack of evidence at the remainder of the kill sites was primarily due to the mortality events occurring over spring, when site access was not possible, and there was typically insufficient evidence that the mortality event had occurred at or near the collar site when I relocated it in summer. In several instances, collars had been moved by a red squirrel (cached and/or chewed on), sometimes making it impossible to find the original kill site. An additional several suspected mortalities were likely not mortalities but rather collars that were dropped because of faulty zip-ties received from the collar manufacturer. Although there was occasionally evidence of a struggle with a predator at the site of a broken collar, this did not necessarily mean that the hare was depredated. Four of the hares that received faulty collar attachments were recaptured in later trap sessions, including one where there was clear evidence of a struggle with a predator at the site where the broken collar was found, which contributed to a cautious threshold for a verified hare mortality site as used in this study.

S1.5 Efforts to control for the influence of heavy snowfall events on horizontal cover measurements

For winter kill site (and replicate) habitat plots, the amount of snow that had accumulated on trees or downed logs around the time of the kill event was considered to potentially influence horizontal cover measurements and was controlled for when possible. Specifically, heavy snow accumulation on branches during a habitat plot would bias horizontal cover measurements if those conditions were not present around the time of the kill event. Although this is an expected concern in any study that includes winter habitat data, and specifically horizontal cover, and cannot be fully controlled for, I attempted to reduce bias of unusually heavy snowfall events that could affect horizontal cover by checking photo documentation of a winter kill site before conducting its associated habitat plots. If needed, snow was scraped or beaten off of branches and logs prior to horizontal cover measurements to try and match snow conditions at the time of the kill event, per photographs.

S1.6 Future direction: analysis of unknown predator kill sites

At quite a few snowshoe hare kill sites in my study, it was not possible to identify the responsible predator species with much certainty. However, many other studies have made presumptions about predator identity by how the carcass was handled. Until recently, there was no other option, unless the kill occurred in winter. Given that such visual identifications from the carcass alone are typically not verifiable, I did not include them in my primary analysis unless particularly diagnostic (as was sometimes the case with raptor kills). A future direction could include a separate analysis that includes some of the kills for which visual evidence suggested the responsible predator, even if not verified by saliva or tracks. One would make these conjectures with the caveat that they are not certain. However, my documentation of handling patterns for known-fate kills (those with definitive predator identifications) could potentially facilitate classification of unknown kills by likely responsible predator. One could then compare these estimates with predictions from known identifications. If conducting this analysis in the future, one could predict the responsible predators at kill sites where no identification was obtained using boosted regression trees (BRT) in R package “dismo” (Elith et al. 2008, Guisan et al. 2017).

S2 – Chapter 2 Supplemental

S2.1 Lynx habitat requirements and response to silviculture treatment

Prior studies have determined that lynx require a combination of mature, structurally-complex forests with at least moderate canopy cover (Squires et al. 2010, 2013, Holbrook et al. 2017), the presence of young, dense regenerating stands (Koehler 1990, Kosterman et al. 2018, Lewis 2011), and forest connectivity (Kosterman et al. 2018). Dense restocking practices after logging could be beneficial once sufficient time (typically at least 20 years) has passed but must be planned carefully because lynx tend to avoid forest openings (Maletzke et al. 2008). Lynx responses to other silviculture treatments are less clear, but in the Northern Rockies, lynx have been found to avoid areas where any type of silvicultural actions had been performed for up to ten years (Holbrook et al. 2018). Areas where thinning treatments are performed are used by lynx earlier (50% use at ~20 years) than areas where selection or regeneration cuts are used (50% use at ~34-40 years); additionally, where selection cuts were implemented within preferred lynx habitat (i.e., mature, multistoried forest), lynx were more likely to avoid the selection cuts (Holbrook et al. 2018).

S2.2 Further details of forest composition variable generation

To represent forest composition in the plot vicinity and reduce dimensionality, I used clustering techniques on my variables representing dominant tree species in each structural layer of the forest (overstory, intermediate, understory) to find natural breaks in frequency of association. Subdominant tree species data were dropped to streamline the classification process. Dominant tree layer variables with <5% observations (n=5 out of 18 total variables) were dropped; the inherent sparsity of this binary index justified a lower threshold for inclusion than the observations of the numeric variables in the main analysis, which received a 25% inclusion threshold. Variables dropped from the forest composition clustering were: intermediate and understory Douglas-fir (*Pseudotsuga menziesii*), intermediate and understory snags, and “other species” in the understory.

Using agglomerative hierarchical clustering and diagnostics on this forest composition data (e.g., Fig. S2.1), I assigned membership for each habitat plot into one of 3 forest composition clusters, thus collapsing the remaining 13 tree dominance variables into a single 3-category variable. Further details are in the main chapter.

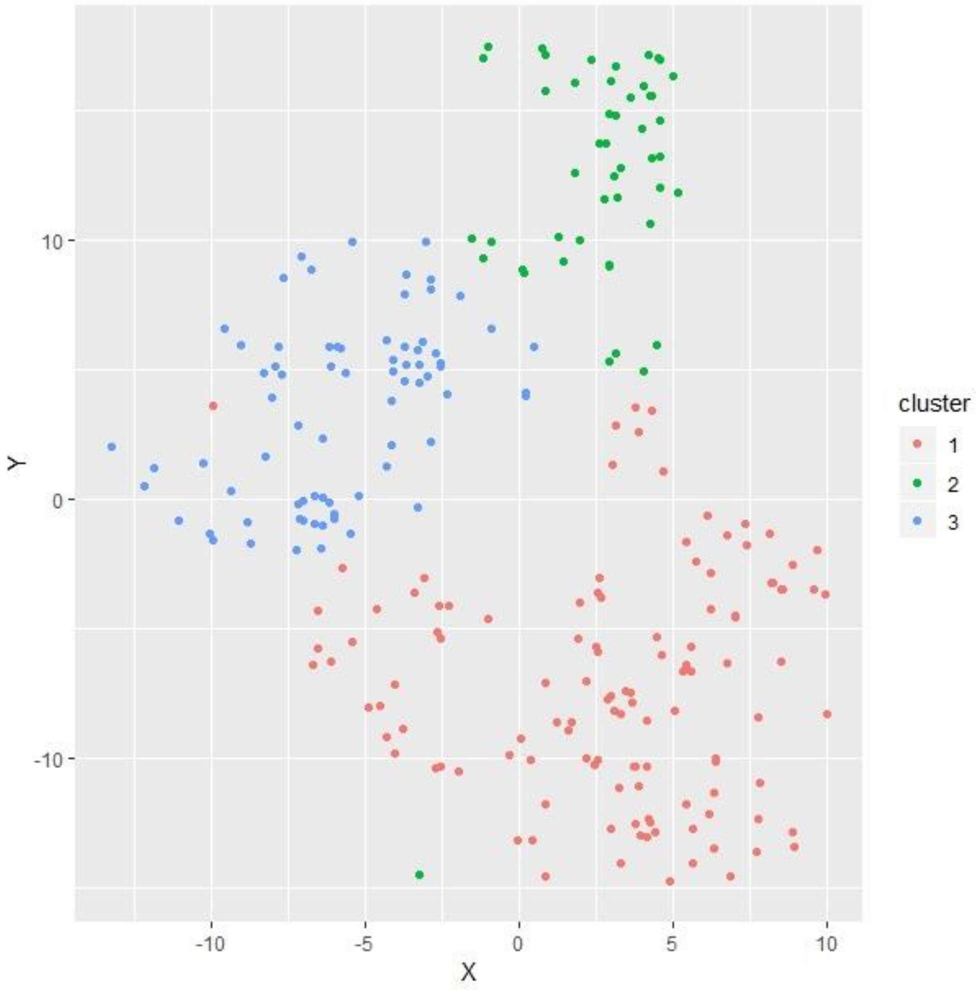

Figure S2.1. Example non-metric multidimensional scaling (NMDS) ordination plot ("metaMDS" in R package vegan) used to visualize and determine appropriate cluster membership for the forest composition variable in the lynx kill site and reference plot dataset.

S2.3 Forest age and structural complexity in the lynx kill site and reference plot dataset

Habitat plots with the maximum forest structural complexity occurred in mature forest plots (Fig. S2.2). However, lynx appeared to target and successfully capture hares in habitats with high structural complexity across all forest age categories (Fig. S2.3). This finding may be in part due to the more granular designations I used for structural complexity, which would have captured more nuanced heterogeneity in forest age and intermixed younger undergrowth and saplings than the coarser forest age categories, although both forest age and structure were measured at the same spatial scale of the plot vicinity. Furthermore, many sites could not be clearly classified as regenerating or mature, or even mixed, particularly if they were at the cusp of an interface between regenerating and mature forest.

