SPATIOTEMPORAL OVERLAP OF SYMPATRIC MESOCARNIVORES IN CENTRAL BRITISH COLUMBIA, CANADA

by

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Abstract

Many wildlife species use similar resources, leading to the potential for overlapping niches. These overlaps can create negative interspecific interactions, including different forms of competition. Niche overlap can be experienced on several different axes, including spatial, temporal, and dietary. There are many factors that may affect species co-occurrence patterns, including population cycles, natural and anthropogenic landscape change, harvest mortality, and changes in resource availability. Effective wildlife management is dependent on an understanding of the interaction between community dynamics and competition. Many mesocarnivores in central British Columbia overlap spatially, temporally, and dietarily. This high degree of overlap means that understanding the mechanisms facilitating their coexistence is particularly important. I used five years of data from remote cameras and fine-scale habitat data from LiDAR to assess patterns in the spatial and temporal co-occurrence of short-tailed weasels (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana*), fishers (*Pekannia pennanti*), wolverines (*Gulo gulo*), and Canada lynx (*Lynx canadensis*). During this study, there were fluctuations in snowshoe hare *(Lepus americanus*) abundance, as well as many predators, specifically decreases in lynx and increases in fisher.

Habitat features, like structural complexity, can facilitate species co-occurrence by allowing for fine-scale niche partitioning. I used multi-species occupancy models to test hypotheses about the relationships between mesocarnivore co-occurrence and habitat. Mesocarnivores were more likely to co-occur at sites with greater complexity of vertical forest structure and at sites closer to riparian zones. Short-tailed weasels, however, did not co-occur with other mustelids in riparian zones. Importantly, I found that habitat covariates associated with co-occurrence were relatively similar over time despite notable changes in the abundance of

predators and prey. My findings highlight the importance of riparian habitats and forest complexity in facilitating species co-occurrence in harvested forests.

Temporal niche partitioning is a second mechanism that allows species to co-exist in space and may occur if one species shifts its temporal activity patterns to avoid interactions with another. I tested the hypothesis that smaller-bodied species would shift their activity in the presence of larger-bodied species. I found partial support for this hypothesis in that marten activity differed in the presence of larger-bodied lynx when lynx were abundant but not when lynx were rare. Furthermore, the activity patterns of the largest mesocarnivores in our study, lynx and wolverine, were unaffected by the presence of smaller species. In contrast with my hypothesis, weasel activity was similar in the presence of larger-bodied species. Collectively, these findings suggest that mesocarnivores may alter their temporal use of habitat to avoid co-occurrence in response to the presence of other species.

Combined, my research provides insight into the mechanisms by which mesocarnivores—species with overlap in diet and habitat—share space. My findings highlight the importance of forest management practices that retain structural complexity and riparian areas to promote the co-existence of sympatric mesocarnivores. Further, my results emphasize the responses of sympatric species to changes in community dynamics, which is important for understanding the effects of population cycles on species co-occurrence.

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Chapter 1: Introduction

Background

Community ecology is a discipline that focuses on the interactions among species that share habitat or habitat features (Mittelbach 2012). Typically, communities are dynamic, with shifts in population distributions and densities across temporal scales. Those dynamics are regulated through various mechanisms such as predator-prey and competitive interactions (Haapakoski et al. 2013; Tilman and Kareiva 1997; Tyson et al. 2010; Zielinkski 2015). Community dynamics are also influenced by environmental conditions, such as habitat availability (Manlick et al. 2017; Smith et al. 2018), climate change (Gouveia et al. 2014), and disease outbreaks (Cunningham et al. 2019). As species adapt and respond to systemic changes, the nature of their relationships may also change. For example, changes in population size may cause localized colonization or extirpation, which in turn influences competition or predation (Cunningham et al. 2019; Kupferman et al. 2021).

Competitive interactions are particularly common among species within a guild that have commonalities in their diets, habitat, or life history strategies (Simberloff and Dayan 1991). These commonalities are referred to as “shared niche axes” and describe the resources for which species may compete (Case and Gilpin 1974). Gause’s Principle of Competitive Exclusion states that no two species at a similar density can compete for the same resources. Thus, species that co-occur exhibit partial or complete niche partitioning along at least one axis (Case and Gilpin 1974; Hardin 1960). There are several ways by which niche partitioning may occur, including spatial niche partitioning where species occupy different spaces (Fisher et al. 2013; Zhong et al. 2016), temporal niche partitioning where species use the same space at different times (Smith et al. 2022), and dietary niche partitioning where species may overlap in space and time but consume different diets (Breault et al. 2023). Additionally, species that overlap on one niche axis may differ at another, a phenomenon known as niche complementarity (Cornhill et al. 2023).

Mammalian mesocarnivores (hereafter mesocarnivores) are a diverse guild that experience varying degrees of interspecific competition. Mesocarnivores include species from the families *Felidae*, *Canidae*, *Procyonidae*, *Mephitidae,* and *Mustelidae* (Prugh et al. 2009). Mesocarnivores are primarily carnivorous and obtain food through hunting or scavenging the kills of larger carnivores (Roemer et al. 2009). To a lesser extent, mesocarnivores also forage on seeds and berries (Breault et al. 2023). Although a single mesocarnivore species has less influence on top-down community dynamics than an apex predator (Wallach et al. 2015), mesocarnivore guilds are often more numerous, diverse, and adaptable than their larger counterparts, and influence community dynamics in multiple ways (Roemer et al. 2009). For example, mesocarnivores can regulate populations of small mammals (Terbough and Estes 2010), thus, playing an important role in seed dispersal (Roemer et al. 2009). Mesocarnivores have evolved in many different habitats, including coastal regions (Ben-David et al. 1996), arid regions (Cunningham et al. 2019), and forested habitats of North America (Evans and Mortelliti 2022; Linnell et al. 2017; Ruggiero et al. 1994).

In the central interior of British Columbia, there is a wide range of mesocarnivores that use forested habitats, including wolverines (*Gulo gulo*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), Canada lynx (*Lynx canadensis*), fishers (*Pekania pennanti*), American marten (*Martes americana*), American mink (*Neogale vison*), and short-tailed weasels (*Mustela erminea*). These species differ greatly in size but have considerable overlap in diet and habitat use (Breault et al. 2023; Cumberland et al. 2001; Donadio et al. 2006, Kupferman et al. 2021; Weir et al. 2009). Previous research has examined some of the relationships between species of this guild, including marten and fisher (Fisher et al. 2013) and fisher and lynx (Mclellan et al. 2018). Few studies, however, have examined the interspecific interactions and niche overlap of these species as a group, particularly in central British Columbia.

The landscape of central British Columbia is largely forested and has experienced large-scale disturbances over the past 30 years due to forest fires (Parminter 2014), mountain pine-beetle outbreaks (Alfaro et al. 2010), and salvage logging (Lewis 2009). Disturbances may have reduced the suitability of habitat for some species, such as marten (Lofroth 1993), and increased the suitability of habitat for other species, such as lynx (Ruggiero et al. 1994). These disturbances may have contributed to changes in populations of the mesocarnivores within this region, which in turn may have altered interspecific interactions among mesocarnivores and their prey.

This study focused on five species of mesocarnivore: wolverine, lynx, fisher, marten, mink, and short-tailed weasels. Except for lynx, these species are all mustelids. The mustelids in this study are often solitary, only grouping up to mate and raise young. Typically, mustelids have long, narrow bodies with very little body fat and therefore, they require high caloric input for thermoregulation (Buskirk 1994). Wolverines are the largest species in this group and often scavenge wolf kills for food (Inman and Packila 2015; Lofroth et al. 2007). Fishers, the next largest mustelid, feed on small mammals, and specialize on porcupines (Raine 1987; Weir 1995; Weir et al. 2005). Marten, a mature forest specialist, target small prey, including snowshoe hares (*Lepus americanus*), red squirrels (*Sciurus vulgaris*), mice (*Muridae*), shrews (*Soricidae*), voles (*Cricetidae*), and passerines (Breault et al. 2023; Cumberland et al. 2001; Poole and Graf 1996). Mink are semi-aquatic and often prey on small mammals such as mice, shrews, and voles, in addition to more aquatic prey (when the conditions are favorable) such as fish, muskrats (*Ondatra zibethicus*), and amphibians (Hoffman et al. 2009; Magnusdottir et al. 2014). Lastly, short-tailed weasels are the smallest member of this group, and primarily target small mammal prey such as shrews, mice, and voles (Breault et al. 2023; Piontek et al. 2015).

Lynx are taxonomically different from mustelids, but they are considered mesocarnivores based on size. Lynx typically travel in family groups of 2–5 individuals at the height of their population cycle whereas they are more often solitary when population densities are low (O'Donoghue et al. 1997; 1998). Lynx are prey specialists, with snowshoe hares being their primary prey (Saunders 1963). Lynx and mustelids have some degree of dietary overlap and may also overlap along other niche axes. Although the specific habitat features that each of these species require varies, all require some degree of forest cover.

Research Purpose

My thesis explored the interspecific interactions among sympatric mesocarnivores, with the goal of providing context to single-species focused management and research. The predator and prey populations have shifted dramatically over time within the wildlife community of my study area (Chisholm, 2023, Crowley, et.al *In review*). Species, specifically fishers, are facing conservation concerns in this area (Fogarty et al. 2022). Having a more holistic understanding of the effects of changes to this community on species interactions may allow researchers and wildlife managers to better manage the habitats of these species. This work will help identify fine-scale habitat features that facilitate species co-occurrence in harvested landscapes, allowing for these features to be retained or created during forest harvesting operations. Accordingly, my specific research objectives were to:

1. Quantify spatial overlap between short-tailed weasels, mink, marten, and fishers in central British Columbia using camera data and fine-scale LiDAR habitat covariates.
2. Compare the temporal activity patterns of short-tailed weasels, mink, marten, fisher, lynx, and wolverine in central British Columbia using time-stamped camera data.

I hypothesized that weasels, mink, marten, and fisher would occupy sites with similar habitat features year to year, but that habitat occupancy would differ slightly among the individual species. I also hypothesized that weasel, mink, and marten co-occupancy would differ between 2015–2016 and 2020–2022 because of the increase of fishers in 2020–2022. I hypothesized that weasel, mink, marten, and fisher would co-occur within riparian habitats, as these areas have the structural complexity that each of these species prefer. Second, I hypothesized that temporal activity patterns of smaller species would differ in the presence of larger species across areas of spatial overlap. I predicted that between the two sampling sessions, the temporal activity patterns of weasel, mink, marten, and lynx would differ because of the changes in snowshoe hare populations.

These results built on the understanding of interspecific interactions among these mesocarnivores. This system is complex, with many of the components that drive interspecific interactions changing constantly (such as predator populations, prey populations, and habitat availability). This study did not seek to quantify the exact mechanisms driving these interactions, but rather explore if interactions were occurring, what abiotic factors affected these interactions, and were they more common spatially or temporally.

Thesis Format

My thesis consists of four chapters: The first chapter introduces the concepts of community ecology and niche partitioning, followed by examples that provide local context for the project. I discuss the ways that species organize themselves on the landscape to avoid negative interactions, and the theories that support these behaviours. I then introduce the study species, mustelids and lynx, and how their behaviours facilitate these interactions. Finally, I describe the research gap that this project aims to fill, which is to better understand the interspecific interactions of mesocarnivores in central British Columbia.

In the second chapter, titled “Riparian areas and fine-scale forest structure drive occupancy patterns of sympatric mustelids”, I used fine-scale habitat data to examine the spatial overlap of short-tailed weasels, American mink, American marten, and fishers. Using both single- and multi-species occupancy models, I evaluated the fit of *a priori* model hypotheses to better understand spatial co-occurrence of the focal species over the span of five years of data.

The third chapter, “Body size and prey density influence interspecific interactions in a diverse mesocarnivore community”, was designed to complement and provide context to the chapter focused on spatial overlap. Here, I used time-stamped camera data from 2015, 2016, 2020, 2021, and 2022 of wolverine, lynx, fisher, marten, mink, and short-tailed weasels to observe and compare temporal activity patterns. I used coefficients of overlap to determine if activity patterns differed from one another. Both the second and third chapters were written as manuscripts for publication, thus there is some introductory information that is repeated in both chapters.

Chapter 4, “Conclusions”, provided a final summation of the results that integrated the findings of both chapters. This chapter allowed me to explore the findings of my research in the context of British Columbia’s wildlife monitoring and forest harvesting practices. This chapter is where general limitations of this study were examined, in addition to future research recommendations.

Study Area

This study was conducted in and around the John Prince Research Forest (JPRF), located in Central British Columbia, Canada. The JPRF was formed as a partnership between the University of Northern British Columbia and the First Nations on whose traditional territory the research forest is situated: Tl'azt'en, Binche Whut'en, and Nak'azdli Whut'en Nations. Study data were collected using a camera grid that spanned a 350km^2 area that covered the entirety of the research forest (16,683 ha), in addition to areas north and west of the forest. The JPRF has experienced a long history of disturbances, from mining activity on the north shore of Pinchi Lake (1940–1975) to forest harvesting activities of various intensities starting in the 1940s. In 1999, when the research forest was established, forest harvesting in the JPRF had slowed. With a limited annual allowable cut, forest harvest occured at a scale, speed, and intensity that was much less than the surrounding area. These areas provide context to "real world conditions" outside of the research forest, to ensure patterns found within JPRF are not indicative of a refugia on the landscape.

This study took place in a forest with a heterogenous mosaic of seral stages, stand types, disturbance levels, and ecotypes. Generally, this area consisted of mixed-wood forests, including tree species such as Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), hybrid white spruce (*Picea glauca x ??*), subalpine fir (*Abies lasiocarpa*), trembling aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), and paper birch (*Betula papyrifera*). This system is classed as the dry Sub-boreal Spruce biogeoclimatic zone (SBSdw3), and is known for short, dry summers (average temperature 17°C), and long, cold winters (average temperature -10°C). The average snowpack is between 0.80m and 1.2m and persists into April. The topography of this area consists of rolling hills characterized by rocky outcroppings of limestone to the south, and of iron-rich soils to the north. There are two large lakes that form parts of the boundary of the research forest, Tezzeron Lake (7989.4 hectares) and Pinchi Lake (5554.2 hectares), in addition to many small lakes, wetlands, and streams.

The heterogenous landscape of JPRF supports a diverse wildlife community, including many large mammals (moose, elk, mule deer, white-tailed deer, wolves, grizzly, and black bears), mesocarnivores (wolverine, red fox, coyote, North American river otters, Canadian lynx, fisher, American marten, American mink, striped skunks, and short-tailed weasels), smaller mammals (snowshoe hares, muskrats, porcupines, red squirrels, flying squirrels, mice, shrews, voles), raptors (bald eagles, great Horned owls, barred owls, red-tailed hawks, goshawks), and other avian species (woodpeckers, passerines, Galliformes, and waterfowl). The diversity of wildlife within this landscape is a result of both natural phenomena, such as cyclical populations, and anthropogenic influences, such as hunting and trapping. Wildlife assemblages in this area are influenced by natural disturbances, such as wildfire, as well as by anthropogenic disturbances, such as forest harvesting. During the monitoring period in JPRF, noticeable changes occurred in the abundance of lynx, snowshoe hares, and fishers. Similar to patterns observed in the Yukon (Krebs et al 2018; Tyson et al. 2010), the lynx and snowshoe hares in JPRF demonstrated cyclical population trends in which the peak of the lynx cycle was estimated to occur in 2016 and a low in the cycle observed in 2021 (Chisholm, 2023, Crowley, et.al *In review*). The change in both predator and prey abundance in this short window of time could have major effects on other species within this system. Specifically, detections of mink and marten decreased whereas detections of fisher, wolverine, and short-tailed weasels increased.

The JPRF has been operating a camera grid within and outside the boundaries of the research forest since 2015. The grid included 42 cameras inside the research forest, 24 cameras to the north of the research forest, and six to the west of the research forest, all with identical monitoring protocols (Fig 1). The camera grid consisted of hexagonal cells of 5.41km^2. A camera was placed near the center of each hexagon. Each camera was mounted to a tree approximately one meter off the ground, and approximately three meters from a hanging bait, which included a small piece of beaver meat and scent lures (Fig 2). The cameras (Bushnell Trophy Cam model 119467 and Bushnell Trophy Cam HD Max Model 119477 [2015-2016], Browning Dark Ops HD Pro Trail Cameras Model BTC-6HDP; Browning, Utah, USA) [2020-2022]) were set to record a video for 10 seconds when triggered by movement.