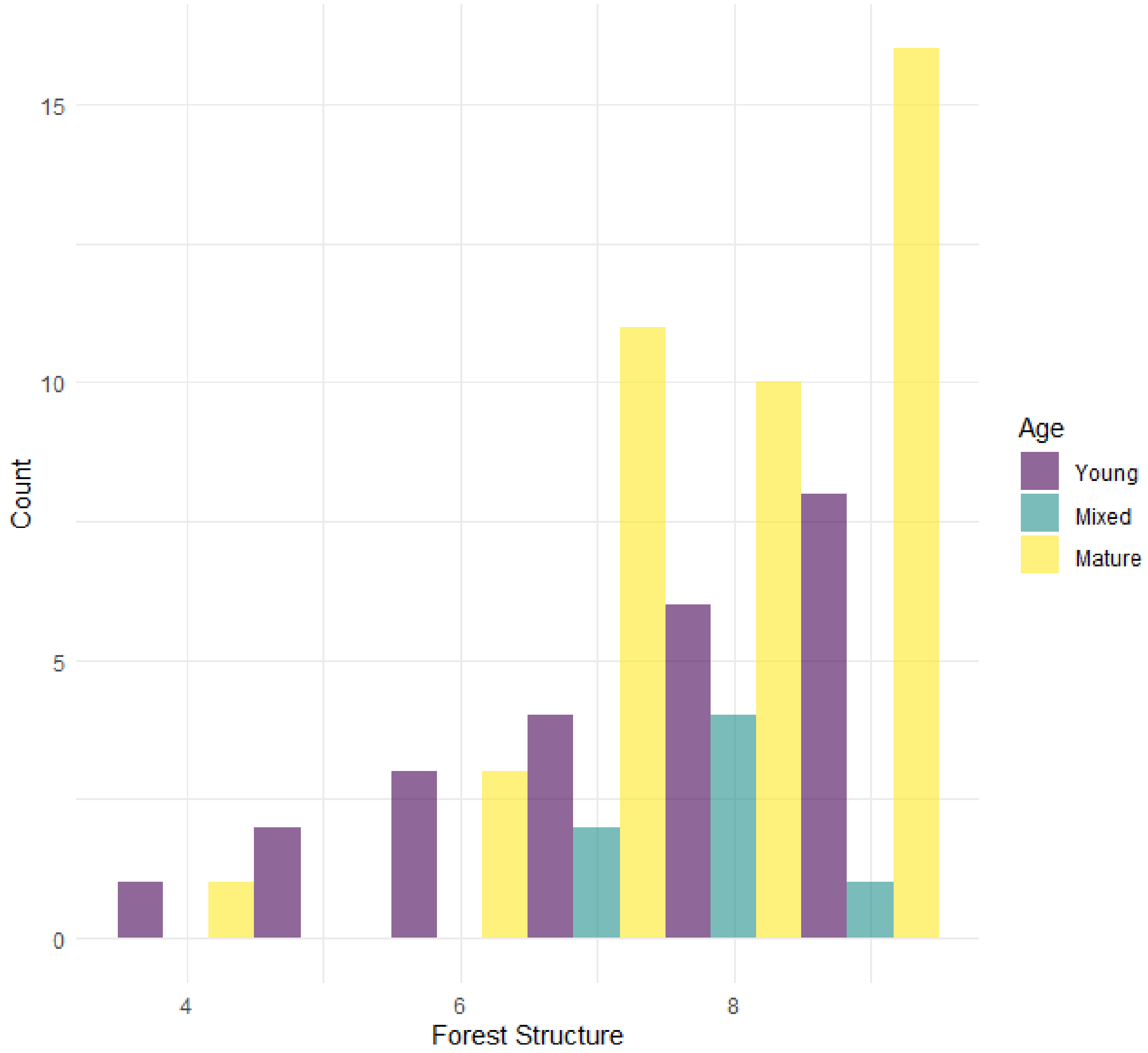

Figure S2.2. Forest structural complexity scores by forest age category for the pooled lynx dataset of kill sites and reference habitat plots. Lynx had more kills in mature forest plots than regenerating (young) forest plots, but this difference was also mostly reflected in the available habitat reference plots. Areas of at least moderately high structural complexity were available to lynx across forest ages.

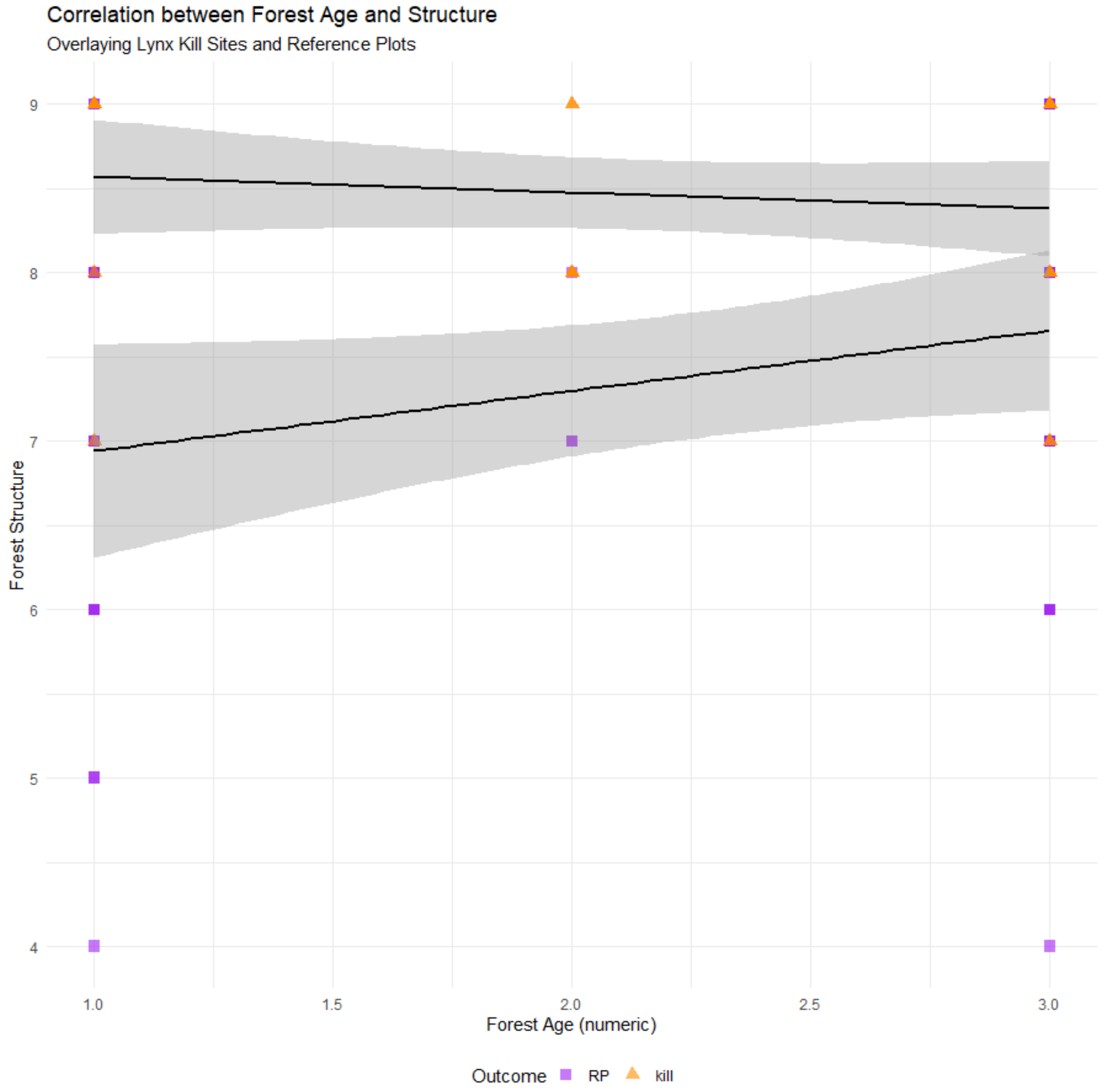

Figure S2.3. Correlation between forest structural complexity scores by forest age at lynx kill sites and reference habitat plots. Lynx kill sites had high structural complexity across forest ages.

S2.4 Stem density at lynx kill sites and reference plots

Most lynx kill sites did not occur in the highest stem density areas (Fig S2.5), but the mean number of stems (sapling and non-sapling trees) was notably higher for lynx than reference plots (232 versus 148, respectively). However, stem density was not retained as an important predictor of a lynx kill site when modeled with the other variables, even at the more liberal penalty threshold in the elastic net modeling. Prior studies in other regions have suggested that lynx are unable to access prey in regenerating forest areas with the highest stem density (Fuller et al. 2007, Ivan and Shenk 2016), but a comparison with habitat along lynx travel routes would have been necessary to conduct a similar analysis in my study because available habitat plots were unlikely to adequately sample the highest stem-density areas on the landscape.