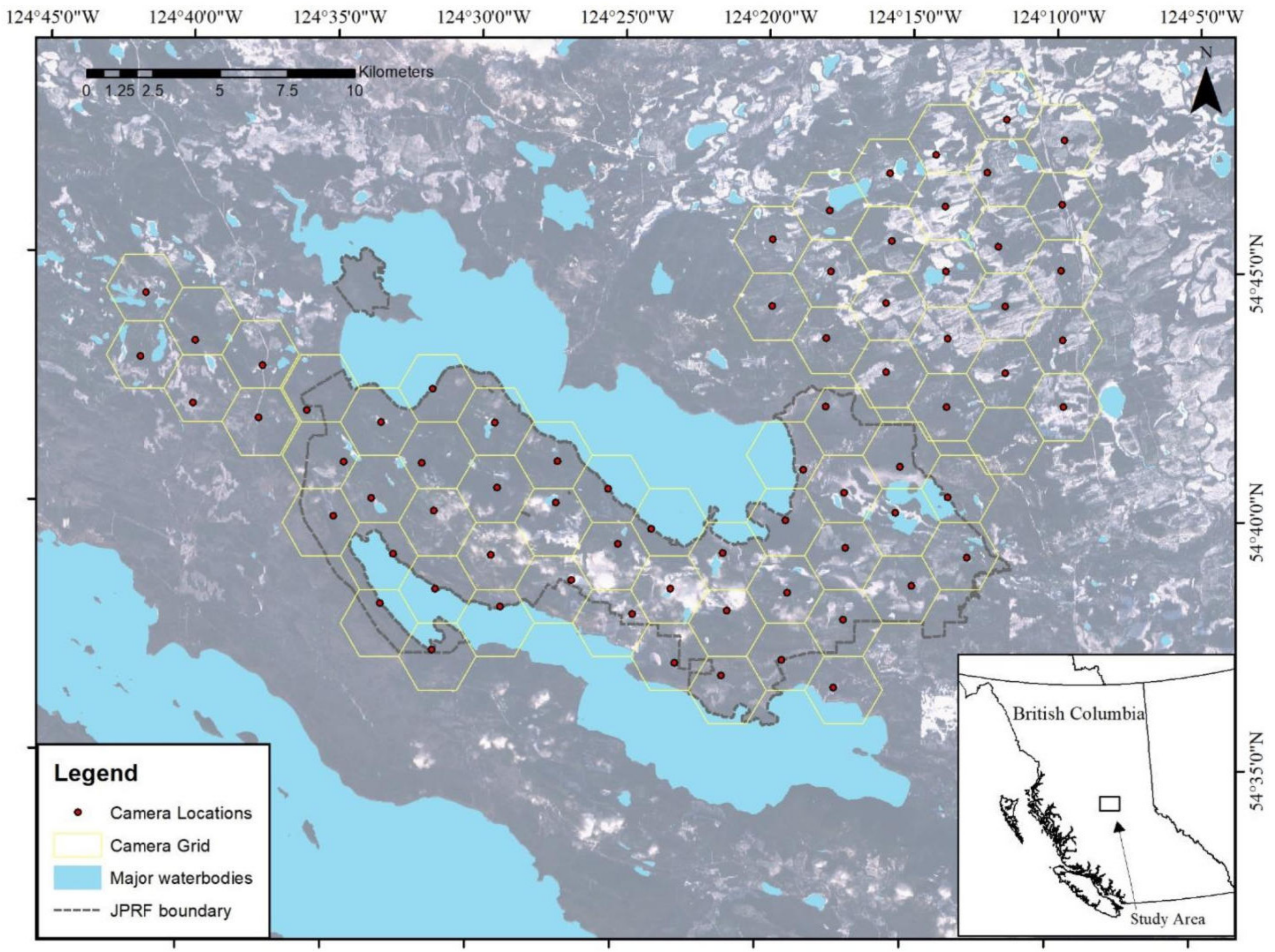

Figure 1: The camera grid used to monitor wildlife in the John Prince Research Forest, British Columbia, Canada. Each yellow hexagon represented a 5.41km^2 area, with the red dot indicating the camera location within the hexagon, for a total of 72 cameras. These cameras were in operation in 2015, 2016, 2020, 2021, and 2022. Darker shaded areas indicate mature forests, while lighter shaded areas indicate areas of forest disturbance.

Cameras were active during two sampling periods: 2015–2016 and 2020–2022. Winter monitoring occurred between February and April, and the cameras were checked every two weeks. Trained technicians watched videos and recorded species, date, and time for each session to produce presence/absence data. A session was described as the amount of time between rebaiting or checking of the camera (winter sessions are 14 days). Initially, a detection was considered independent if a species was detected once within five minutes. This short independent detection interval was designed so that different projects could use different intervals for independent detections. As described below, I used two different intervals to define an independent detection. To determine camera effort, a camera was considered “active” if it was in operation for more than 50% of the days during the 14-day monitoring session. Cameras with less than 50% active days were dropped from that session, and cameras with less than 50% active sessions were dropped from the analyses completely for that year.

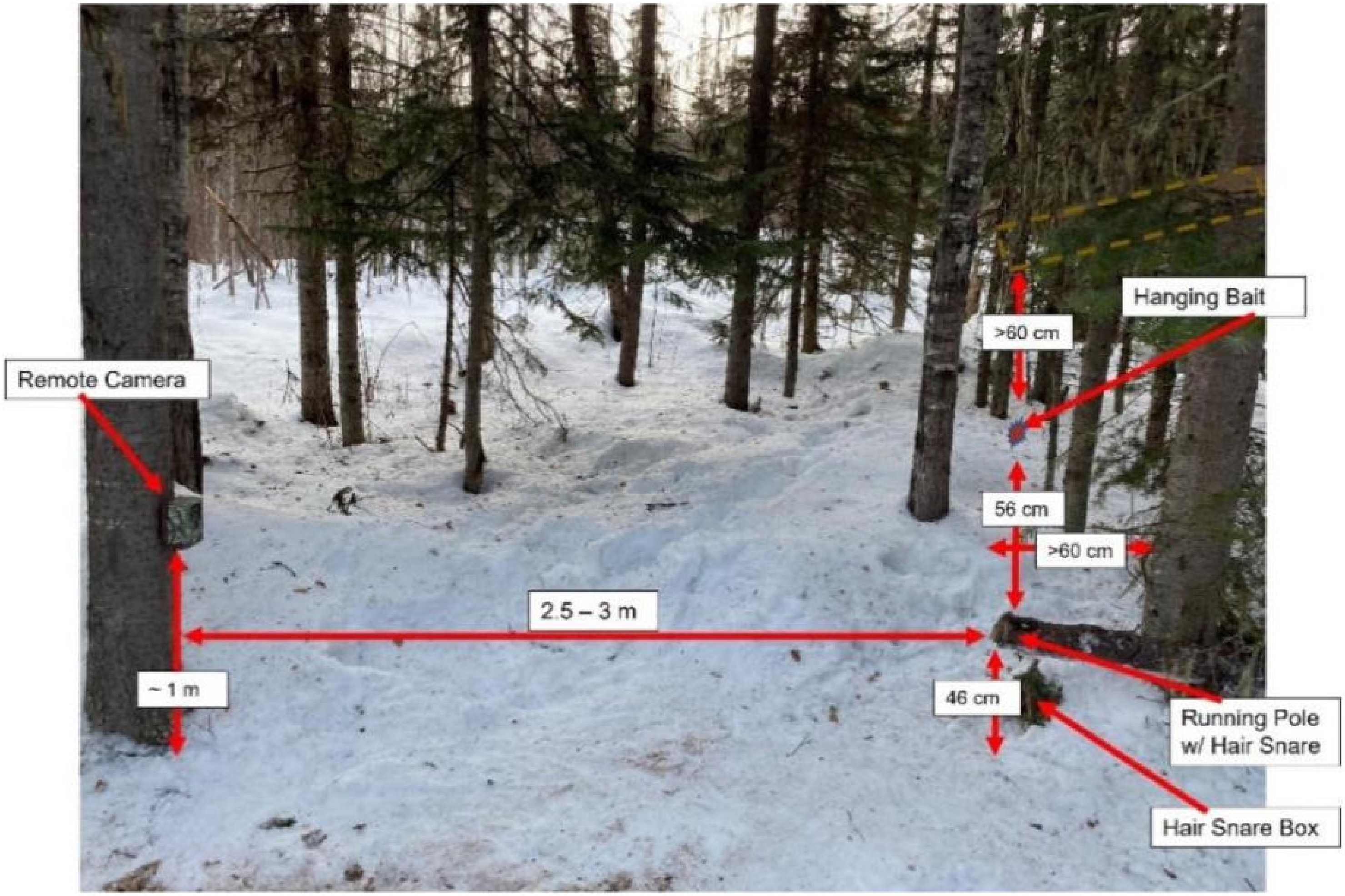

Figure 2: Typical camera trap set-up, including measurements between camera and bait set, within the John Prince Research Forest, British Columbia, Canada.

Chapter 2: Riparian areas and fine-scale forest structure drive occupancy patterns of sympatric mustelids

Introduction

Sympatric species interact in complex ways and may compete for shared resources such as food and space (Whittaker and Levin 1975). One mechanism that facilitates species co-occurrence is spatial niche partitioning, which can occur when species occupy different sites or when species use different microhabitats within a site (Tilman and Kareiva 1997). Patterns in spatial niche partitioning, however, are complex and are influenced by community dynamics such as the relative abundance of predators, competitors, and food resources (Murray et a. 2023). Habitat characteristics that influence species interactions and resource availability also have strong effects on spatial niche partitioning and, by extension, patterns in species co-occurrence (Zhong et al. 2016). Understanding variation in species co-occurrence can provide insight into mechanisms that allow species to share space.

Forest harvesting is one form of environmental change that can influence interspecific interactions through changes in population dynamics and habitat characteristics (Evans and Mortelliti 2022). For example, forest harvesting can lead to increased abundance of species that use early seral stands (Parsons et al. 2020) and reduced abundance of species that depend on more mature seral stands (Fuller and Harrison 2005). Forest harvesting may interact with natural cycles in population dynamics (Ferron et al. 1998). Better understanding the effects of population dynamics driven by forest harvesting and in conjunction with natural population cycles is important for understanding the mechanisms by which organisms share space.

Changes in habitat characteristics in harvested forests can influence interspecific interactions (Delheimer et al. 2023; Wiebe et al. 2014). For example, harvested stands often have reduced complexity of forest structure compared with mature forest, which may not provide the necessary fine-scale habitat features for many species. These features include cover (Barbeito et al. 2009; Seip et al. 2018; Wiebe et al. 2014), rest sites and dens (Weir et al. 2012), or openings (Massé and Côté 2012). The height, species, density, age, and condition of trees within a forest stand influence the wildlife species that occupy that stand (McComb 2016). Dense, tall stands often block sunlight from reaching the ground and may leave less shrub cover in the understorey (West et al. 1981), while sparse, open stands may facilitate growth of the shrub community and regenerating trees, creating abundant near-ground cover and browsing opportunities (Halls and Alcaniz 1968; West et al. 1981). Downed wood, or coarse woody debris (CWD), can provide cover and hunting grounds for small species, and in places where there is deep snow, protection from avian predators in subnivean habitats (Wiebe et al. 2014). Dead standing snags provide cavities for dens as well as nests, resting sites, and security cover (Edworthy et al. 2018). These fine-scale characteristics contribute to structural diversity and increase the potential for co-occurrence among species within a forest stand.

Riparian areas are one habitat type that is typically retained during forest harvesting. Riparian is a general term describing a diverse group of habitats, including shorelines of large lakes, edges of wetlands, large rivers, and small forest streams (Verry et al. 2004). Each of these types of riparian habitat may maintain different assemblages of species, depending on the structure available. Riparian habitats are often complex, with many of the fine-scale characteristics that may support a more diverse, species rich community of wildlife (Hamilton et al. 2015; Hannon et al. 2002; Sabo et al. 2005; Shirley 2004). Riparian areas are often comprised of complex structure, caused by gaps in the canopy and the abundance of water (Verry et al. 2004). These areas create a ecotone between two habitat types, which may naturally support a more diverse community of species (Kremsater and Bunnell 1999). While riparian management has historically been focussed on aquatic species, there has been a shift to also explore the importance of these areas to more terrestrial species. When mature forests are harvested, many animal species can become displaced and may retreat to the nearest suitable habitat to ensure survival (Courtois et al. 2008). For example, American marten (*Martes americana*) are a species that almost exclusively use mature forests and will likely move into nearby riparian habitats post-harvest (Chapin et al. 1998). Riparian specialists, such as American mink (*Neogale vison*), now may have to compete with marten within this restricted habitat (Hodder et al. 2017; Kiseleva 2012).

Mesocarnivores are a diverse guild of species with considerable potential for competitive interspecific interactions due to similar dietary and habitat needs (Roemer et al. 2009). These species are sensitive to habitat change, including forest harvesting, and many undergo cyclical population dynamics (Chapin et al.1998; Linnell et al. 2017a; Sullivan and Sullivan 2021). These circumstances provide an opportunity to better understand the effects of population changes and forest harvesting on spatial niche partitioning among species.

We used a long-term dataset to investigate patterns of co-occurrence among sympatric mesocarnivores in a harvested forest landscape in Central British Columbia, Canada. This allowed for an analysis of changes in space use during two contrasting periods when the abundance of predators and prey differed. We used camera traps and Light Detection and Ranging (LiDAR) data to evaluate fine-scale winter habitat co-occurrence patterns of four forest-dwelling mustelids including American marten, American mink, short-tailed weasel (*Mustela erminea*), and fisher (*Pekania pennanti*). These sympatric species often have similar diets (Breault et al. 2023) and habitat needs (Evans and Mortelliti 2022; Hodder et al. 2017; Manlick et al. 2017; Suffice et al. 2020) that may increase spatial co-occurrence and the potential for competitive interactions (Murray et al. 2023; Sanglas and Palomares 2022). We used fine-scale LiDAR derived forest inventory data to facilitate investigations of animal occurrence at spatial scales similar to animal movements. Locally, fishers were rarely detected until 2020, and this change allowed us to study the interactions of other species before and during the increase of this relatively uncommon species in the community.

We hypothesized that (1) habitat covariates associated with the occupancy of weasel, mink, marten, and fisher would be consistent among years and with previous literature on habitat use of each species. For example, we predicted weasels would occupy habitats with greater volumes of coarse woody debris (Linnell et al. 2017a), mink would occupy habitats closer to riparian areas (Hodder et al. 2017), marten would occupy mature forest with greater canopy closure above 10m (Lofroth 1993), and fishers would occupy habitats with less snow depth (Krohn et al. 1995). We tested this first hypothesis using single-species occupancy models. We hypothesized (2) that the habitat covariates associated with co-occupancy of short-tailed weasel, mink, and marten would differ in years with high fisher abundance. Lastly, because this system is within a disturbed landscape, we hypothesized that (3) the focal species would be more likely to co-occur in riparian habitat, which is retained during timber harvest. We tested these last two hypotheses using multi-species occupancy models.

Methods

Study Area

This study took place in and adjacent to the John Prince Research Forest (JPRF), encompassing an area of approximately 350 km^2 of mixed-wood stands between 54°35’–54°45’ N latitude and 124°10’–124°36’ W longitude. The portion of the study area adjacent to the JPRF extended beyond the research forest to the north, an area with more intensive forest harvesting.

The study area includes a variety of habitat types and seral stages. Tree species include Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), hybrid white spruce (*Picea glauca x engelmannii*), subalpine fir (*Abies lasiocarpa*), trembling aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), and paper birch (*Betula papyrifera*). The area ranges in elevation from 700–1267 m above sea level and experiences short, warm summers (average temperature 17°C) and long, cold winters (average temperature -10°C) with an average snowpack between 0.80 m and 1.2 m.