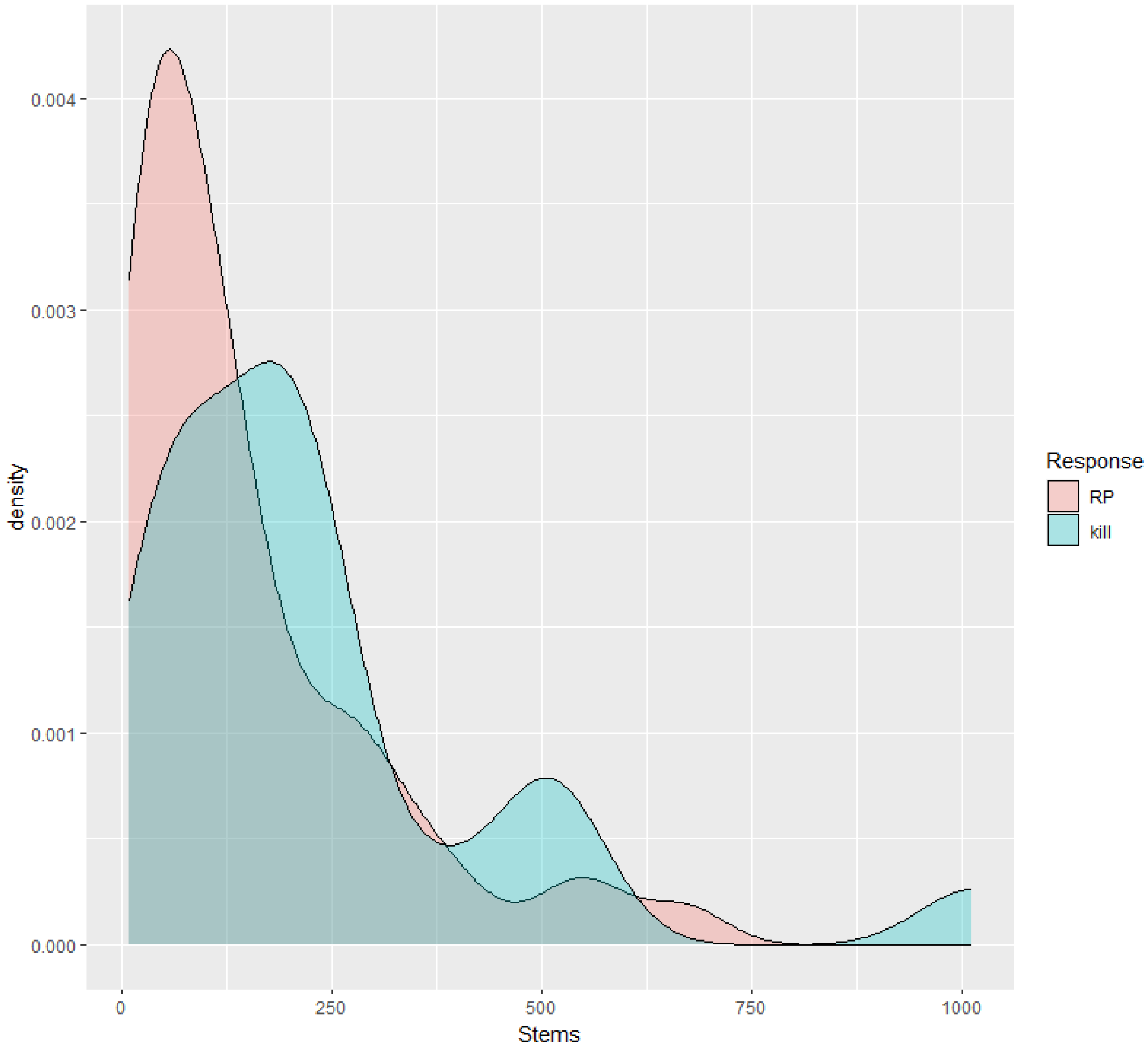

Figure S2.4. Probability density plot of stem density, that is, the number of tree and sapling trunks in the 0.1 ha fixed-radius plots at lynx kill sites and reference habitat (RP) plots. Although stem density was higher overall at lynx kill sites, this variable was not retained as a strong predictor of a lynx kill in the elastic net analysis.

S2.5 Potential evidence for forest age interface at lynx kill sites

Within lynx kills only and comparing only lynx kill habitat with trap site forest age, I found some additional evidence that lynx might be catching hares more than was expected when comparing the broader-level stand age (forest age where a hare was live-trapped) with forest age at the scale of the kill site plot, with lynx killing hares more often than expected within mature or mixed-age forest relative to the age of the overall stand (Supplemental S2), which could provide further support for an accessibility hypothesis. Hares that I monitored with radio-telemetry in this study had been live-trapped in both mature (n_{hares} = 107) and regenerating (n_{hares} = 116) forest stands, and lynx ultimately killed hares across forest age types (Fig. S2.5), despite the higher hare density in the regenerating forest type (Jensen 2020), which offers some support for the accessibility hypothesis if lynx were not targeting hares exclusively in the regenerating forest with the highest stem density. I could not rule out that some of this pattern was due to available habitat on the landscape, however, given that this was the general pattern surrounding regenerating forest stands on the landscape in this area. Nonetheless, this pattern should not have been detected if lynx were targeting hares in the highest stem density stands that supported the higher hare abundance.

Forest age is directly affected by management decisions and timber harvest schedules, which supported further exploration of any patterns in lynx foraging success by forest age. Despite forest age categories alone not predicting a lynx kill site, I found limited evidence that an interface between mature and regenerating forest affected where lynx made kills. A variable representing “habitat interface” was originally included in the lynx kill site elastic net modeling at lambda min but was ultimately dropped due to infrequent observation (present at <25% of all plots). Habitat interface was a visual assessment of whether the plot was more situated at or adjacent to a habitat interface between clearly different-aged habitats. Although a “present” habitat interface was sometimes at the edge of a clearing, it was more commonly an interface between regenerating and mature forest. This characteristic was assessed at a broader scale than cover type (i.e., at the plot vicinity level). Lynx kill sites occurred at a habitat interface twice as often as reference plots, but small sample size limited inference and justification for inclusion.

Another approach to assess forest age at lynx kill sites was a comparison between forest age where hares were trapped (i.e., stand-level forest age) and where a kill occurred, and this study found some evidence for lynx kill sites occurring in a different forest age type than the stand where hares were trapped more often than expected, but only for the regenerating stands. It was not possible to directly include trap stand age in the main analysis for lynx kill sites because there would be no difference between replicate and kill site plots. Instead, to explore whether lynx captured hares in the same forest age where the hares were originally trapped and collared, I used a Fisher's Exact Test on only the lynx kill site plots (i.e., no reference plots) to compare expected and observed proportions for trap site age (forest stand age where a hare was first trapped) and the forest age where a hare was captured by lynx. There was a significant association between stand-scale age type and whether a lynx kill site occurred in the same and contiguous habitat (Fisher Exact Test; $p = 0.0162$), with kills occurring in or at the interface of mature or mixed forest more often than expected. Hares trapped in mature stands were always caught by lynx at a spot designated as mature. In contrast, hares that were originally from regenerating stands were caught by lynx in or at the edge of mature or mixed forest 46% of the time. However, this pattern was generally also reflected in replicate plots (Fig. S2.5), but the parallel is not unexpected because hares that were trapped in the regenerating stand and subsequently killed in an adjacent habitat type would inevitably have replicates that similarly fell outside of the main stand type, given that the reference plots were only 100 m away. Although the phenomenon could be due to differences in available foraging habitat for lynx in the study area, with regenerating stands being in a more diverse-aged matrix than mature stands in general in this region, I would nonetheless expect lynx to capture hares almost exclusively in the regenerating stands where they originated if accessibility were not a hindrance, given that hare density is typically higher within the regenerating stands than in the surrounding matrix (e.g., Walker 2005). As a secondary test to the main analyses, this comparison of forest age at trap sites and kill sites could provide further insight into an accessibility hypothesis because kill site forest age should not differ from trap site forest age if lynx can access mature and the denser regenerating stands with equal ease. An alternative study design could help clarify whether lynx capture hares more than expected in mature forest when it is adjacent to regenerating forest.