The JPRF has a history of logging dating back to the 1940s. Following the establishment of the JPRF in 1999, logging continued, but at a smaller scale, and often in consideration of research and wildlife habitat objectives. Past and current practices have created a mosaic of stand ages, composition, and complexity. Riparian features in the study area include large lakes, Tezzeron Lake (7989.4 hectares) and Pinchi Lake (5554.2 hectares), many small lakes, wetlands, and streams.

The JPRF supports a wide range of wildlife species, including a diverse group of mesocarnivores such as wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), Canada lynx (*Lynx canadensis*), fisher, American marten, American mink, and short-tailed weasel. Monitoring data between 2015 and 2022 indicated that these species had experienced shifts in population densities, notably a reduction in abundance of Canada lynx (Crowley et. al, *In review*). Lynx declines may be linked to decreased abundance of snowshoe hares (Chisholm 2023; Krebs et al. 2018). Other species, such as marten and mink, experienced declines in detections during this period as well, whereas the number of detections of wolverine, fisher, and short-tailed weasels increased.

Camera Grid Design

The JPRF operated a camera grid of 66 cameras since 2015 to observe mammal communities. The cameras were active during two separate sampling periods, 2015–2016 and 2020–2022. The camera grid spanned the extent of the research forest, with each hexagonal grid cell covering an area of 5.41km^2 (Figure 1). Cameras were placed near the center of each of the 66 hexagons. Each camera was mounted to a tree approximately 1 meter off the ground and 3 meters away from a hanging bait, which included a small piece of beaver meat and a scent lure (Figure 2). The cameras (Bushnell Trophy Cam model 119467 and Bushnell Trophy Cam HD Max Model 119477 [2015-2016], Browning Dark Ops HD Pro Trail Cameras Model BTC-6HDP; Browning, Utah, USA) [2020-2022]) were set to record a video for 10 seconds when triggered by movement. The cameras were checked and the sites rebaited every 14 days in the winter.

Trained technicians watched every video and recorded the species, the date, and the time observed in the video. For analyses presented here, we used data from February 1 to April 15 of each year. A session was described as the number of days between researcher visits to a camera (winter sessions were 14 days). A detection was considered independent if a species was detected once or more within 24-hours, so each session had a score 1–14 detections for each species. For example, if a weasel was identified in 20 videos on day one of the session, there would be one weasel detection recorded for that day. A camera that was in operation for more than 50% of the days during the 14-day session was considered "active". Cameras active for less than 50% of days within a session were excluded from that session, and cameras with less than 50% active sessions were removed from the analyses for that year.

Covariates

We used Light Detection and Ranging (LiDAR) data and field measurements to quantify nine covariates that we hypothesized would characterize the habitat of the focal species (Table 1).

Table 1: Detection and occupancy covariates used for modeling occupancy of short-tailed weasel (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana*), and fisher (*Pekania pennanti*) in the John Prince Research Forest, British Columbia, Canada, during the winters of 2015–2016 and 2020–2022.

Detection Covariates and units	**Covariate name**	**Source**	**Range**
Temperature (C°)	temp	Stuart Lake Weather Station	-15.9 – 7.3
Average time with bait (days)	bait	Camera detections	2.2 – 17.5
Occupancy Covariates and units	**Covariate name**	**Source**	
Canopy closure between 0-3 m (%)	cc0-3	LiDAR	18.3 – 83.2
Canopy closure between 3 -10 m (%)	cc3-10	LiDAR	24.3 – 92.7
Canopy closure above 10 m (%)	cc10	LiDAR	0 – 87.6
Distance to nearest riparian feature (m)	rip_dist	LiDAR	0.01 – 445.5
Dominant tree type	tree_type	Field measurements	-
Coarse Woody Debris (m^3)	cwd	Field data collected at sites	1.8 – 240.6
Snow depth (cm)	sd	Field data collected at sites	21.0 – 85.9

We considered temperature and time since bait as detection covariates in our occupancy models. Temperature data were collected from Environment Canada’s National Climate Data and Information Archive as the average temperature for the area for each session. Temperature may influence detections in different ways. For example, animals may reduce movements during warm temperatures if the snowpack becomes soft and difficult to move through or during cold temperatures to conserve energy (Zalewski 2001). We used bait and scent lure to increase the likelihood of detections, but if the bait was consumed early in the session, the likelihood of detection would decrease over time. The bait covariate was calculated by averaging the number of days between being baited and the first mesocarnivore detection.

We used seven variables to represent various aspects of habitat within the occupancy models. Occupancy covariates were derived from LiDAR or field measurements. LiDAR data were collected between August 14 and September 10, 2015, with an average realized pulse density of 8–10 pulses/m^2. These data provided a detailed image of the landscape and were refined into metrics that represented vegetation structure at the time of data collection.

Covariates were extracted from a 50-meter radius centered on the camera location. These covariates included representations of canopy closure for vertical layers in the canopy ranging in height above ground from 0–3m, 3–10m, and above 10m, as well as distance to riparian features. The canopy closure covariates described the complexity of the stand in each height class; a higher value represented more complexity at that height above ground. The canopy closure measurements at 3–10m and above 10m were corrected for winter conditions (without leaves) in deciduous-dominant sites as LiDAR data were collected during summer (Crowley et. al, *In review*). Canopy closure in the 0–3m height class reflected the relative amount of low shrubs and regenerating trees. Canopy closure in the 3–10 m height class represented tall shrubs and regenerating trees that were more than 3 m in heigh. Notably, canopy closure between 3–10 m represented multiple habitats, primarily regenerating coniferous plantations and shrubby riparian forests. Canopy closure above 10m represented the cover from taller and mature trees. Distance to riparian habitats described how close the camera location was to riparian features including small streams, rivers, wetlands, or lakes.

Covariates reflecting tree composition, coarse woody debris, and snow conditions were recorded at each camera site. Tree composition was classified as deciduous, coniferous, or mixed based on dominant trees within a circular plot with an 11.28-m radius centred on the camera site. Sites were classified as deciduous if >75% of the trees within the plot were deciduous and coniferous if >75% of trees within the plot were coniferous. Sites with <75% of either type of tree were categorized as mixed. Coarse woody debris volume was measured at each site using three 50m long transects radiating out from the camera location (Stevens 1997). Snow depth was measured at the beginning of every session (once every two weeks) by pushing a stick with a measuring tape attached into the snow column vertically until it hit the ground.

Tolerance scores were used to assess these covariates for excessive collinearity (Menard 2002) with a threshold of 0.1. All scores were > 0.1.

Occupancy Models

Single species occupancy models

I used the single-season, single-species occupancy models to test my first hypothesis, that habitats associated with occupancy of the four focal species (i.e., weasels, mink, marten, and fishers) would vary among years. I fit models using the R package "unmarked" (Fiske and Chandler 2011). A species was considered present if detected on one or more days during a two-week session. Weasels occurred at a large proportion of sites across years (e.g., 61 out of 66 sites in 2022). This high occupancy rate caused several of the models to be overparameterized or non-convergent. Accordingly, I developed an adapted index of presence or absence to correct for the large number of weasel detections. Specifically, in 2015, 2016, 2020, and 2021, weasels were considered absent at sites with 0 or 1 detections within a two-week session and present at sites with 2 or more detections. In 2022, weasels were considered absent at sites with <3 detections within a two-week session, and present at sites with 3 or more detections. This correction still included 45 of 66 (68% naïve occupancy) sites with detections in 2022. This correction may better represent the core habitat of weasels, by distinguishing between habitats where weasels are found in high versus low densities. Fishers were detected only once in each of 2015 and 2016, so only models for 2020, 2021, and 2022 were built for fishers.

I defined a set of 12 models that represented *a-priori* hypotheses explaining habitat occupancy of the focal species, in addition to a null model (Table 2). Models for each year and species were run separately in the "unmarked" package in R and then compared to the null model using an Akaike information criterion with a correction for small sample size (AIC_c) ranking. (Mazerolle 2023). Before fitting the occupancy covariates, I identified detection covariates by comparing three models with either temperature, time since bait, or a constant on the detection parameter and a constant on the occupancy parameter. I did not use temperature and time since bait together to avoid model overparameterization. The covariates from the highest AIC_c ranked model for detection was used in subsequent models to evaluate models with different combinations of occupancy covariates. Occupancy covariates from models that held 75% of the model weights were considered to have substantial support and were used in subsequent multi-species modelling.

I used the Mackenzie-Bailey goodness of fit test (Mackenzie and Bailey 2004) to perform model validation on the single-species models to determine if the highest ranked models fit the data adequately. If the *c*-hat value of the global model was above the threshold, the models were ranked using QAIC*c* to address overdispersion of the data.

Table 2: Single-species occupancy models for short-tailed weasel (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana*), and fisher (*Pekania pennanti*) in 2015, 2016, 2020, 2021, and 2022 in the John Prince Research Forest, British Columbia, Canada.

Model Name	Covariates included
Full habitat model	cc0_3 + cc3_10 + cc10 + rip_dist + tree_type + cwd
Vertical structure	cwd + cc0_3 + cc3_10 + cc10
Mature Forest type	cc10 + tree_type
Riparian structure	cc0_3 + cc3_10 + rip_dist
Type of riparian	rip_dist + tree_type
Ground- to mid- story complexity	cc0_3 + cc3_10
Riparian	rip_dist
Ground complexity	cc0_3
Mid-story complexity	cc3_10
Mature stand canopy closure	cc10
Coarse Woody Debris	cwd
Snow depth	sd
Null	(no occupancy covariates)

Multi-species Occupancy Models

To evaluate hypotheses 2 and 3, all possible species combinations were run from the two “seasons” of sampling (nine combinations), with the highest AICc-ranked single-species occupancy models or covariates being used from each species, in addition to distance to riparian and mid-story complexity (cc3–10m) to test hypothesis 3 (Table 3). I compared the multi-species models to a null model, then ranked them based on AICc scores for small sample sizes (Fiske and Chandler 2011; Mazerolle 2023). Conditional two-species models were built for the two periods of sampling: the first period was the winters of 2015, 2016 and the second period was the winters of 2020, 2021, and 2022. Species detections were combined for the years included in each season (2015/2016 and 2020/2021/2022). The multi-species occupancy models produced 3 types of results for each model, and each scenario was presented for each of the covariates within the model.

- Scenario 1: likelihood of occupancy when species one is present while species two is absent.
- Scenario 2: likelihood of occupancy when species two is present and species one is absent.
- Scenario 3: likelihood of occupancy when both species are present.

Table 3: Multi-species occupancy models for each period (2015–2016 and 2020–2022) and species pairings between short-tailed weasels (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana*), and fisher (*Pekania pennanti*) in the John Prince Research Forest, British Columbia, Canada.

Species pair	Years	Top single-species models included in each multi-species framework
Marten and Weasel	2015–2016	Mid-story complexity, ground- to mid-story complexity, mature forest, distance to riparian.
Marten and Mink	2015–2016	Mid-story complexity, ground complexity, mature forest, distance to riparian.
Mink and Weasel	2015–2016	Mid-story complexity, ground complexity, distance to riparian.
Fisher and Mink	2020–2022	Mid-story complexity, distance to riparian, snow depth.
Fisher and Marten	2020–2022	Mid-story complexity, ground complexity, mature forest, snow depth.
Fisher and Weasel	2020–2022	Mid-story complexity, distance to riparian, mature forest, snow depth.
Marten and Weasel	2020–2022	Mid-story complexity, ground complexity, distance to riparian.
Marten and Mink	2020–2022	Mid-story complexity, distance to riparian.
Mink and Weasel	2020–2022	Mid-story complexity, mature forest, distance to riparian.

Results

From the 66 cameras, 13971 videos were captured of the four focal species between February 1 and April 15 of 2015, 2016, 2020, 2021, and 2022. The average camera effort was 94% active across all years, with 2% of the sessions dropped in 2015, 2016, 2020, 2021, and 7% in 2022. Three sites were dropped completely in 2022, with less than 50% active sessions in total for the year. There were 269 videos of fishers, resulting in 64 independent detections at 30 sites. Two fisher detections, one in 2015 and another in 2016, were not used in the analyses. There were 5188 videos of marten, resulting in 377 independent detections at 55 sites, and 432 videos of mink, resulting in 76 independent detections at 30 sites. There were 8082 videos of weasels, resulting in 349 independent detections at all 66 sites. Once weasel detections were re-classified into high versus low weasel detections, there were 242 independent detections at 41 sites.

Detection covariates identified using single-species occupancy models

Of 18 species-year combinations, the null model for detection was ranked highest ten times. The model with temperature as a detection covariate was ranked highest seven times, four times for weasels, once for mink, and twice for marten. The direction of the effect of temperature varied among years and species; weasels were more likely to be detected when temperatures were warmer in 2020, 2021, and 2022 and less likely to be detected when temperatures were warmer in 2015. Mink were less likely to be detected when temperatures were warmer in 2016. Marten were more likely to be detected when temperatures were warmer in 2020 and 2021. The temperature covariate was only significant for weasel in 2022, mink in 2016, and marten in 2020 and 2021. Time since bait was identified as a detection covariate in only one model—for weasel detections in 2016. Weasels were less likely to be detected the longer the time since bait was added to the site; however, the effect was not significant.

Habitat covariates associated with occupancy among years for each species

I used single-species occupancy models to test hypothesis 1, which was that habitat covariates associated with occupancy would be similar among years for each species and that habitat covariates associated with occupancy would reflect species-specific habitat requirements.

Overall, the top model testing the association between habitat covariates and occupancy differed among years for each species, with covariates being most variable among years for weasel and less variable for mink, marten, and fisher (Table 4). The null model for occupancy was only the highest ranked in weasel models, in 2015, 2020, 2021, and 2022. Complete model outputs for each species and each year can be found in Appendix 1.

Habitat covariates associated with occupancy were inconsistent among years for weasels, with almost no interannual pattern to habitat occupancy. Weasels were less likely to occupy sites closer to riparian habitats in 2021 and 2022; however, the relationship was not statistically significant in both years and ranked below the null model. Canopy closure between 0–3m occurred in some of the highest-ranked models in 3 of 5 years, but the directionality of the relationship was inconsistent; the association was positive in 2015 and 2022 and negative in 2020. The null model ranked the highest in 4 of the 5 years.

The 'riparian' model was ranked highest for mink in four of the five years of the study. Mink were less likely to occupy sites at greater distances from riparian; this relationship was significant in 2020 and 2022. In 2016, the 'mid-canopy' model was ranked highest. Mink were less likely to occupy sites with greater mid-canopy complexity (cc3–10), but the relationship was not significant.

Marten were less likely to occupy sites with greater canopy closure between 3–10 m in 4 of 5 years; coefficients for this relationship were significant in all years. Marten were also less likely to occupy sites with greater proportions of canopy closure between 0–3m in 3 of 5 years, but the relationship was only significant in 2015. In 2020, the CWD model was the highest ranked; the association was positive but not significant.

The top models for fisher were ‘snow depth’ in 2020, ‘riparian’ in 2021, and ‘snow depth and riparian’ in 2022 (Table 4). Overall, fishers were less likely to occupy sites farther from riparian and with greater snow depths; the only significant coefficient, however, was distance to riparian in 2021.

Table 4: Coefficients for occupancy (ρ) and detection (ψ) parameters, AIC*c* ranking, and model weight from single species, single season occupancy models built for short-tailed weasel (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana*), and fishers (*Pekania pennanti*) using detections from cameras deployed in the winters of 2015, 2016, 2020, 2021, and 2022 in the John Prince Research Forest, British Columbia, Canada. Models shown were the highest AIC*c* ranked of candidate models compared for each species and year. Models with a (.) are the null models. Coefficients in bold font were statistically significant ($p=<0.05$). AIC*c* values with a (*) are representative of QAIC*c* values.