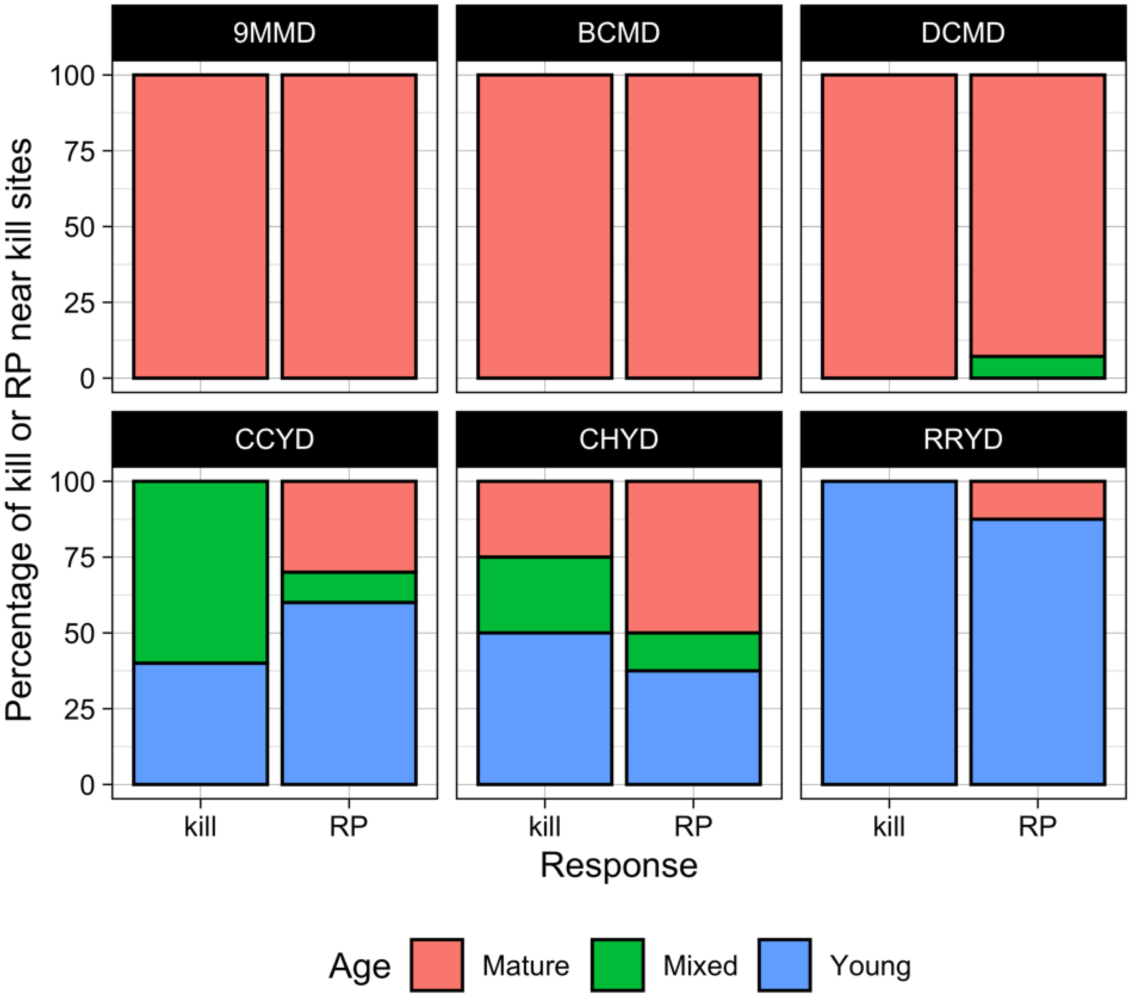

Figure S2.5. Proportion of forest ages at lynx kill locations and reference plots ("RP") across each of the 6 hare-trapping forest stands (broader scale). The top row shows the 3 mature dense forest ("MD") stands and the bottom row shows the regenerating, young dense ("YD") stands. Forest age at lynx kill sites significantly differed from the overall stand age of where the hare was originally trapped (p=0.0162; Fisher Exact Test), but this pattern could not be ruled out as being due to available habitat.

S2.6 Possible seasonal differences in lynx foraging strategies

Sample sizes in this study likely were too small to detect much seasonal difference, particularly because the structure of the main analysis did not allow lynx kill site and reference habitat plots to vary across seasons. I also conducted season-specific analyses (Wilcoxon rank tests) but ultimately discarded their findings as overly optimistic and not sufficiently rigorous. However, descriptive *post hoc* analyses suggested that the two strongest predictors (nearby ambush features and forest structure), which were the two variables most closely tied to the accessibility hypothesis, differed between kill sites and reference plots in the winter and fall, but not the spring. Conversely, increasing horizontal cover, a variable supporting the abundance hypothesis, appeared more important in the spring and in summer. Because seasonal snow melt impeded site access to biologists during the spring snow melt, relatively fewer kill sites were measured during the spring in particular, which could have contributed to the observed seasonal differences in lynx kill site habitat. However, seasonal accessibility issues for humans could also belie accessibility issues to lynx, necessitating the use of different foraging strategies during the wet and muddy spring. Lynx may also utilize a different foraging strategy in the spring and summer to take advantage of changing hare abundance and presence on the landscape (e.g., the hare breeding season), shifting habitats based on hare abundance to an extent, as has been suggested in the limited seasonal studies on lynx foraging (Squires et al. 2010). Nonetheless, these inferences are more limited, and the only variable with much magnitude of seasonal differences compared to available habitat was presence of nearby ambush features, which were scored higher in winter, despite their apparent importance throughout the year. Future studies may further parse out seasonal differences, particularly if able to obtain more kill site data during spring and summer.

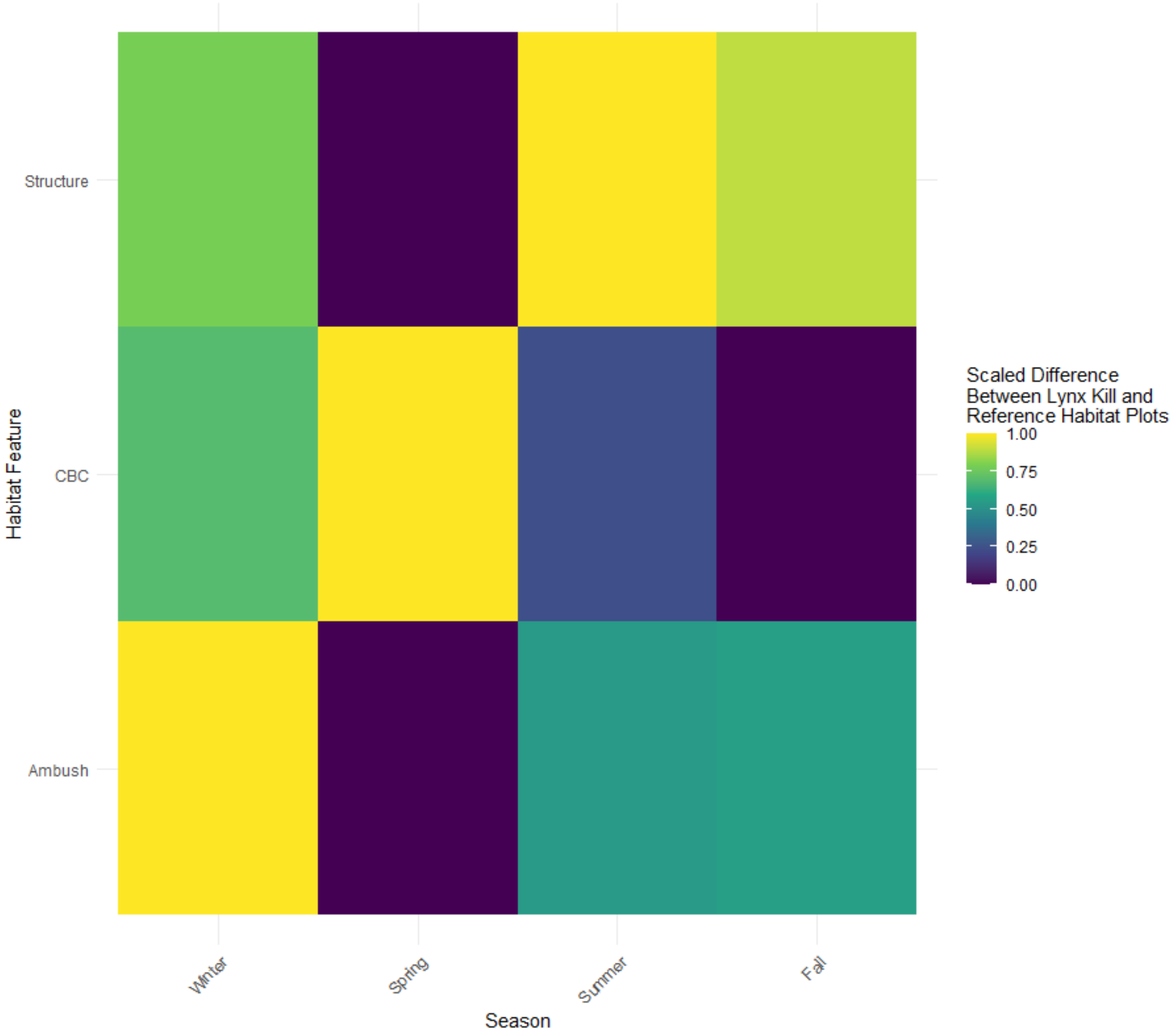

Figure S2.6. Descriptive plot showing relative seasonal variation between lynx kill sites and reference habitat plots for the top three numeric habitat variables identified as important in elastic net modeling: nearby ambush features (within 6 m), horizontal coverboard (CBC) cover at 0.5-1 m height, and forest structural complexity. Differences between kill sites and available habitat reference plots are scaled for relative comparison between the three habitat variables on the y-axis. Note that values for spring may be less reliable due to having the smallest sample size and the spring habitat data being collected in summer due to site access issues, although this would be less likely to influence the ambush or forest structure measurements. Ambush features *were used at lynx kill sites more so in winter but were important throughout most of the year. Forest structural complexity was important across most seasons but may have been more important to lynx in summer. Horizontal cover (CBC) at 0.5-1 m height was not as strongly predictive of a lynx kill on the landscape in the main analysis compared to ambush and structure variables but appeared to be more important in snow-on seasons.*

S2.7 Additional hare mortality site involving a lynx

At one additional predation event not included in this analysis, a lynx likely finished killing the hare and consumed it (along with her two subadult kittens) but did not appear to be the first to attack the hare. Rather, the hare was first captured by a great-horned owl and confiscated by the lynx, which killed the great-horned owl. I deduced the situation from the layout and location of lynx snow tracks and sit spot impressions, hare tracks, owl droppings on the nearby tall stump, and forensic analysis of the owl carcass. See "Evidence for interference competition" in Supplemental section S3 for further details.