Species	Year	Model	ρ(temp)	ρ(bait_time)	ψ(cc0-3)	ψ(cc3-10)	ψ(cc10)	ψ(rip_dist)	ψ(cwd)	ψ(sd)	AIC*c*	ωi
Weasel	2015	ρ (temp) ψ (.)	-0.16								57.33 *	0.31
	2016	ρ (bait_time) ψ (cc3-10)		-0.16		0.03					163.4 *	0.29
	2020	ρ (temp) ψ (.)	0.53								189.76	0.23
	2021	ρ (temp) ψ (.)	0.13								169.27 *	0.21
	2022	ρ (temp) ψ (.)	**0.09**								162.82 *	0.26
Mink	2015	ρ (.) ψ (rip_dist)						-0.04			149.51	0.55
	2016	ρ (temp) ψ (cc3-10)	**-0.27**			-0.1					114.38	0.42
	2020	ρ (.) ψ (rip_dist)						**-0.04**			86.75	0.2
	2021	ρ (.) ψ (rip_dist)						-0.1			41.24	0.57
	2022	ρ (.) ψ (rip_dist)						**-0.07**			138.11	0.31
Marten	2015	ρ (.) ψ (cc0-3)			**-0.07**						84.53 *	0.22
	2016	ρ (.) ψ (cc3-10)				**-0.09**					166.68 *	0.50
	2020	ρ (temp) ψ (cwd)	**0.37**						0.01		174.30 *	0.20
	2021	ρ (temp) ψ (rip_dist)	**0.38**					**-0.05**			91.56 *	0.42
	2022	ρ (.) ψ (cc3-10)				**-0.05**					166.39 *	0.21
Fisher	2020	ρ (.) ψ (sd)								-0.04	166.57	0.25
	2021	ρ (.) ψ (rip_dist)						**-0.05**			128.3	0.4
	2022	ρ (.) ψ (rip_dist + sd)						-0.04		-0.16	154.22	0.26

Habitat variables associated with species co-occurrence during periods of high and low fisher abundance.

Multi-species occupancy models were used to test my second hypothesis, which was that habitat covariates that influenced co-occurrence of mink, marten, and weasels differed during two time periods with contrasting fisher abundance. Overall, similar habitat covariates were associated with species co-occurrence in 2015–2016 and in 2020–2022. Moreover, the direction of the relationships with the covariates (positive or negative) was also relatively consistent between periods. Complete model outputs for each species pair and each time period can be found in Appendix 2.

The highest-ranked co-occurrence covariates for marten and weasels in 2015–2016 were canopy closure between 3–10m and canopy closure between 0–3m. In 2020–2022, the highest-ranked covariate was canopy closure between 3–10m (Table 5). Marten and weasels were more likely to co-occur at sites with a lower percent cover between 3-10m, but this relationship was not significant in either period.

The highest-ranked covariate for mink and marten in both 2015–2016 and 2020–2022 was canopy closure between 3–10m (Table 5). Sites where both mink and marten were detected were more likely to have greater complexity between 3–10m, although the relationship was not significant in either period. In both periods, sites with marten but not mink had a negative association with canopy closure between 3–10m (2015–2016 p=0.09, 2020–2022 p=0.004).

The highest ranked covariate for mink and weasel differed between the two periods. In 2015–2016, the highest-ranked covariate was cc3–10m, whereas in 2020–2022 it was distance to riparian (Table 5). In 2015–2016 there was a negative relationship with cc3–10m at sites where both mink and weasels were detected (p=0.05), whereas in 2020–2022 there was a positive relationship with increased distance to riparian habitats.

Table 5: Coefficients for occupancy (ρ) and detection (ψ) parameters, AIC*c* ranking, and model weight from multi-species, multi-season occupancy models built for short-tailed weasel (*Mustela erminea*) (W), American mink (*Neogale vison*) (MK), American marten (*Martes americana*) (MN), and fishers (*Pekania pennanti*) (FR) using detections from cameras deployed in the winters of 2015, 2016, 2020, 2021, and 2022 in the John Prince Research Forest, British Columbia, Canada. Models shown held 75% of the cumulative model weight of candidate models compared for each species pairing and years. Coefficients in bold font were statistically significant(p=<0.05). Covariate abbreviations cc0-3 represents canopy closure from 0-3m, cc3-10 represents canopy closure between 3-10m, cc10 represents canopy closure above 10m, and riparian represents the distance from the camera location to a riparian feature.

Species	Year	Formula	Model output	cc0-3	cc3-10	cc10	riparian	AIC*c*	ΔAIC*c*	AIC*c* ω_i
MN + W	2015-2016	ρ(.)ρ(.)ψ(cc3_10+cc0_3)	MN + W	**0.2**	-0.07			850.59	0	0.89
			MN no W	**-0.3**	-0.05					
			W no MN	-0.2	0.08					
	2020-2022	ρ(.) ρ(.) ψ (cc3_10)	MN + W		-0.03			1771.12	0	1
			MN no W		-0.04					
			W no MN		-0.02					
MN + MK	2015-2016	ρ(.)ρ(.) ψ cc3_10	MN + MK		0.1			819.11	0	0.81
			MN no MK		-0.1					
			MK no MN		-0.1					
	2020-2022	ρ(.) ρ(.) ψ (cc3_10)	MN + MK		0.08			1164.73	0	0.5
			MN no MK		**-0.09**					
			MK no MN		-0.07					
		ρ(.) ρ(.) ψ (dist_rip)	MN + MK				-0.05	1165.03	0.29	0.43
			MN no MK				0.009			
			MK no MN				-0.005			
MK + W	2015-2016	ρ(.) ρ(.) ψ cc3_10	MK + W		**-0.1**			594.82	0	0.63
			MK no W		0.04					
			W no MK		0.1					
	2020-2022	ρ(.) ρ(.) ψ (dist_rip)	MK + W				0.2	1173.89	0	0.99

			MK no W				-0.3			
			W no MK				0.007			
FR + MK	2020-2022	ρ(.) ρ(.) ψ (dist_rip)	FR + MK				-0.2	717.68	0	0.99
			FR no MK				-0.003			
			MK no FR				-0.01			
FR + MN	2020-2022	ρ(.) ρ(.) ψ (cc3_10)	FR + MN		0.04			1316.76	0	0.94
			FR no MN		-0.002					
			MN no FR		**-0.09**					
FR + W	2020-2022	ρ(.) ρ(.) ψ (cc10)	FR + W			-0.6		1351.93	0	0.99
			FR no W			0.6				
			W no FR			0.6				

Riparian co-occurrence

I used two-species occupancy models to evaluate our third hypothesis, which is that species pairs would be more likely to co-occur in riparian habitat. I considered two models to be representative of riparian habitat: distance to riparian and mid-story complexity (i.e., canopy closure between 3 and 10 m or cc3–10m). Specifically, a high proportion of mid-story complexity characterized by LiDAR may represent riparian habitat. Distance to riparian was ranked as one of the highest models three times, all in 2020–2022 (Table 5). Although none of the associations between co-occurrence and distance to riparian were significant, the direction of the trend supported our hypothesis in two of three cases. Specifically, fisher and mink were more likely to co-occur at sites closer to riparian habitats (Table 5). Similarly, mink and marten were more likely to co-occur at sites closer to riparian. By contrast, mink and weasels were more likely to co-occur at sites farther from riparian (Table 5).

Either mid-story complexity or riparian distance occurred in top models for all species in both time periods except for the second-ranked model for mink and weasel in 2015–2016 and the fisher and weasel model in 2020–2022 (Table 5). Marten and mink were more likely to co-occur at sites with greater midstory complexity or closer to riparian in both time periods. Similarly, fisher were more likely to co-occur with marten and mink at sites closer to riparian. In contrast, weasels were less likely to co-occur with mink at sites with greater mid-story complexity in both time periods. Weasels were also less likely to co-occur with marten at sites with greater midstory complexity in 2015–2016 and at distances closer to riparian in 2020–2022. Riparian distance and mid-story complexity were not associated with the co-occurrence of fisher and weasels. Notably, the only significant association between species co-occurrence and riparian distance or midstory canopy was for mink and weasels in 2015–2016 (cc3-10, p=0.05).

Discussion

These results showed that forest-dwelling mustelids demonstrated variability in the habitats that they occupied, but co-occupancy was similar over time. The increase in fisher detections did not appear to affect the co-occurrence of weasels, mink, or marten, which was unexpected. We also found that the co-occurrence of mustelids was associated with forest structure and riparian areas in every year of the study, emphasizing the importance of riparian habitats for these animals.

Single-species occupancy

The results of the single-species occupancy models showed that each species occupied different habitats year to year. My hypothesis was that each species would have predictable occupancy patterns in specific habitats by displaying similar, if not the same, occupancy patterns every year.

Mink showed the most consistent occupancy patterns among years and were more likely to occupy habitats near riparian sites in 4 of the 5 years of the study. The importance of riparian habitat to mink in our study aligns with much of the literature in North America (Ben-David et al. 1996; Hodder et al. 2018; Schooley et al. 2012). In 2016, however, riparian was not identified as an important covariate associated with the occupancy of a site by a mink. Greater use of areas outside riparian areas might be expected if intra-specific competition were greater in 2016 compared with other years. Although the number of mink detections fluctuated among years, 2016 was not the highest or the lowest year for mink detections, suggesting that increased mink detections probably did not influence mink habitat use in that year. Species such as lynx (Crowley et. al. *In review*) and marten, however, had the greatest number of detections in 2016, suggesting that interference competition may have led to greater occupancy outside riparian habitats by mink. Mink have more general diets than marten in our study area and may therefore respond to increased presence of marten by foraging at sites outside riparian areas (Breault et al. 2023).

In general, marten were less likely to occupy sites with greater mid-story complexity (i.e., canopy cover between 3–10m). Canopy closure 3–10m may describe multiple habitat types, the two most common being regenerating stands and riparian forests. Marten were associated negatively with cc3-10m as it often represented a regenerating stand. This negative association with regenerating forests was determined through comparisons with the results of the riparian covariates, and mapping of the cc3–10m covariate, where marten were more likely to occupy habitats closer to riparian, but less likely to occupy habitats with high cc3–10m. I hypothesized that marten would occupy sites with greater canopy closure above 10m in every year, suggesting that marten occupy mature forests (Buskirk 1994). However, we found marten were more likely to avoid young forests than they were to occupy mature forests, which is consistent with other studies in North America showing that marten avoid regenerating clear cuts (Fuller and Harrison 2005). Our findings suggest that marten may occupy other habitats, such as areas with mature forest characteristics, to avoid occupying regenerating clear cuts. In 2015 and 2020, the null model was within 2 $\Delta \text{AIC}c$ of the highest ranked models, suggesting that those results have limited strength.

Fishers occupied habitats that had some similarities among years, although there were only three years of data to compare. Fishers were less likely to occupy sites with greater snow depths in two of three years, which is consistent with findings of other studies (Evans and Mortelliti 2022; Krohn et al. 1995). Fishers have difficulty moving and hunting above snow (Powell et al. 2003) and likely forage less efficiently in subnivean environments compared with marten and weasels (Fitzgerald 1977; Jung et al. 2021). Fishers were more likely to be detected at sites closer to riparian in two of the three years. Female fishers use large diameter trees for maternal dens in the spring (Weir et al. 2012) that are often found in riparian habitats. (Heemskerk et al. 2009). Riparian habitats also share characteristics with mature forest that fishers often use, including CWD, understory complexity, and canopy closure (Weir 1995). In 2020 and 2022, the null model was within two ΔAIC*c* of the highest ranked models. This suggests that the inferences drawn from these findings are limited, and these results may not have as much strength as findings from years without a highly ranked null model.

Weasels had the least consistent patterns of occupancy over the five years. The high naïve occupancy rate of weasels may have contributed to the variation in covariates associated with occupancy, particularly in 2022. Surprisingly, weasels did not occupy sites associated with greater volumes of coarse woody debris. One explanation may be that weasels are less likely to be detected on camera because there is more cover at sites with greater volumes of coarse woody debris. Alternatively, weasels may be habitat generalists and occurrence patterns may be driven more by prey availability than habitat characteristics. Moreover, our finding that weasels were more likely to occur at higher densities at sites farther away from riparian areas in two of five years contrasted with studies of habitat use by weasels in more arid sites in Oregon (Linnell et al. 2017a), New Mexico (Frey and Calkins 2014), and Poland (Zub et al. 2008). One explanation for these differences could be the availability of cover in non-riparian habitats in our study area. Alternatively, the high diversity of predators and competitors that use riparian habitats in our system could displace weasels. Previous studies have also observed that sexual dimorphism and age affect habitat selection by weasels (Linnell et al. 2017a), which also could have influenced our findings, as males and females may use different habitats, adding noise to these results. The null model was very highly ranked for all years of weasel occupancy. This suggests that the inferences drawn from the weasel results have limited strength.

Although the highest AIC*c*-ranked models are discussed above, it is important to consider that for some species, including weasels, marten, and mink, these models poorly fit the data during some of the years of the study. This lack of a strong fit limits the inferences that can be drawn from these data. Sample size (both large and small), as well as high naïve occupancy, could be potential explanations for some of this poor model fit, and future studies could aim to use different modelling techniques to achieve a more parsimonious model fit.

Before and during fishers

The increase in fisher detections from 2015–2022 did not appear to affect the co-occurrence patterns among marten, mink, and weasels. I hypothesized that an increase in the fisher population would cause a top-down trophic cascade in our system (Wallach et al. 2015), either directly through predation or indirectly through competition for shared resources. Studies have shown that fisher diets occasionally include marten, short-tailed weasels, and other fishers (Weir et al. 2005), and that marten and fisher have extensive dietary overlap (Manlick et al. 2017). Dietary competition may occur between fisher and other species in our study area, but data on fisher diets in our system do not yet exist. Spatial analysis alone cannot completely quantify competition in these complex systems (Murray et al. 2023). Although patterns of co-occurrence did not change when fishers increased, the temporal activity patterns of species may have changed to avoid negative interactions with fishers (Kupferman et al. 2021). Further studies of co-occurrence relationships should include analyses of temporal activity patterns.

Between 2015–2016 and 2020–2022, the number of detections of marten and mink decreased but detections of weasels increased. Number of detections can be used as a rough estimate of abundance (Kenney et al. 2024; Mace et al. 1994), but further population studies are required to determine if the increase in fishers led to a decrease in marten and mink, and a possible release of weasels. In addition, this system experienced a steep decline in both snowshoe hares (*Lepus americanus*) and Canada lynx (*Lynx canadensis*) between 2015–2022 (Chisholm 2023; Crowley, et.al *In review*). Cyclical population changes, synchronous with the snowshoe hare cycle, have been observed for mink and weasels in Alberta (Keith and Cary 1991) and other species in the Yukon (Boutin et al. 1995). This large shift in both the predator and prey community may have contributed to the changes in mustelid detections in this study.

The similarity in co-occurrence patterns among weasels, mink, and marten with the increase of fishers could reflect long-term associations among these species. Few fisher detections in 2015–2016 (one detection each year) led to the assumption that the existing community had developed without fishers. If fishers were a novel species in the system, however, weasel, mink, and marten would probably have shown a change in occupancy patterns upon fisher colonization, possibly to avoid fishers, as in similar cases of novel competitors (Wallach et al. 2015). Thus, fishers have likely evolved with the other species in this community and are an uncommon species experiencing population fluctuations. Alternatively, there may not be a detectable difference in weasel, mink, and marten occupancy in response to changes in fisher detections because fishers have not yet reached a threshold above which the effects of fisher increases are observable. This could be due to the methods used (camera trap data), or the gap between the observed periods is too short to measure an effect. Further research could examine this relationship over a longer temporal scale, or in a different system, to see if fishers change how other mesocarnivores use habitats.

Riparian co-occurrence

My results show that mink, marten, and fisher co-occurred closer to riparian features. This partially aligns with my third hypothesis, that the four focal species would overlap in riparian habitats. I hypothesized that weasels would also occupy riparian habitats, because riparian areas often have high densities of small mammals (Doyle 1990; Frey and Calkins 2014) and more complex structure (Sullivan and Sullivan 2021), often associated with weasel habitat (Frey and Calkins 2014). However, I found that weasels occurred at lower detection rates at sites with mink, marten, and fisher in riparian areas. Moreover, weasels occurred at lower detection rates at sites closer to riparian habitat even in the absence of competitors. Possible reasons for lower weasel detection rates in riparian areas include increased risk of predation by fishers (Weir et al. 2005), competition for prey with marten (Breault et al. 2023), the potential competition for cover with mink, or a combination of these possibilities. Our findings contrast with those from more arid systems where weasels are often found in riparian habitats (Doyle 1990; Frey and Calkins 2014; Sullivan and Sullivan 2021), but in those systems the highest amount of cover is found in riparian habitats (Frey and Calkins 2014). In the temperate system where this study was conducted, there is more cover available outside of riparian areas, which could explain why our result contrasts with previous studies. Other studies in BC have shown weasels to be more likely to use open, less complex areas, such as in early-seral habitat (Mowat et al. 2000), which is more consistent with our results.

The co-occurrence of mink, marten, and fisher at sites closer to riparian habitat is surprising due to the high dietary overlap among these species (Breault et al. 2023; Hodder et al.

2017; Manlick et al. 2017). One mechanism facilitating spatial overlap of these species in riparian areas could be the complexity of riparian habitat, which may allow for fine-scale niche partitioning within occupied sites. Alternatively, these species may avoid direct competition in riparian areas if they use riparian habitats primarily for travel rather than for long-term residency. Riparian habitats include streams, rivers, and lakeshores, which can serve as relatively easy travel corridors in winter (Perault and Lomolino 2000; Santos et al. 2011). Regardless of the mechanism, our findings highlight the importance of riparian areas for the co-occurrence of these three species.

Conclusion

I found that the occupancy patterns of weasels, mink, marten, and fishers varied among years, but that riparian and forest structure consistently influenced occupancy. I found that the increase in fishers did not change co-occurrence patterns among weasel, mink, and marten, suggesting that the hierarchy of size is not a driving factor in space-use for mink and marten. However, I found that the combination of these three species (fisher, mink, marten) could potentially affect space use by weasels in riparian areas. My results demonstrate the importance of retaining riparian areas with high mid-story complexity on the landscape to facilitate co-occurrence of mustelid species, and the need for further assessment of weasel habitat needs.

Chapter 3: Body size and prey density influence activity patterns in a diverse mesocarnivore community.

Introduction

Sympatric species occur within the same geographic space and may use similar resources, such as dietary items or habitat features (Case and Gilpin 1974). Niche overlap can lead to interactions between species, often if two or more of the axes overlap. For example, if a pair of species overlap spatially and temporally, they are more likely to interact as they are active at the same time in the same space (Whittaker and Levin 1975).

Interactions between species can be benign or antagonistic, and the latter could lead to altered behaviours to avoid such interactions, known as niche partitioning (Bianchi et al. 2016; Sidorovich et al. 2008; Zhong et al. 2016). Species can avoid undesirable interactions by utilizing unique niches in which they no longer compete for resources. Heterogenous environments provide a diverse range of habitats to allow for spatial niche partitioning, but if a species cannot partition spatially, then changing the timing of their activities will allow for temporal niche partitioning. Niche shifts can be driven by differences in size as larger individuals may indirectly affect how smaller individuals interact with a resource (Palomares and Caro 1999). Another form of niche partitioning is known as niche complementarity (Cornhill et al. 2023; Pepi and McMunn 2021), in which species that have similarities in one niche will differ in another to avoid interactions. Shifts in space use, time of activity, or prey can occur between species, but can also occur between individuals within a species (Rouse et al. 2021). Intraspecific interactions can be caused by changes to the availability of resources: either through a decrease in the resource, or an increase in demand for the resource, such an increase in population (Cunningham et al. 2019).

Changes to populations and distributions of species can be caused by many factors, including availability of food, and environmental conditions (Boutin et al. 1995; Anthony et al. 1987; Ricci et al. 2013; Tilman and Kareiva 1997). Shifts in prey communities can occur over short temporal periods, particularly in cyclical species, resulting in adaptive pressures on dependent predators (Fitzgerald 1977; O'Donoghue et al. 1998). Carnivore species that have narrow dietary niches may have more noticeable shifts in temporal activity patterns when their primary prey species decline (Palomares and Caro 1999), which has been observed for Canada lynx (*Lynx canadensis*) during declines in their primary prey, snowshoe hare (*Lepus americanus*) (Bowman et al. 2006; Crowley et al. *In review*). As the abundance of lynx decline, the mesocarnivore community may shift in relative species composition (Elmhagen and Rushton 2007). Shifts in mesocarnivore temporal activity caused by changes in densities or distributions of another carnivore have been observed in Alaska (Kupferman et al. 2021), Australia (Cunningham et al. 2019), and the United States (LaPoint et al. 2015).

Mammalian mesocarnivores (hereafter mesocarnivores) are medium-sized predators that include members of *Canidae, Felidae,* and *Mustelidae* (Prugh et al. 2009; Roemer et al. 2009). Mesocarnivores play important roles in many ecosystems through prey regulation and seed dispersal, and can influence the structure of ecological communities (Roemer et al. 2009). Forest-dwelling mesocarnivores have evolved with a wide range of life history traits and behaviours that maximize their ability to exploit their realized niche within forested habitats. The forests of British Columbia (BC), Canada, support a diverse group of mesocarnivores, including wolverines (*Gulo gulo*), Canada lynx, coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), fishers (*Pekania pennanti*), American marten (*Martes americana*), American mink (*Neogale vison)*, and short-tailed weasels (*Mustela erminea*). These species share many similarities, including habitat features, life history traits, and prey species, but have evolved niche separation to minimize competition for shared resources (Ben-David et al. 1996; Frey and Calkins 2014; Whittaker and Levin 1975). Extreme conditions during winter can be a challenging time for these species, especially for smaller mustelids (marten, mink, and weasels) whose long, slender body shape requires enormous caloric input to maintain homeostasis (Dunstone 1993; Marchand 2013). Marten, mink, and weasels use subnivean habitats beneath the snow to access small mammals and thermal cover during the winter (Jung et al. 2021; King and Powell 2006). Others, such as wolverine, lynx, and fisher, have larger home ranges to find food within, primarily carrion for wolverines (Lofroth et al. 2007), snowshoe hares for lynx (Squires and Ruggiero 2007), and a variety of medium- to small-sized prey for fishers (Weir et al. 2005).

While each of these individual species have been studied in BC, their interactions with one another are poorly understood (but see Crowley et al. *In review*). Due to the amount of niche overlap for many of these species, it is likely that they compete on one or more niche axis during certain times of the year. The goal of this study was to better understand the temporal overlap and potential competitive interactions between wolverine, lynx, fisher, marten, mink, and weasels. I used five years of camera data from the John Prince Research Forest in Central BC, to assess the spatiotemporal overlap of the focal species. There were two separate periods of observation that represented distinct periods of prey availability: the winters of 2015–2016, and 2020–2022. The first objective was to determine if smaller mesocarnivores experienced interference competition from larger mesocarnivores. I hypothesized that smaller species would have different activity patterns in the presence of larger species, while similar sized species would have no differences. My second objective was to test for differences in temporal pattern among the study species. I hypothesized that weasel, mink, marten, and lynx would have significantly different activity patterns between the two time periods.

Methods

Study Area

This study took place in and adjacent to the John Prince Research Forest (JPRF), encompassing an area of approximately 350km^2 of mixed-wood stands between 54°35’–54°45’ N latitude and 124°10’–124°36’ W longitude. The JPRF is comanaged by Tl’azt’en, Binche Whut’en, and Nak’azdli First Nations and the University of Northern British Columbia. Forest harvesting occurs within the JPRF, but at a much different scale and intensity than in the adjacent areas. The study area is mostly forested with stands in a variety of seral stages. The area also encompasses a variety of other habitat types, including riparian areas and rock bluffs. Tree species in the study area include Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), hybrid white spruce (*Picea glauca x ?*), subalpine fir (*Abies lasiocarpa*), trembling aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), and paper birch (*Betula papyrifera*). The climate is characterized by warm summers (average 17°C) and cold winters (average -10°C), with average snow depths between 0.80 m and 1.2 m.

The JPRF supports a wide range of wildlife species, including a diverse group of mesocarnivores such as short-tailed weasels, American mink, American marten, fisher, wolverine, and Canada lynx. Monitoring data between 2015 and 2022 demonstrated that these species have experienced shifts in population densities, notably a significant decline in Canada lynx (Crowley et al, *In review*). Lynx declines may be linked to the population cycle of snowshoe hares (Krebs et al. 2018), which have been monitored in the research forest since 2017 and have also been declining (unpublished thesis, Chisholm J 2023). Other species, such as marten and mink experienced declines in detections during this period, whereas detections of wolverine, fisher, and weasels increased.

Camera grid

A grid of 66 cameras was installed in and around the research forest between 2015–2016. Six additional cameras were added in 2020–2022 for a total of 72 cameras. All cameras were set to Pacific Standard Time (Coordinated Universal Time minus 8 hours) and did not change for daylight savings time. The cameras were checked, and the sites rebaited every two weeks in the winter. Trained technicians watched videos and recorded species, number of individuals, date, and time for each session. A session was defined as the amount of time between rebaiting or checking of the camera (winter sessions were 14 days).

A detection was considered independent if no detections of the same species occurred within 30 minutes of the first detection. Numerous independence thresholds have been reported in the literature: 24 hours (Schuette et al. 2013), 12 hours (Di Bitetti et al. 2009), 1 hour (Cruz et al. 2014), 30 minutes (Khan et al. 2022; Smith et al. 2022; Watabe and Saito 2022), and 15 minutes (Kupferman et al. 2021). To test the sensitivity of this selection for these species, the data were organized with independent detections occurring at 5-, 30-, and 180-minute intervals. The average amount of time that individuals of all focal species spent in front of the camera was less than three minutes for every year of the study. We ran the same statistical tests on the three time intervals and found that all intervals produced similar results. We used 30-minute intervals as it was the most supported time interval in the literature and makes sense ecologically for the focal species within this study. To determine camera effort, a camera was considered “active” if it recorded videos for more than 50% of the days during the 14-day session. Cameras with less than 50% active days were dropped from that session, and cameras with less than 50% active sessions were dropped from the analyses for that year.

Temporal activity analyses

Six species were chosen to explore patterns in mesocarnivore temporal activity: wolverine, lynx, fisher, marten, mink, and short-tailed weasels (hereafter, weasels). Detections of these species were recorded during winter for five years: 2015, 2016, 2020, 2021, and 2022. Daily temporal activity pattern curves of each of the six species were plotted to compare 24-hour activity patterns between species, and over different time periods using the overlap package in R (Ridout and Linkie 2009). The coefficient of overlap (Δ) was then calculated for all pair-wise combinations of species of interest if there were at least 10 detections of both species (Fisher 1995). The coefficient of overlap (Δ) is calculated using a kernel density function, and ranges from 0–1, with 0 representing no overlap and 1 representing full overlap. The coefficient Δ_1 was used for any species comparisons where there were <75 detections of one of the species, while the coefficient Δ_4 was used for all other pairs >75 detections, and 95% confidence intervals were calculated after bootstrapping 1000 samples.

I used the Watson-Wheeler test to determine if there were differences in activity patterns between paired species, ("circular" package in R; Agnostelli and Lund 2017). The data were subset to test for potential differences in activity pattern of the less dominant species at sites with and without the dominant species. Sites with at least one detection of both species were considered the overlap sites, while sites where species 1 was detected and species 2 was absent, were considered the non-overlap sites. These conditions were applied to each species pairing and an overlap index was calculated for each distribution (species 1 with and without species 2).

To test Hypothesis 1, we observed the overlap of species with differences in size (every pair except marten and mink who are similar in size) in both time periods when applicable. We calculated a coefficient of overlap for the smaller species with and without the larger species to determine level of overlap, then we conducted the Watson-Wheeler test to determine if the activity patterns differed with and without the larger species.

To test Hypothesis 2, we contrasted the activity patterns of weasel, mink, marten, and lynx between 2015–2016 and 2020–2022. These were the only species that were detected often enough in both periods to be included in these analyses. We calculated a coefficient of overlap for each species between the two periods to determine level of overlap, then we conducted the Watson-Wheeler test to determine if the activity patterns differed between periods.

Results

There was a total of 360 camera days between February 1 and Apr 15 in 2015, 2016, 2020, 2021, and 2022, which resulted in 1985 independent weasel detections, 114 independent mink detections, 1164 independent marten detections, 109 independent fisher detections, 164 independent wolverine detections, and 1245 independent lynx detections. Between 2015–2016 there were only 2 fisher detections and 20 wolverine detections, so those species were excluded from analyses for those years.

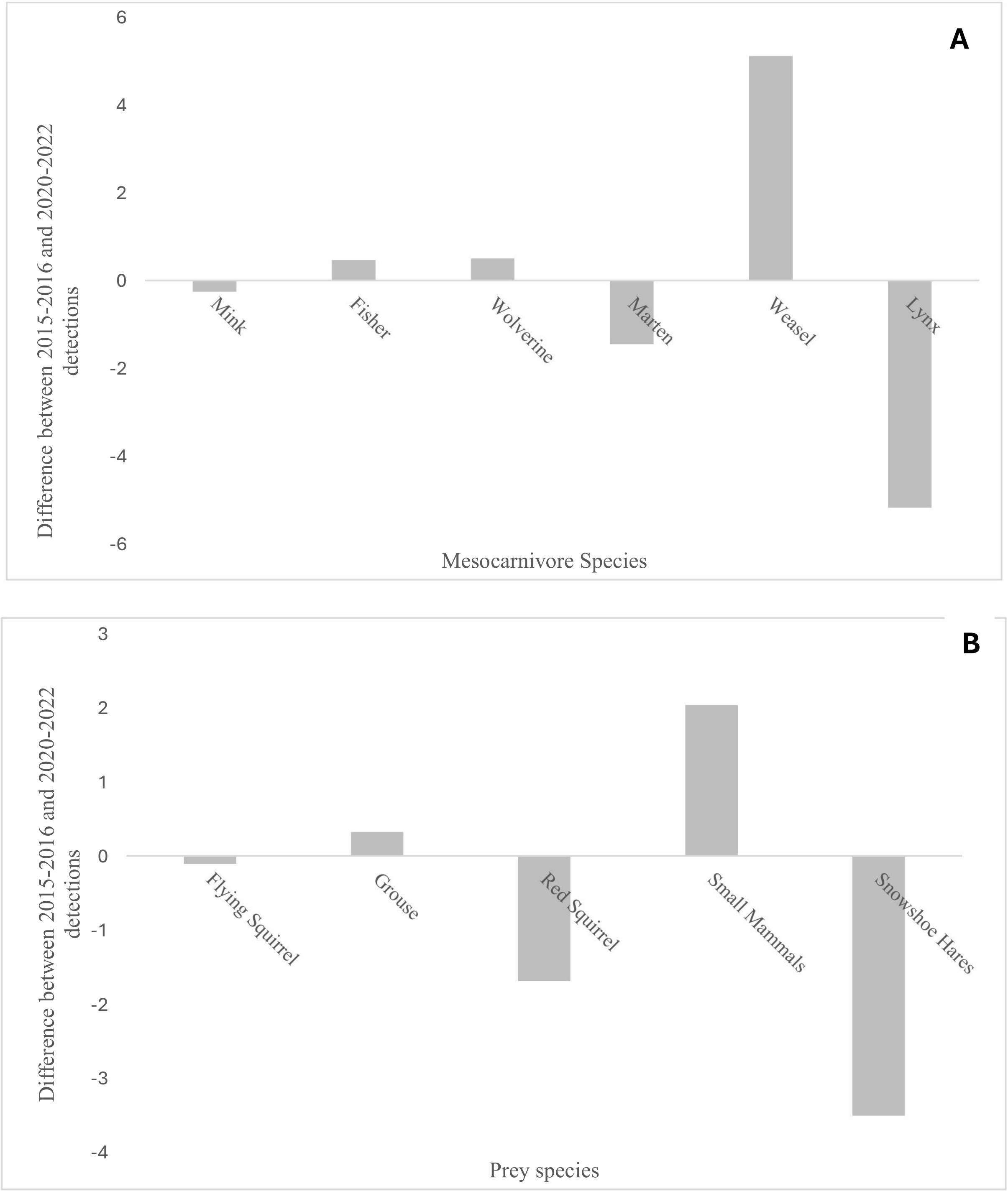

Figure 3: Differences of 30-min independent detections of mesocarnivore species (A): short-tailed weasel (*Mustela erminea*), American mink *(Neogale vison*), American marten (*Martes americana*), Canada lynx (*Lynx canadensis),* fisher (*Pekania pennanti*), wolverine (*Gulo gulo*), and prey species (B): snowshoe hares (*Lepus americanus*), red squirrels (*Sciurus vulgaris*), flying squirrels (*Glaucomys sabrinus*), grouse, and small mammals between Feb 1–Apr 15 of 2015–2016 and 2020–2022 (corrected for camera days) in the John Prince Research Forest,

British Columbia, Canada. Between 2015–2016 there were 137 active camera days, and between 2020–2022 there were 223 active camera days. Small mammal detections may be underrepresented in the winter camera data, so these were collected from Jun 1–Aug 31 of 2016, 2020, and 2021.