S3 – Chapter 3 Supplemental

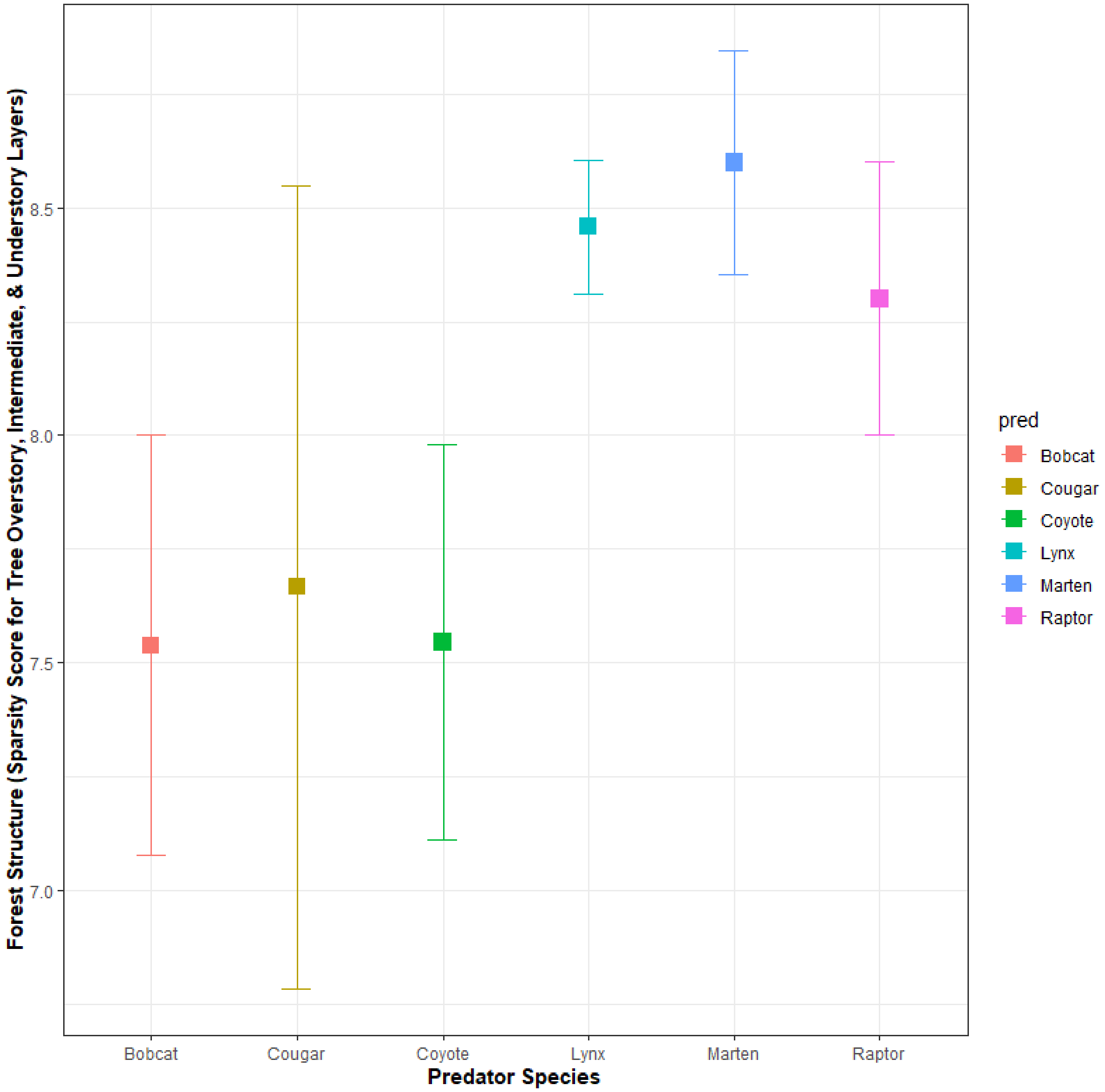

Figure S3.1. Predator species by amount of structure present in the understory, intermediate layer, and overstory at kill sites. Structure was scored numerically from 0 (absent in that layer) to 3 (fully present in that layer.)

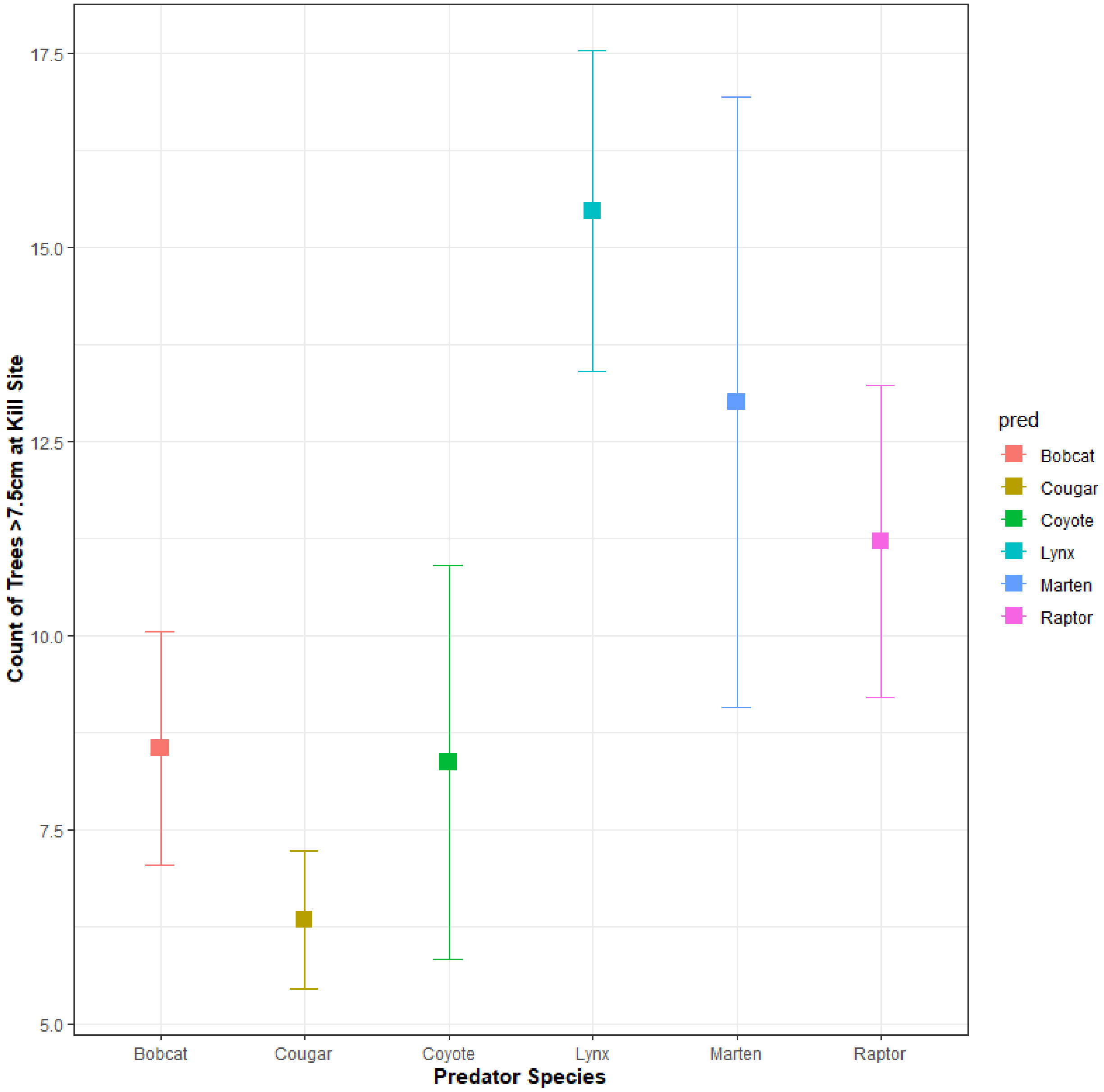

Figure S3.2. Predator species by number of non-sapling trees at kill sites plots.