Overall, most species showed a moderate to high degree of temporal overlap (Table 6). Fisher and marten had the highest coefficient of overlap (Δ_4=0.86). All other species comparisons had a coefficient of overlap between 0.62–0.82. The only species comparison that had a coefficient of overlap below 50 was between weasels and marten (Δ_4=0.44).

Table 6: Comparisons between 2015–2016 and 2020–2022 at sites where short-tailed weasels (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana*), fisher (*Pekania pennanti*), Canada lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*) co-occur in the John Prince Research Forest, British Columbia, Canada. The coefficient of overlap (Δ), bootstrap mean (BS), and 95% confidence interval (CI) are presented, derived from the kernel density function. A coefficient of 1 means complete temporal overlap whereas a coefficient of 0 means no overlap. The p-values (p) were calculated from the Watson-Wheeler test, describing the probability that curves for the two species come from an equal distribution. Values in bolded show significantly different activity patterns (p<0.05).

Year	Species pair	Δ	*BS*	*CI*	*p*
2015-2016	Mink andmarten	0.72	0.70	0.58–0.82	**< 0.001**
	Marten and lynx	0.77	0.68	0.71–0.84	**< 0.001**
	Weasel and lynx	0.74	0.75	0.67 - 0.79	**< 0.001**
	Weasel and marten	0.44	0.45	0.34 - 0.50	**< 0.001**
2020-2022	Mink and marten	0.73	0.72	0.59 - 0.86	**0.03**
	Marten and lynx	0.74	0.77	0.67 - 0.83	**0.007**
	Weasel and lynx	0.67	0.69	0.61 - 0.74	**< 0.001**
	Weasel and marten	0.64	0.65	0.59 - 0.67	**< 0.001**
	Weasel and fisher	0.62	0.86	0.55 - 0.69	**< 0.001**
	Marten and fisher	0.86	0.85	0.79 - 0.95	0.6
	Fisher and wolverine	0.77	0.76	0.66 - 0.87	**0.03**
	Fisher and lynx	0.82	0.82	0.73 - 0.92	0.24
	Wolverine and lynx	0.67	0.70	0.58 - 0.76	**< 0.001**

Testing the size-dominance hypothesis: differences in activity patterns in the presence of other species

We evaluated whether the activity patterns of each species differed in the presence of larger species. Some pairs of species could not be compared because they did not overlap spatially at enough sites to warrant statistical analysis (<10 detections), but species pairings used for comparisons had a high degree of spatial overlap. Mink were more nocturnal at sites with marten compared to sites without marten (p=0.07) in 2015/2016 (Table 7 and Fig 4A). Marten were more nocturnal at sites where fisher were present compared to sites without fisher (2020–2022, p=0.01), and sites where lynx were present compared to sites without lynx (2015–2016, p=0.01) (Table 7 and Figure 4B and C). Fisher were more active midday at sites where lynx were present compared to sites without lynx (p=0.007) (Fig 4D). The activity patterns of other species pairs were not significant.

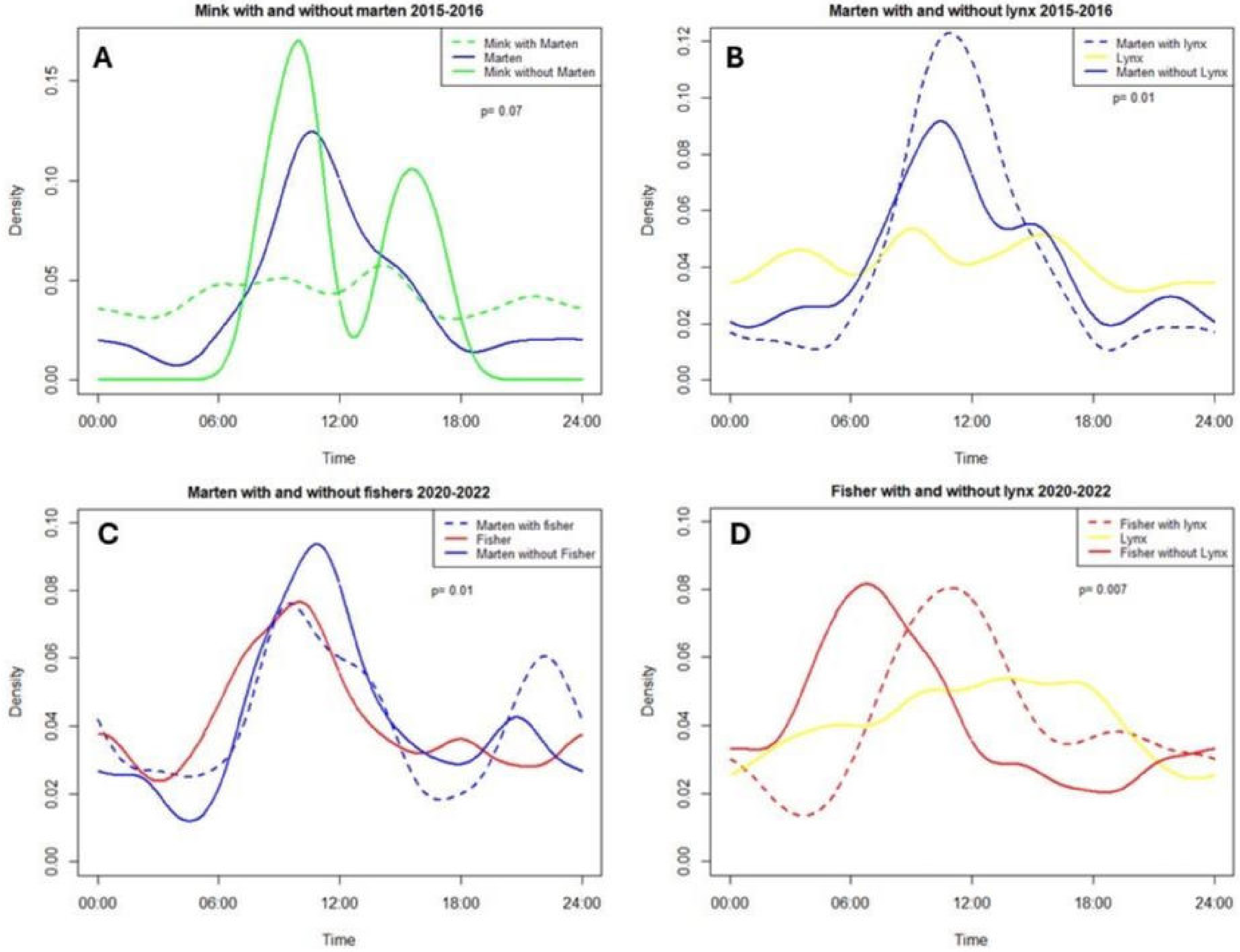

Figure 4: Temporal overlap of American mink (*Neogale vison*) with and without American marten (*Martes americana*) (**A**), American marten with and without Canadian lynx (*Lynx canadensis*) (**B**), American marten with and without fisher (*Pekannia pennanti*) (**C**), and fisher with and without Canada lynx (**D**) in the John Prince Research Forest, British Columbia, Canada, between 2015–2016 and 2020–2022.

Table 7: Single species comparisons of temporal activity patterns during 2015–2016 and 2020–2022 at sites with and without a competitor for short-tailed weasel (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana*), fisher (*Pekania pennanti*), wolverine (*Gulo gulo*), and Canada lynx (*Lynx canadensis*) in the John Prince Research Forest, British Columbia, Canada. The coefficient of overlap (Δ), bootstrap mean (BS), 95% confidence interval (CI) were derived from the kernel density function. A coefficient of 1 means complete temporal overlap whereas a coefficient of 0 means no overlap. The p-value (p) shown was calculated from the Watson-Wheeler test, describing the probability that the two curves come from an equal distribution. Values in bold font depict significantly different activity patterns (p=<0.05). Percentage of total sites where species 1 was detected without species two is represented (SP1), and the proportion of the total species 1 sites where species 2 was also detected is represented (SP1+SP2).

Year	Species comparison	Δ	*BS*	*CI*	*p*	*SP1*	*SP1+SP2*
2015–2016	Mink with and without Marten	0.48	0.50	0.42–0.78	0.07	17	83
	Marten with and without Lynx	0.84	0.84	0.77–0.91	**0.01**	24	73
	Weasels with and without Lynx	0.71	0.70	0.55–0.86	0.44	17	83
	Weasels with and without Marten	0.89	0.86	0.82–0.96	0.7	28	70
2020–2022	Mink with and without Marten	0.61	0.56	0.51–0.94	0.51	16	84
	Marten with and without Lynx	0.95	0.91	0.90–0.99	0.72	38	62
	Weasels with and without Lynx	0.93	0.92	0.89–0.97	0.15	28	72
	Weasels with and without Marten	0.92	0.90	0.88–0.95	0.62	30	70
	Marten with and without Fishers	0.87	0.87	0.81–0.93	**0.01**	46	52
	Fishers with and without Wolverines	0.86	0.79	0.73–0.98	0.4	37	63
	Weasels with and without Fishers	0.96	0.72	0.90–1.02	0.56	51	49
	Wolverine with and without Lynx	0.89	0.78	0.76–1.03	0.86	23	77
	Fishers with and without Lynx	0.74	0.711	0.59–0.89	**0.007**	31	69
	Lynx with and without Fishers	0.94	0.90	0.87–0.99	0.86	54	46

Differences in activity patterns of single species between time periods

Mink, marten, and lynx activity patterns were different between the two time periods (Table 8). Mink were more active midday in 2015–2016 and more nocturnal in 2020–2022 (p=0.06). We also found that the total number of mink detections decreased from 0.47 to 0.22 detections per camera day in 2015–2016 to 2020–2022 respectively (Fig 3). Marten were more diurnal in 2015–2016, while in 2020–2022 they were more nocturnal (p=<0.001). The number of marten detections decreased from 4.13 to 2.67 marten detections per camera day in 2015–2016 to 2020–2022 (Fig 3). Lynx were more active throughout the day in 2015–2016, with peaks around 5AM, 8AM, and 3PM, while in 2020–2022, lynx activity peaked at 1PM (p=0.006). The largest drop in detections was observed for lynx, from 6.66 to 1.49 lynx detections per camera day. Weasel activity patterns were similar between the time periods (p=0.92). The activity patterns of all four species had high coefficients of overlap between the time periods.

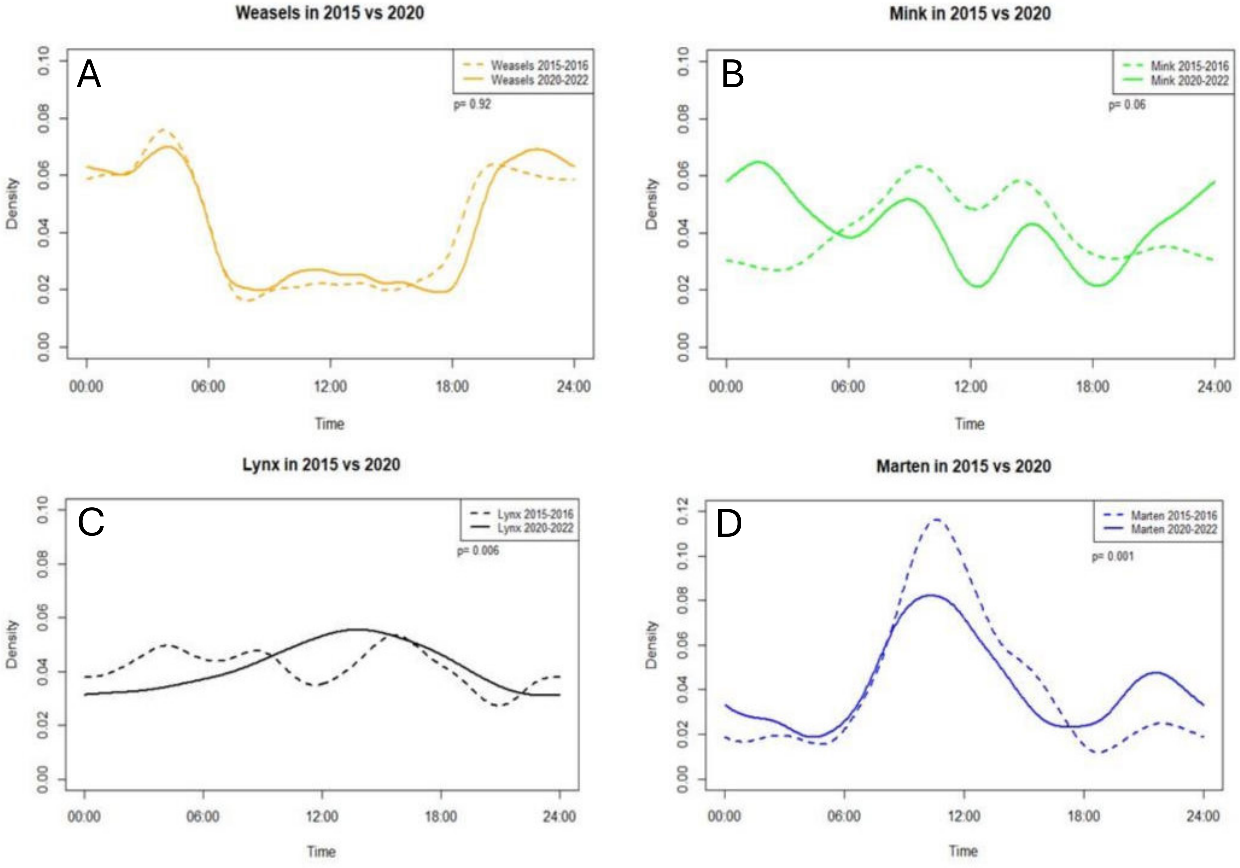

Figure 5: Differences in temporal activity patterns between 2015–2016 and 2020–2022 for A: short-tailed weasel (*Mustela erminea*), B: American mink (*Neogale vison*), C: Canada lynx (*Lynx canadensis*), and D: American marten (*Martes americana*), in the John Prince Research Forest, British Columbia, Canada.

Table 8: Single species comparisons of activity patterns from 2015–2016 and 2020–2022 of short-tailed weasel (*Mustela erminea*), American mink (*Neogale vison*), American marten (*Martes americana),* and Canada lynx (*Lynx canadensis*) in the John Prince Research Forest, British Columbia, Canada. The coefficient of overlap (Δ_4), bootstrap mean (BS), and 95% confidence interval (CI) are presented, derived from the kernel density function. A coefficient of 1 means complete temporal overlap whereas a coefficient of 0 means no overlap. The p-value (p) was calculated from the Watson-Wheeler test and reflects the probability that the curves for the two time periods come from an equal distribution. P-values in bold font describe significantly different distributions ($p<0.05$).

Species	Δ_4	*BS*	*CI*	*p*
Weasel 2015 and Weasel 2020	0.94	0.92	0.91–0.98	0.92

Mink 2015 and Mink 2020	0.81	0.76	0.67–0.94	0.06
Marten 2015 and Marten 2020	0.84	0.84	0.78–0.89	**<0.001**
Lynx 2015 and Lynx 2020	0.9	0.9	0.85–0.95	**0.006**

Discussion:

Our results demonstrated that the activity patterns of the focal species shifted in the presence of other species and between time periods. In the presence of larger species, some species shifted their activity patterns, including marten with lynx and fishers, and fishers with lynx. Other factors, such as changes in the detections of predators and prey, also appeared to change the activity patterns of mink, marten, and lynx. In contrast with other species, weasel activity did not change in the presence of larger competitors or in responses to changes in the prey community.

Size-dominance

I found support for the size-dominance hypothesis as well as the temporal niche complementarity theory. Marten and mink altered their activity patterns to avoid times when other species were most active. Other species, such as fisher, had different activity patterns in the presence of lynx, but the shifts in their activity patterns were not consistent with avoidance of other species. The activity patterns of weasels, lynx, and wolverines did not differ in the presence of other species. This could be due to the magnitude of the size differences between species, as weasels are much smaller than all other species, and lynx and wolverines are much larger than all the other species. Species that were closest in size, such as mink, marten, and fisher, appeared to have a greater effect on each other's activity patterns, suggesting that a smaller size difference could mean more niche overlap on multiple axes.

Marten activity patterns differed when fishers or lynx were detected at the same site, which may be the strongest support of the size-dominance hypothesis. In the presence of both species, marten were less active midday and slightly more active at night compared with sites where fishers and lynx were absent. By contrast, the activity peaks for both fishers and lynx occurred at midday. Fishers and lynx are larger than marten and overlap on both the spatial and dietary niche axes (Fisher et al. 2013; Krohn et al. 1995; Squires and Ruggiero 2007); therefore, changing their activity to avoid temporal overlap could help marten avoid competitive interactions with these larger species. Specifically, marten were less active mid-day when fisher activity was highest. The competitive relationship between marten and fisher has been well documented in Eastern North America (Croose et al. 2019; Evans and Mortelliti 2022; Krohn et al. 1995; Raine 1987). Eastern populations of fisher and marten have high degrees of spatial overlap (Croose et al. 2019), increasing the likelihood for competitive interactions. Studies in Alberta, Canada, have shown marten and fisher do not overlap spatially (Fisher et al. 2013), but few studies have been conducted in British Columbia (see Chapter 2). Fisher predation upon marten, while uncommon, is not unprecedented in British Columbia (Weir et al. 2005), and could contribute to martens' avoidance of fishers, in addition to competition for resources.

As further evidence that marten activity patterns were influenced by the presence of lynx, the relationship between marten activity patterns and lynx presence changed over time. Specifically, marten activity patterns differed in the presence of lynx only in 2015–2016 but not in 2020–2022. Lynx detections were much less in 2020–2022, probably reflecting a decline in lynx density (Crowley et al. *In review*). This shift in marten activity during the period of abundant lynx could be due to the foraging patterns of lynx. When lynx are abundant they hunt in family groups of 2–5 individuals, while when in low densities, group hunting is less common

(O’Donoghue et al. 1998). Solitary lynx may be more confined to sites with greater snowshoe hare densities (Poole 1994), which typically are not optimal marten habitat, possibly leading to less spatial overlap with marten.

Mink activity patterns also differed in the presence of other species, specifically the similar-sized marten. This finding is surprising as mink are considered exploitative in areas where they are invasive (Santulli et al. 2014). In areas where mink are native species, however, their dominance over other species has less support (Hodder et al. 2017). In our system, mink activity patterns differed in the presence of marten (2015–2016) in a way that suggested mink avoided peak marten activity. Mink and marten are roughly the same size (Ruggiero et al. 1994; Geptner et al. 1989), so this finding does not provide support for the size dominance hypothesis, rather it suggests that the two species exhibit temporal niche complementarity. Mink and marten have high levels of overlap both spatially and in their winter diets (Breault et al. 2023; Hoffman et al. 2009; Kiseleva 2012; Poole and Graf 1996). By avoiding periods of peak marten activity, mink may reduce competitive interactions with marten over shared resources. Notably, the shift in activity by mink in the presence of marten may be seasonally exclusive. In the summer, mink can separate spatially from marten by accessing more aquatic prey species but are limited to terrestrial prey in the winter (Hodder et al. 2017). Moreover, the shift in activity by mink may be density dependent. Mink activity patterns only differed from marten in 2015–2016 when detections of the two species were greater compared with in 2020–2022 when detections of both species were less.

Fishers changed their activity pattern in the presence of lynx. At sites where lynx were present, fishers adjusted the peak of their activity to overlap more with the peak of lynx activity. This suggests that fisher were not avoiding lynx, but they were shifting their activity to match that of the lynx. That activity pattern does not support the size-dominance hypothesis. Fishers may be accessing a prey species at the same time as lynx. For example, snowshoe hares are a prey species of both species (Squires and Ruggiero 2007; Weir et al. 2005). There is little evidence of competitive interactions between lynx and fishers in western North America; however, cases of fisher predation on lynx is documented in Maine, USA (Mclellan et al. 2018). While unlikely, the shift in fisher activity pattern could reflect predatory behaviour by fishers toward lynx, especially during the period when lynx were more solitary and vulnerable due to food scarcity.

The activity patterns of lynx and wolverine did not differ in the presence of other species, suggesting that their activity patterns were not influenced by co-occurrence with competitors. This finding provides further support for the size-dominance hypothesis, as lynx and wolverine were the two largest species in this study. Alternatively, this finding could also be a result of the spatial scale of this study. Wolverines have the largest home ranges of all the species in this study (Banci and Harestad 1990) and could be active at sites transiently and not long enough to affect the activity patterns of other species. Wolverine detections were low, but similar in number to fisher detections that yielded significant results when activity patterns were compared with other species. Wolverine may exploit different spatial and dietary niches compared with the other species in this study, due in part to their larger body size and home range.

The activity patterns of weasels were similar in the presence of larger species. This finding does not support our size-dominance hypothesis, possibly due to the degree of size difference between weasels and the other species. Since weasels are much smaller, they may avoid competition with the larger species by exploiting different resources or through different behaviours rather than through temporal changes in activity. For example, weasels often use subnivean spaces in winter to access to food and cover (Simms 1979). Marten also use subnivean spaces (Jung et al. 2021), but not to the same extent as weasels. Moreover, marten cannot use the same small interstitial spaces as weasels. Weasels might experience more competition with marten in summer when the subnivean zone is unavailable. Local populations of marten and weasels have complete dietary overlap in the summer (Breault et al. 2023), which suggests that temporal niche partitioning between marten and weasels might be more important in summer than winter.

Changes over time hypothesis

The abundance of mesocarnivores and their prey shifted between the two time periods. Detections of mink, marten, lynx, snowshoe hares, and red squirrels decreased in 2020–2022 compared with 2015–2016. By contrast, detections of weasels, fishers, wolverines, and small mammals increased between time periods. During 2015–2016, snowshoe hares were experiencing the height of their abundance in their cyclical population (Chisholm 2023). In contrast, 2020–2022 was a low in the local snowshoe hare cycle. This change in snowshoe hare availability may cause predators of hares to change their activity patterns to find other prey, and ultimately, could lead to population declines.

Weasel activity did not change between the two time periods, possibly because they were not reliant on snowshoe hares in winter. Although weasels may target immature snowshoe hares (Simms 1979), they typically prey on smaller mammals, such as mice, shrews, and voles (Fitzgerald 1977). As further evidence that the decline in hares had little effect on weasels, the number of weasel detections was greater in the second period than the first when hare abundance was less. In addition, detections of small mammals increased in the second time period as did detections of weasels, which could reflect cyclical population dynamics between weasels and prey such as voles (Fitzgerald 1977; Haapakoski et al. 2013). These results suggest that weasels do not alter their activity patterns according to shifts in snowshoe hare abundance. Another shift that occurred between time periods was the abundance of other predators. Specifically, mink, marten, and lynx decreased, and fisher and wolverine increased. The winter diets of fisher have included weasels (Linnell et al. 2017; Weir et al. 2005), but our results suggested that weasels did not change their activity pattern when the predator community shifted. Weasels are sexually dimorphic, and differences have been observed between male and female spatial niches (Lisgo et al. 2002). Perhaps there are differences in temporal activity patterns between male and female weasels that are difficult to differentiate using camera data. Further research into the differences in temporal activity between male and female weasels may be helpful in interpreting these results, as differences in activity between males and females would add noise to our findings. These findings also suggest that weasels may be less sensitive to intraspecific competition since their activity patterns were not more spread out over a 24-hour period as they increased in abundance, which might be indicative of intraspecific competition (Cunningham et al. 2019).

Mink activity patterns differed between the two time periods. Mink were more nocturnal in 2020–2022 than 2015–2016, which could have been a response to avoid fishers, which were active during the day and more abundant in 2020–2022. Alternatively, mink may not show a strong response to declines in snowshoe hares due to their generalist diet consisting largely of aquatic species in the summer and terrestrial species in winter (Hodder et al. 2017). The mink response may also be non-significant due to low detection rates, resulting in a small sample size, especially in the second period. Finally, activity patterns and habitats of male and female mink can be quite different (Harrington et al. 2009; Hodder et al. 2017; Hodder et al. 2018) but due to our data source (camera data), we were unable to verify the sex of mink on camera. This uncertainty may have led to noise in the data, making patterns less clear.

There was strong statistical support for a change in marten activity patterns between the two periods, which could reflect prey-switching behaviour by marten. Snowshoe hares and red squirrels are large parts of local marten diet (Breault et al. 2023). Marten became slightly more active at night, with a pulse of activity around 10:00pm in 2020–2022. This may mean there is a prey species that is more nocturnal, such as snowshoe hares or flying squirrels, that marten may be targeting, although there is little support showing flying squirrels being a part of marten diets (Cumberland et al. 2001). Alternatively, marten may be avoiding competitors who are also targeting snowshoe hares and red squirrels by increasing activity at times when these competitors were less active. It is unlikely that marten were experiencing significant intraspecific competition, as the activity pattern during the height of marten abundance was more peaked, and less spread out throughout the 24-hour period which may be indicative of intraspecific temporal partitioning (Cunningham et al. 2019). The activity pattern in 2020–2022, when marten were less abundant, showed a broader distribution of activity throughout the 24-hour period.

Lynx activity was significantly different between the two periods. The main prey species of lynx is snowshoe hares, and as snowshoe hare detections decrease, changes in lynx behaviour are expected. With fewer hares, lynx may switch prey species, which may explain the decrease in nocturnal activity by lynx in 2020–2022 (Coblentz 2020). There were also fewer overall detections of lynx in 2020–2022, which could result in different activity patterns. Support of intraspecific competition during 2015–2016 can be seen in the broad range of active times of lynx, while 2020–2022 shows a more central peak (Cunningham et al. 2019). Our data showed that there were many lynx groups of up to five individuals between 2015–2016, with no family groups detected between 2020–2022. This change from group to solitary activity may also contribute to changes in activity patterns, as groups may target different prey species. Moreover, solitary animals may be more vulnerable to predation than groups of animals and therefore may be more likely to alter their activity patterns to avoid predators.

Conclusion

This study found that mesocarnivore activity patterns changed in the presence of other mesocarnivore species in the JPRF, and over time. These results provide insights on strategies to maintain spatial co-occurrence and possible mechanisms to avoid competition within a diverse community of mesocarnivores. These changes may be driven by prey availability or competition, but other factors such as changes to habitats, disturbances, and weather may all lead to shifts in daily activity patterns. Further monitoring of this community during different seasons and over a longer time period would help determine how further predator and prey fluctuations may influence the interspecific interactions of mesocarnivores. This study allows researchers to better understand this guild of animals and how they interact with one another, which is important for adding context to single species monitoring efforts. In addition, this study underscores the importance of long-term monitoring to fully grasp the complex ecology of these species and their interactions with one another.

Chapter 4: Conclusion

Research Summary

Mesocarnivores are a diverse guild that provide many ecosystem services across a variety of habitats around the world. In British Columbia, these species and their interactions are poorly understood. Many studies in BC have focused on a single species (Lofroth 1993; Lofroth et al. 2007; Weir et al. 2005), but often within-guild interactions provide more information about the conclusions from single-species research (Croose et al. 2019; Evans and Mortelliti 2022; Kupferman et al. 2021). Some mesocarnivores in BC are facing population declines, such as fishers (Fogarty et al. 2022), whereas the population size and conservation concern of other mesocarnivores is unknown. These species face challenges including reduced habitat availability, climate change, trapping, and declines in prey (Evans and Mortelliti 2022; Fogarty et al. 2022; Frey and Calkins 2014; Kelly and Hodges 2020; Wiebe et al. 2014). As forest habitat continues to be altered, understanding the variation in species interactions over space and time may aid in management and monitoring of forest-dwelling members of the mesocarnivore guild.

Accordingly, my research focused on better understanding patterns of co-occurrence among sympatric mesocarnivores in a harvested forest ecosystem. I used remote camera data to observe the spatiotemporal overlap of five species in Central British Columbia over the course of five winters. In Chapter 2, I used single- and multi-species occupancy models to examine the spatial overlap of fishers, marten, mink, and weasels. The results from these analyses allowed me to identify habitat variables associated with co-occurrence of these species.

Spatially, fisher, marten, mink, and weasels had moderate overlap. I found that fisher, marten, and mink co-occurred within habitats closer to riparian features. By contrast, weasels did not occupy habitat adjacent or within riparian areas. I found that patterns of co-occurrence did not change between weasel, marten, and mink during the period of low fisher detections compared to the period of higher fisher detections. For all species, fine-scale forest structure influenced occupancy in every year of the study.

Patterns of spatial co-occurrence for these species suggested that riparian features and forest structure provided important habitat for mesocarnivores in BC (Sauder and Rachlow 2015; Suffice et al. 2020; Wiebe et al. 2014). In contrast with other study species, weasels were less likely to occur in riparian habitats. Weasels often use shrub cover, coarse woody debris, and canopy cover that typically occurs within riparian areas (Frey and Calkins 2014; Linnell et al. 2017a; Lisgo et al. 2002; Zub et al. 2008). However, my findings suggested that during winter weasels avoided camera sites that contained riparian habitat, possibly due to competition with or predation by other species.

By comparing species co-occurrence during two periods of contrasting fisher abundance, I found that the increase in fisher detections between time periods did not change the co-occurrence patterns of weasel, mink, and marten. My findings suggest that fishers may have experienced a decline in population density during the first period of this study, shown through the lack of change to mink, marten, and weasel occupancy patterns. Differences in fisher abundance between time periods could be the result of shifts in trapping pressure, changes abundance of prey or competitors, or habitat limitations.

In Chapter 3, I used kernel-density estimators to quantify the temporal overlap of wolverines, lynx, fisher, marten, mink, and short-tailed weasels. Temporal overlap was moderate to high for most species' pairings (Δ 0.44–0.86). The daily activity patterns of weasels, lynx, and wolverine did not differ in the presence of any other species. By contrast, the daily activity patterns of mink, marten, and fishers differed in the presence of other species. Specifically, mink activity differed in the presence of marten, marten activity differed in the presence of lynx and fisher, and fisher activity differed in the presence of lynx. Between the two time periods, the activity patterns of lynx, marten, and mink differed. The activity patterns of weasels were similar between time periods.

The temporal activity patterns that I quantified for mesocarnivores in the JPRF reflected patterns observed in South-eastern Alaska (Kupferman et al. 2021). My findings showed support for the size-dominance hypothesis, specifically among marten and larger species such as fisher and lynx. Additionally, I found that species closer in size were more likely to show differences in temporal activity in the presence of one another, such as mink and marten, possibly due to the high degree of niche overlap between these species during winter. Species that differed in temporal activity patterns in the presence of one another were all the closest in size.

I found differences in species activity patterns between the two monitoring periods, likely due to the decline in snowshoe hare abundance (Chisholm 2023). This reduction in prey biomass may have triggered cascading effects, such as the decrease in lynx, marten, and mink detections, and the increase in fisher and wolverine detections (possibly released due to decreased competition from lynx). These findings draw attention to the importance of long-term monitoring to fully understand the complexity and plasticity of community dynamics. Further research should continue to monitor these species over time to gain a fuller understanding of the effects of cyclical population patterns on temporal activity.

Using both spatial and temporal data to assess the overlap between these mesocarnivores provided a more holistic understanding of species interactions. Consideration of spatial and temporal data provided important context to each of these chapters on their own and identified important nuances in these data. Although spatial overlap can suggest the potential for interaction, looking at the temporal activity allowed us to better understand the degree of overlap, and how often these species interact. These complimentary approaches provided a richer understanding of this system and may allow for more specific research questions to be asked.