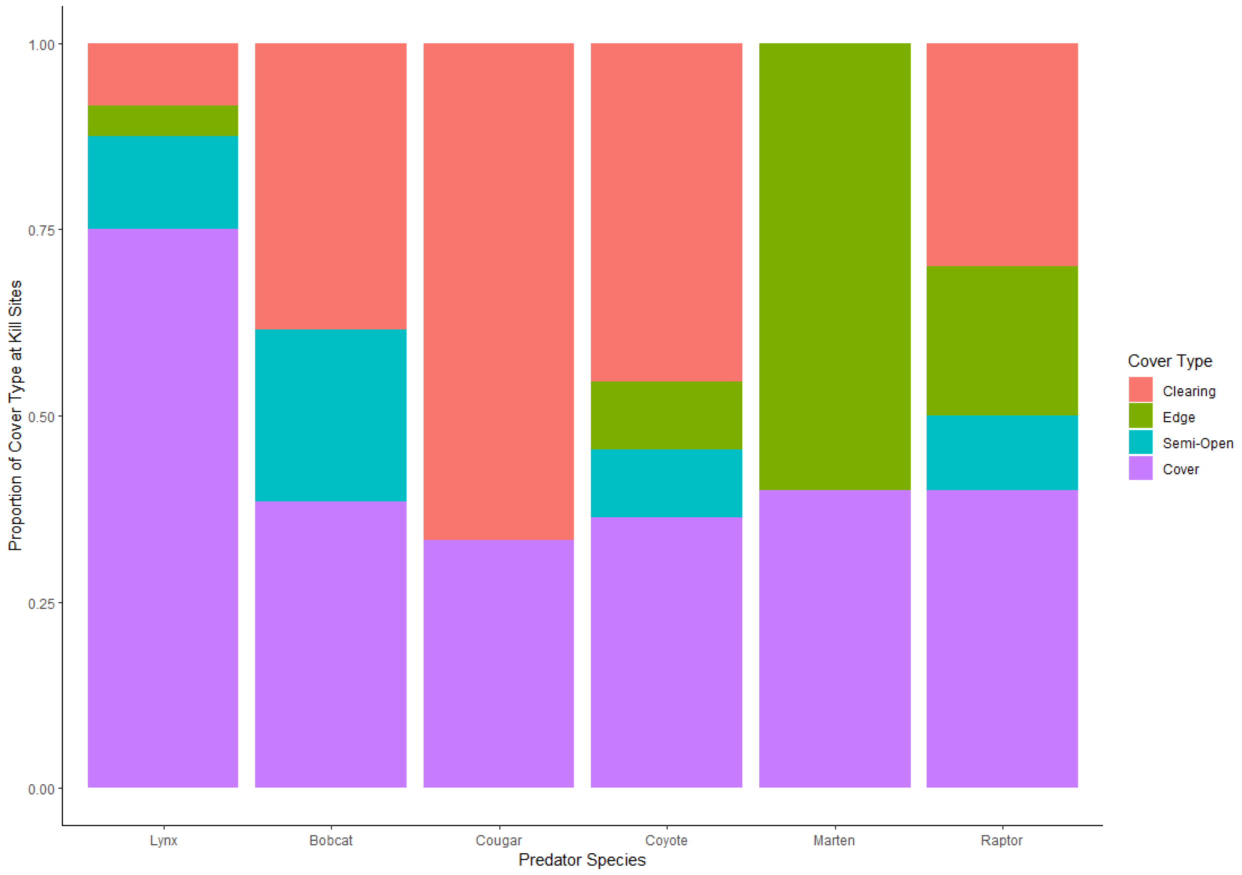

Figure S3.3. Percentage of kills by cover type for each predator species.

S3.1 Field data collection

Over the course of field work, I determined that 75.8% of potential mortalities (n=120 investigated mortalities) were predation events. Although many kill sites could not be assigned to a responsible predator with enough certainty to include in this analysis, the saliva-swabbing results provided more identifications than any other method (Peelle et al. 2019). A total of 120 potential mortalities were investigated, and 91 were determined to be mortality events and attributable to predation by any predator species.

S3.2 Other predators

Certain hare predators are more difficult to categorize purely based on the lines of generalists and specialists or hunting mode (e.g., pine martens, which are forest specialists but not prey specialists). Nonetheless, it is possible to make some predictions based on natural history and to test those predictions with predator-specific modeling. The number of pine marten-attributable hare kills was too low to likely make much inference, but their preference for mature forest may make it possible to categorize them to an extent. For example, snow depth and forest biomass are expected to have a positive effect on pine marten presence (Siren 2020) and thus, presumably, kill site habitat.

The primary raptors anticipated to depredate hares in the study area were great-horned owls and northern goshawk, both of which I observed in the area, and each was directly implicated at least once in hare kills. (Note, raptors do not salivate as much as mammals, making it extremely unlikely that raptor-attributable kills could be narrowed down to the species responsible by swabbing the remains and collar.) With great-horned owls appearing to be the most abundant raptor in the study area, I will focus on their natural history for my supplemental predictions. Great-horned owls are considered generalists, consuming a vast array of prey types (Donázar et al. 1989) and occurring across a broad range of habitats in North America. However, raptors large enough to catch hares are still restricted to using areas with trees large enough to support them and for nesting. Great-horned owls have been shown to have higher success at catching hares in more open habitat, appear to choose juveniles over adults, and select hares in good physical condition (Rohner and Krebs 1996). Indeed, Murray (2002) found that hares in poorer condition were more likely to be killed by mammalian than avian predators. This pattern of raptors catching hares in superior condition and more open areas would suggest that the hares using high-risk open areas with quality forage have benefited from the trade-off, at least until the time of the predation event. Conversely, hares in poorer condition being caught in the open would suggest condition-dependent risk-taking.

S3.3 Anecdotal note on evidence of interference competition

At one kill site currently attributed to raptor, the hare first captured by a great horned owl kill was actually confiscated by a female lynx with kittens in tow and killed by the lynx; it is unknown whether the hare was actually terminated by the lynx or the owl, but evidence at the site indicated that both predators were watching the same highly active hare runway, and the lynx was seated for some time in cover behind the owl's perch on a stump; whitewash evidenced that the owl's back was to the lynx. The lynx tracks indicated a fast gait towards the kill site, where the lynx incapacitated the owl (head injury with puncture wounds that matched the morphology of typical lynx dentition) and presumably finished killing the hare before sharing it with her subadult kittens. The owl was not consumed by the lynx family.

Figure S3.4. Hare predation site where a female lynx with kits killed a great-horned owl and confiscated the hare in it had captured, demonstrating anecdotal evidence of interference competition.

S4 - Chapter 4 Supplemental

S4.1 Continued discussion of survival covariate justifications

Body size has also been linked to increased survival in hares (Sievert and Keith 1985, Murray 2002, Wirsing et al. 2002*b*, Abele et al. 2013). In the southern range, hare body size is related to length of the growing season, which differs from northern populations, where body size increases with latitude and snow depth (Gigliotti et al. 2020). With growing season and thus food availability being a presumed driver of body size in southern populations, one might expect larger hares to be in better body condition, which could lead to increased survival because hares in better health can afford to practice more predator-sensitive foraging. However, due to the correlation between hare size and condition and to reduce the number of models considered, body size was not included in the Cox survival modeling. Although using the residuals of a regression for body condition would have reduced this correlation, this approach is not as accurate as a scaled mass index (SMI), the metric I ultimately used, at reflecting body condition (Peig and Green 2009, 2010).

S4.2 Crude mortality rates for survival analysis

I used 90-day Kaplan-Meier (KM) survival estimates to model seasonal survival, both for consistency with standard practice in wildlife literature and to align with the plots. However, I will also report basic ("crude") mortality rates, which are number of deaths divided by the total follow-up time in that strata (level of each covariate), in this supplemental material. The 90-day KM survival estimates required extensive right-censoring because of the anticipated change in juvenile weights over time. These 90-day survival estimates demonstrated the same overall pattern as the "crude" mortality rates but provided less-precise estimates because of having a lower temporal sample size, although the 90-day interval did approximate the length of seasons used in my analysis. However, crude mortality rates are more commonly used in human literature. While not intended to replace the more robust Cox proportional hazard analysis, which controlled for a baseline hazard and thus allowed for modeling of multiple predictors of hare survival, a strength of crude mortality rates as a starting point for basic reporting is that they do not require an arbitrary cut-off date for survival probability of the overall population sampled and instead use simple Poisson-based estimate. This could be particularly helpful for datasets like mine that were limited by extensive censoring to handle time-varying covariates that could not be consistently measured (e.g., hare body condition)

Table S4.1. Crude mortality rates of snowshoe hares per 1000 exposure-days by season, sex, and stand age.

Stand Age	Sex	Season	Deaths	Exposure-days	Mortality rate	Lower	Upper	SE
All	All	summer	39	15839	2.5	1.7	3.2	0.4
All	All	autumn	30	18985	1.6	1.0	2.1	0.3
All	All	winter	18	17661	1.0	0.5	1.5	0.2
All	All	spring	44	13179	3.3	2.4	4.3	0.5
All	f	summer	26	7359	3.5	2.2	4.9	0.7
All	f	autumn	21	8893	2.4	1.4	3.4	0.5
All	f	winter	8	8179	1.0	0.3	1.7	0.3
All	f	spring	19	6252	3.0	1.7	4.4	0.7
All	m	summer	13	8184	1.6	0.7	2.5	0.4
All	m	autumn	9	9540	0.9	0.3	1.6	0.3
All	m	winter	9	9004	1.0	0.3	1.7	0.3
All	m	spring	22	6680	3.3	1.9	4.7	0.7
mature	All	summer	16	7195	2.2	1.1	3.3	0.6
mature	All	autumn	13	8179	1.6	0.7	2.5	0.4
mature	All	winter	12	7872	1.5	0.7	2.4	0.4
mature	All	spring	21	5873	3.6	2.0	5.1	0.8
regenerating	All	summer	23	8644	2.7	1.6	3.7	0.6
regenerating	All	autumn	17	10806	1.6	0.8	2.3	0.4
regenerating	All	winter	6	9789	0.6	0.1	1.1	0.3
regenerating	All	spring	23	7306	3.1	1.9	4.4	0.7

S4.3 Further detail on censoring to address time-varying hare measurements

Of the 109 collared hares that were recaptured, 76 of these had repeat measurements of weight and hind foot length because individuals recaptured within the same season were typically not remeasured. It is common to not recapture all individuals in subsequent seasons, and recapture of particular individuals was not a priority of the study compared to tracking survival via radiotelemetry, but the limited per-individual remeasurements for hares that were likely still growing prevented inference about younger individuals. Hares that never reached the minimum weight cutoff of 900 g were censored after 100 days (n = 27 individuals, 10 of which were mortalities). Although only a few juvenile mortalities remained in the final dataset after censoring for stability of the time-varying internal covariates, thus preventing analysis of an age factor, there were 23 mortalities in hares under 900 g at the last time they were measured (out of 40 total including unknown fates), 17 of which were considered juveniles (i.e., were under 800 g, out of 29 total including unknown fates). Further analysis that is less strict in censoring cutoffs could provide further insight into juvenile survival patterns.

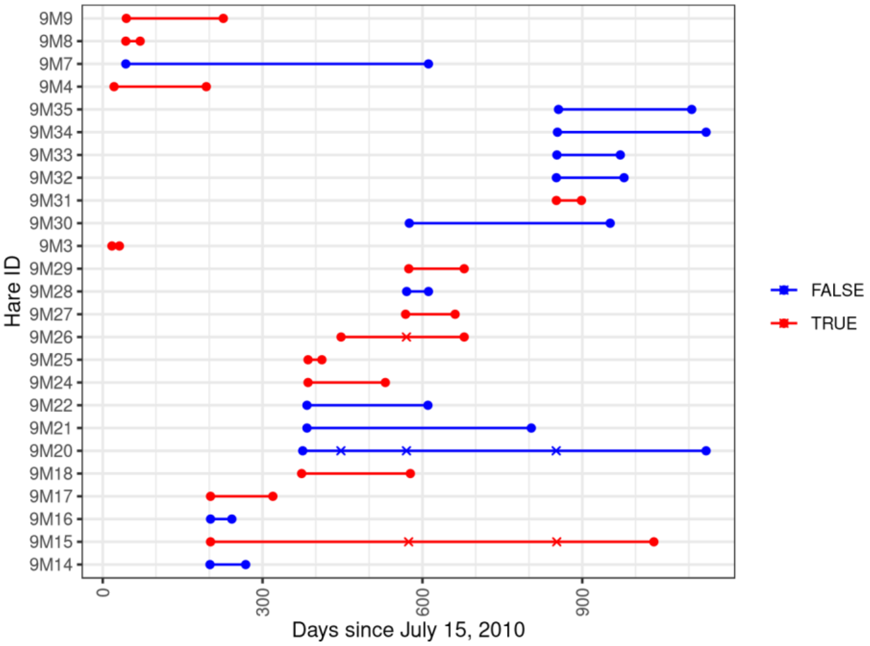

Figure S4.2. Follow-up time and status at last known alive date for hares at site 9MMD. Crosses indicate times at which hares were recaptured.

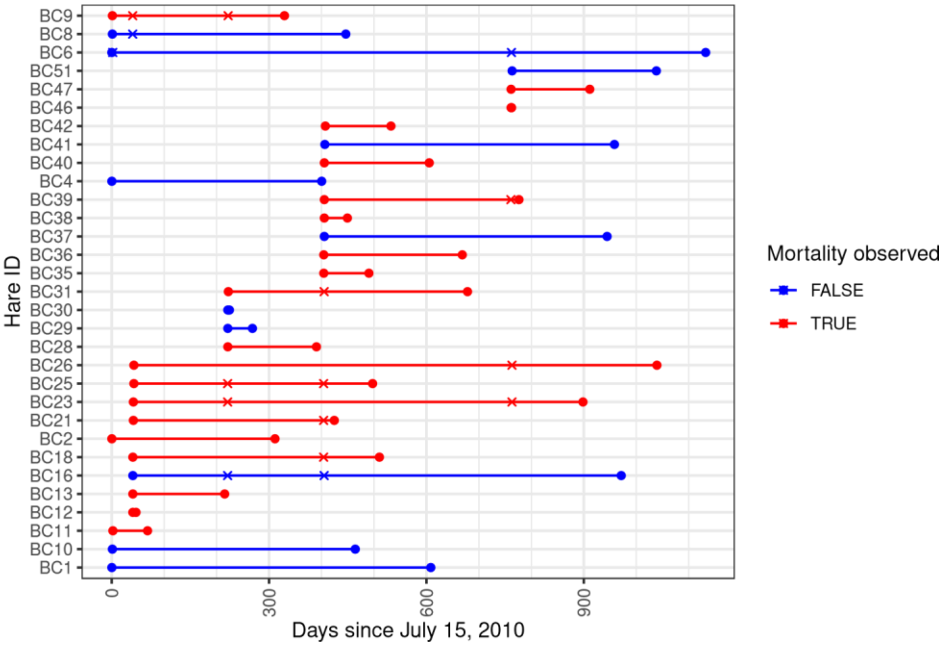

Figure S4.3. Follow-up time and status at last known alive date for hares at site BCMD. Crosses indicate times at which hares were recaptured.

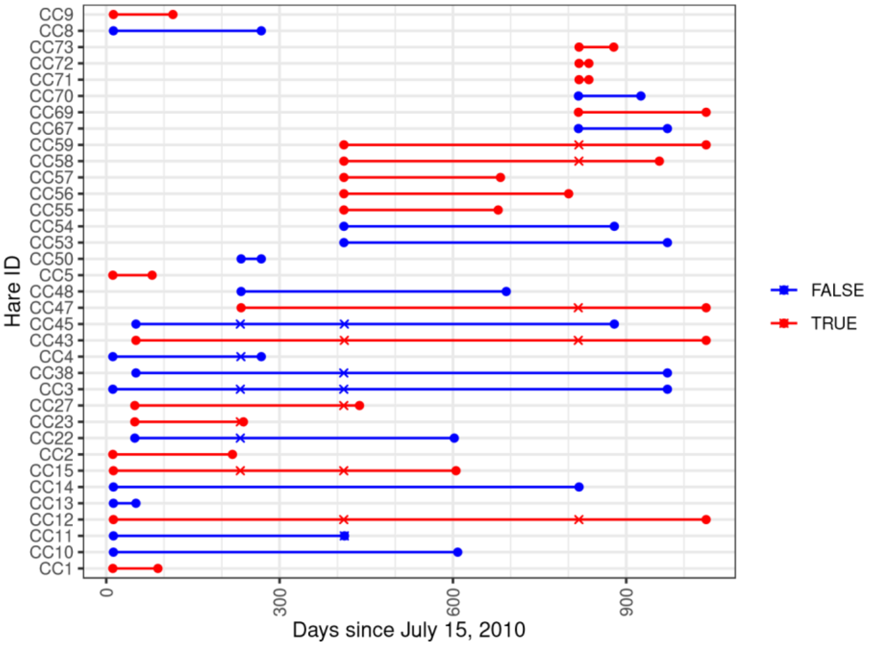

Figure S4.4. Follow-up time and status at last known alive date for hares at site CCYD. Crosses indicate times at which hares were recaptured.

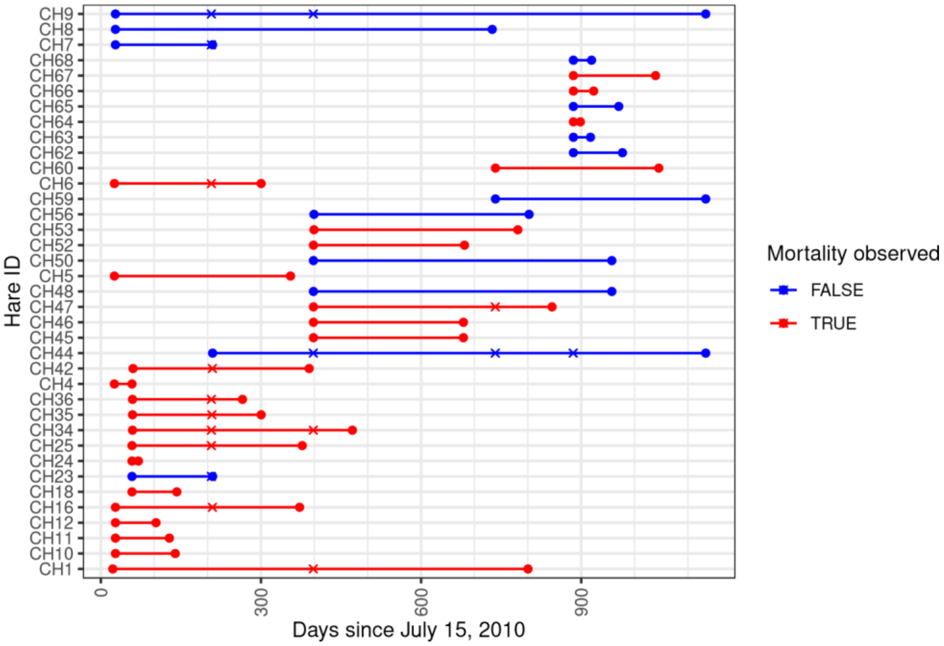

Figure S4.5. Follow-up time and status at last known alive date for hares at site CHYD. Crosses indicate times at which hares were recaptured.

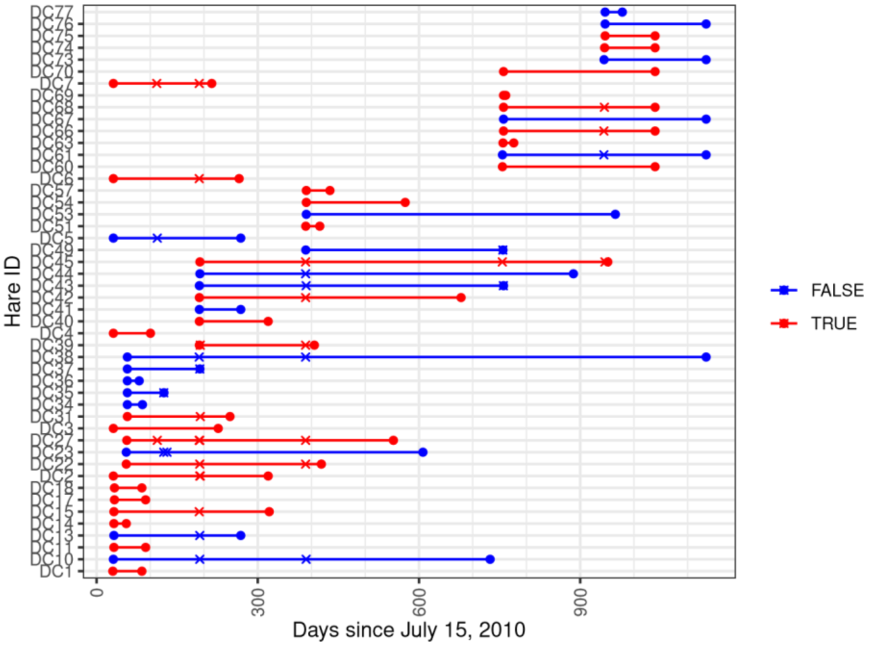

Figure S4.6. Follow-up time and status at last known alive date for hares at site DCMD. Crosses indicate times at which hares were recaptured.

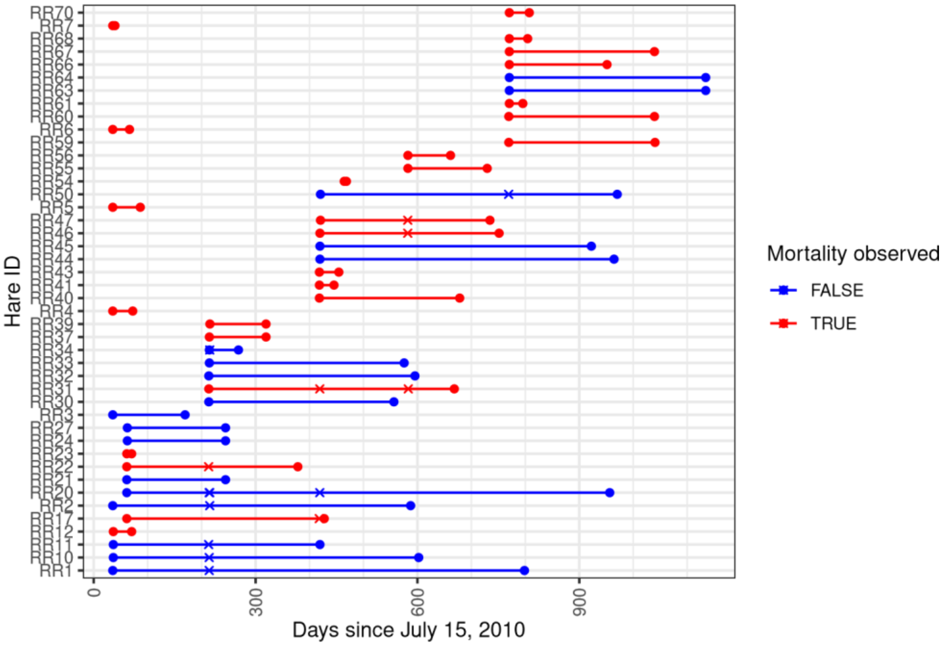

Figure S4.7. Follow-up time and status at last known alive date for hares at site RRYD. Crosses indicate times at which hares were recaptured.

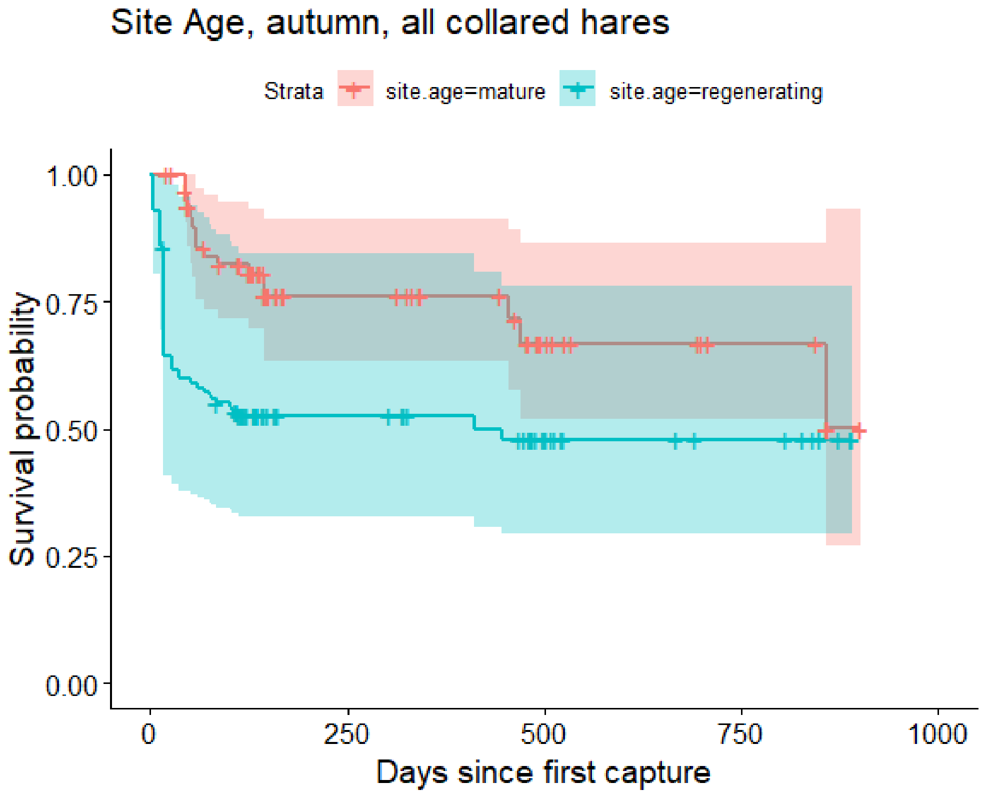

Figure S4.8. Survival by forest trapping site age in autumn. Hare survival by forest stand age in autumn showed some differences but was not retained as a top predictor in the cox modeling.

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