Limitations

This study focused on species that were relatively rare and cryptic, leading to small sample sizes of detections. Sample sizes were one of the constraints of this work, as many of the spatial models would not converge due to few independent detections of mink and fisher in some seasons, and many detections of weasels at many sites in other seasons. In addition, while I used fine-scale covariates derived from LiDAR for my analyses, these data were collected during leaf-on summer conditions while my animal detection data were collected during leaf-off, winter conditions. This difference in timing of habitat measurements could influence model interpretation though I attempted to mitigate these potential issues through winter measurements of canopy closure that allowed for corrections to be made to the summer data. Some of the top-ranked single-species models showed poor model fit, specifically for certain years for weasel, marten, and mink. The models with poor fit limit the inferences that can be drawn about these data and should be considered when reading the spatial results of this thesis. Further research could use other modelling techniques, such as generalized linear models, to potentially find better fitting models for these species. And finally, while I discuss broad themes of interspecific interactions and competition in this thesis, I was not able to quantify prey abundances, and therefore could not quantitatively evaluate competitive interactions among these species (Blanchet et al. 2020; Murray et al. 2023), but future studies could.

In the temporal chapter of this thesis, I assumed that changes to species interactions were potentially caused by the presence of another species, but I understand that there are many other possible explanations for these changes in activity patterns that were not measured in this thesis, such as variations in predators or competitors, prey communities, conspecifics, or environmental factors.

Management and Monitoring Implications

The findings of my research suggest that riparian habitats and forest structure provide many of the necessary fine-scale features that mesocarnivores require. As such, these important habitats or features should be conserved or replicated wherever possible. Forest legislation in BC already requires that buffers of intact forest be retained along aquatic features, primarily fish habitat (Young 2000), but further efforts should be made to allow for functional connectivity of these habitats for terrestrial wildlife.

My results suggest that marten are occupying sites in mature forests rather than in regenerating plantations, which aligns with much of the current literature on marten habitat (Delheimer et al. 2023; Fuller and Harrison 2005). Forest harvesting planners should account for the habitat needs of marten when creating buffers around riparian features, which could be done by creating or maintaining functional movement corridors. My results indicated that marten were occupying sites with more mature trees, so retaining some mature trees within a block may increase occupancy of these disturbed areas by marten. CWD corridors leading to block edges can facilitate movement for marten and weasels (Seip et al. 2018), while the retention of hardwoods and naturally regenerating trees may increase the value of harvested areas as habitat for other mesocarnivores. Other species, such as fishers, are less constrained by overhead cover. My results indicate that fisher are occupying riparian habitats. Retaining large diameter black cottonwood trees, often found in wetter, riparian sites, can provide maternal denning habitat for fishers (Weir et al. 2012), and is a simple strategy to retain fine-scale habitat features for this species.

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Appendix 1 – Single-species, single season occupancy models ranked by AIC*c* for fisher (*Pekania pennanti*), American marten (*Martes americana*), American mink (*Neogale vison*), and short-tailed weasel (*Mustela erminea*) in 2015, 2016, 2020, 2021, and 2022 in the John Prince Research Forest, British Columbia, Canada.

Species	**Year**	**Model Name**	**rank**	**AIC*c***	**ΔAIC*c***	**AIC*c* ω_i**
Fisher	2020	Average snow depth	1	166.57	0	0.21
Fisher	2020	Null	2	166.83	0.26	0.18
Fisher	2020	Average snow depth and distance to riparian	3	167.48	0.91	0.13
Fisher	2020	Average snow depth and coarse woody debris	4	168.39	1.82	0.08
Fisher	2020	Riparian	5	168.48	1.91	0.08
Fisher	2020	CWD	6	168.56	1.99	0.08
Fisher	2020	Ground complexity	7	168.64	2.07	0.07
Fisher	2020	Mid-canopy	8	168.88	2.31	0.06
Fisher	2020	Mature forest	9	169.79	3.21	0.04
Fisher	2020	Mid-canopy+floor	10	170.85	4.28	0.02
Fisher	2020	Mature forest+tree_type	11	171.41	4.84	0.02
Fisher	2020	Riparian_tree_type	12	172.28	5.7	0.01
Fisher	2020	Riparian_area	13	172.86	6.29	0.01
Fisher	2020	Vertical complexity	14	173.94	7.36	0.01
Fisher	2020	Full	15	180.25	13.68	0
Fisher	2021	Riparian	1	128.3	0	0.43
Fisher	2021	Riparian_tree_type	2	129.18	0.88	0.28
Fisher	2021	Full	3	131.65	3.35	0.08
Fisher	2021	Vertical complexity	4	132.78	4.49	0.05
Fisher	2021	Ground complexity	5	132.86	4.56	0.04
Fisher	2021	CWD	6	132.93	4.63	0.04
Fisher	2021	Mature forest	7	134.13	5.83	0.02
Fisher	2021	Average snow depth and distance to riparian	8	134.24	5.94	0.02
Fisher	2021	Mid-canopy+floor	9	135.05	6.75	0.01
Fisher	2021	Average snow depth and coarse woody debris	10	135.18	6.88	0.01
Fisher	2021	Null	11	136.48	8.18	0.01
Fisher	2021	Average snow depth	12	138.38	10.08	0
Fisher	2021	Mid-canopy	13	138.61	10.31	0
Fisher	2021	Riparian_area	14	140.41	12.11	0
Fisher	2022	Average snow depth and distance to riparian	1	154.22	0	0.21
Fisher	2022	Null	2	154.46	0.24	0.19
Fisher	2022	Average snow depth	3	155.4	1.18	0.12
Fisher	2022	Riparian	4	155.42	1.2	0.12

Fisher	2022	CWD	5	155.78	1.56	0.1
Fisher	2022	Mid-canopy	6	156.66	2.44	0.06
Fisher	2022	Ground complexity	7	156.66	2.44	0.06
Fisher	2022	Average snow depth and coarse woody debris	8	157.27	3.05	0.05
Fisher	2022	Mature forest	9	157.88	3.66	0.03
Fisher	2022	Mid-canopy+floor	10	158.92	4.7	0.02
Fisher	2022	Riparian_tree_type	11	159.78	5.56	0.01
Fisher	2022	Riparian_area	12	159.94	5.72	0.01
Fisher	2022	Mature forest+tree_type	13	160.68	6.46	0.01
Fisher	2022	Vertical complexity	14	162.17	7.95	0
Fisher	2022	Full	15	168.36	14.14	0
Mink	2015	Riparian	1	149.51	0	0.55
Mink	2015	Riparian_tree_type	2	150.28	0.77	0.37
Mink	2015	Riparian_area	3	153.9	4.39	0.06
Mink	2015	Null	4	158.31	8.8	0.01
Mink	2015	Ground complexity	5	160.01	10.5	0
Mink	2015	Mid-canopy	6	160.13	10.63	0
Mink	2015	CWD	7	160.19	10.69	0
Mink	2015	Mature forest+tree_type	8	161.43	11.92	0
Mink	2015	Mid-canopy+floor	9	161.76	12.25	0
Mink	2015	Mature forest	10	162.06	12.55	0
Mink	2015	Vertical complexity	11	166.14	16.63	0
Mink	2016	Mid-canopy	1	114.38	0	0.42
Mink	2016	Vertical complexity	2	115.71	1.33	0.21
Mink	2016	Mid-canopy+floor	3	116.67	2.28	0.13
Mink	2016	Mature forest+tree_type	4	118.44	4.05	0.05
Mink	2016	Riparian_area	5	118.68	4.29	0.05
Mink	2016	Riparian_tree_type	6	119.53	5.15	0.03
Mink	2016	Null	7	119.81	5.42	0.03
Mink	2016	Full	8	120.17	5.79	0.02
Mink	2016	Riparian	9	120.38	6	0.02
Mink	2016	CWD	10	120.76	6.38	0.02
Mink	2016	Ground complexity	11	121.95	7.57	0.01
Mink	2016	Mature forest	12	123.1	8.72	0.01
Mink	2020	Riparian	1	86.75	0	0.37
Mink	2020	Null	2	86.78	0.02	0.37
Mink	2020	Ground complexity	3	88.73	1.98	0.14
Mink	2020	Mature forest+tree_type	4	89.11	2.35	0.12
Mink	2021	Riparian	1	41.24	0	0.49

Mink	2021	Riparian_tree_type	2	43.37	2.13	0.17
Mink	2021	Null	3	43.83	2.59	0.13
Mink	2021	Mid-canopy+floor	4	45.34	4.1	0.06
Mink	2021	Ground complexity	5	45.92	4.68	0.05
Mink	2021	Average snow depth	6	46.01	4.77	0.05
Mink	2021	Average snow depth and distance to riparian	7	47.87	6.63	0.02
Mink	2021	Mature forest	8	48.12	6.88	0.02
Mink	2021	Vertical complexity	9	49.16	7.91	0.01
Mink	2021	Riparian_area	10	50.61	9.37	0
Mink	2022	Riparian	1	138.11	0	0.31
Mink	2022	Riparian_tree_type	2	138.36	0.25	0.27
Mink	2022	Average snow depth and distance to riparian	3	138.39	0.28	0.27
Mink	2022	Riparian_area	4	139.77	1.66	0.14
Mink	2022	Full	5	146.07	7.96	0.01
Mink	2022	Mid-canopy	6	149.49	11.38	0
Mink	2022	Average snow depth	7	149.85	11.74	0
Mink	2022	Mid-canopy+floor	8	151.58	13.47	0
Mink	2022	Average snow depth and coarse woody debris	9	151.68	13.57	0
Mink	2022	Null	10	151.91	13.8	0
Mink	2022	Vertical complexity	11	152.12	14.01	0
Mink	2022	Mature forest+tree_type	12	152.22	14.11	0
Mink	2022	CWD	13	153.05	14.94	0
Mink	2022	Ground complexity	14	154.1	15.99	0
Mink	2022	Mature forest	15	155.3	17.19	0
Marten	2015	Mid-canopy+floor	1	280.99	0	0.38
Marten	2015	Vertical complexity	2	282.27	1.27	0.2
Marten	2015	Riparian_area	3	282.87	1.88	0.15
Marten	2015	Full	4	284	3.01	0.08
Marten	2015	Ground complexity	5	284.09	3.1	0.08
Marten	2015	Mature forest+tree_type	6	284.36	3.37	0.07
Marten	2015	Mid-canopy	7	286.34	5.34	0.03
Marten	2015	Riparian_tree_type	8	287.62	6.63	0.01
Marten	2015	Mature forest	9	290.73	9.73	0
Marten	2015	Null	10	291.72	10.72	0
Marten	2015	CWD	11	292.03	11.03	0
Marten	2015	Riparian	12	293.9	12.91	0
Marten	2016	Mid-canopy+floor	1	358.66	0	0.4
Marten	2016	Mid-canopy	2	358.77	0.11	0.37
Marten	2016	Riparian_area	3	360.97	2.31	0.12

Marten	2016	Vertical complexity	4	361.49	2.83	0.1
Marten	2016	Full	5	367.07	8.42	0.01
Marten	2016	Ground complexity	6	369.84	11.19	0
Marten	2016	Null	7	373.18	14.52	0
Marten	2016	CWD	8	374.82	16.17	0
Marten	2016	Riparian	9	375.35	16.69	0
Marten	2016	Mature forest+tree_type	10	375.81	17.15	0
Marten	2016	Mature forest	11	376.42	17.77	0
Marten	2016	Riparian_tree_type	12	376.57	17.91	0
Marten	2020	Vertical complexity	1	280.89	0	0.25
Marten	2020	CWD	2	281.36	0.47	0.2
Marten	2020	Mature forest	3	281.73	0.84	0.16
Marten	2020	SnoW_depth_and_CWD	4	282.99	2.1	0.09
Marten	2020	Null	5	283.09	2.2	0.08
Marten	2020	Mid-canopy	6	283.95	3.06	0.05
Marten	2020	Average snow depth	7	284.33	3.45	0.04
Marten	2020	Full	8	284.9	4.01	0.03
Marten	2020	Ground complexity	9	285.14	4.26	0.03
Marten	2020	Riparian	10	285.23	4.34	0.03
Marten	2020	Mid-canopy+floor	11	286.25	5.36	0.02
Marten	2020	Mature forest+tree_type	12	287.26	6.37	0.01
Marten	2020	Riparian_area	13	288.52	7.63	0.01
Marten	2020	Riparian_tree_type	14	289.98	9.09	0
Marten	2021	Riparian	1	113.38	0	0.4
Marten	2021	Riparian_tree_type	2	114.42	1.04	0.24
Marten	2021	Average snow depth and distance to riparian	3	115.71	2.32	0.12
Marten	2021	Full	4	117.18	3.79	0.06
Marten	2021	Ground complexity	5	117.93	4.54	0.04
Marten	2021	CWD	6	118	4.61	0.04
Marten	2021	Vertical complexity	7	118.05	4.66	0.04
Marten	2021	Mature forest	8	119.27	5.89	0.02
Marten	2021	Mid-canopy+floor	9	120.19	6.8	0.01
Marten	2021	Average snow depth and coarse woody debris	10	120.32	6.94	0.01
Marten	2021	Null	11	121.48	8.1	0.01
Marten	2021	Average snow depth	12	123.45	10.07	0
Marten	2021	Mid-canopy	13	123.68	10.3	0
Marten	2021	Mature forest+tree_type	14	125.64	12.25	0
Marten	2022	Riparian_area	1	349.93	0	0.25
Marten	2022	Vertical complexity	2	349.93	0	0.25

Marten	2022	Mid-canopy+floor	3	350.01	0.08	0.24
Marten	2022	Mid-canopy	4	351.82	1.9	0.1
Marten	2022	Full	5	352.4	2.47	0.07
Marten	2022	Ground complexity	6	353.44	3.52	0.04
Marten	2022	Mature forest+tree_type	7	355.47	5.55	0.02
Marten	2022	Riparian_tree_type	8	355.59	5.67	0.01
Marten	2022	Riparian	9	357.33	7.4	0.01
Marten	2022	Mature forest	10	357.84	7.91	0
Marten	2022	Null	11	358.05	8.12	0
Marten	2022	Average snow depth and distance to riparian	12	358.7	8.77	0
Marten	2022	CWD	13	359.08	9.15	0
Marten	2022	Average snow depth	14	359.14	9.21	0
Marten	2022	Average snow depth and coarse woody debris	15	359.89	9.96	0
Weasel	2015	Ground complexity	1	126.96	0	0.23
Weasel	2015	Null	2	127.59	0.63	0.17
Weasel	2015	Mature forest	3	127.94	0.98	0.14
Weasel	2015	Riparian	4	128.26	1.31	0.12
Weasel	2015	CWD	5	128.64	1.68	0.1
Weasel	2015	Mid-canopy+floor	6	129.21	2.26	0.07
Weasel	2015	Mid-canopy	7	129.85	2.89	0.05
Weasel	2015	Riparian_area	8	130.87	3.91	0.03
Weasel	2015	Mature forest+tree_type	9	131	4.05	0.03
Weasel	2015	Riparian_tree_type	10	131.39	4.43	0.03
Weasel	2015	Vertical complexity	11	131.88	4.92	0.02
Weasel	2016	Mid-canopy	1	182.4	0	0.32
Weasel	2016	Null	2	182.97	0.58	0.24
Weasel	2016	Mid-canopy+floor	3	184.53	2.14	0.11
Weasel	2016	CWD	4	185.16	2.76	0.08
Weasel	2016	Ground complexity	5	185.19	2.79	0.08
Weasel	2016	Riparian	6	185.22	2.83	0.08
Weasel	2016	Riparian_area	7	186.76	4.36	0.04
Weasel	2016	Mature forest	8	187.19	4.8	0.03
Weasel	2016	Vertical complexity	9	189	6.61	0.01
Weasel	2016	Mature forest+tree_type	10	189.61	7.22	0.01
Weasel	2016	Riparian_tree_type	11	189.78	7.39	0.01
Weasel	2016	Full	12	195.22	12.82	0
Weasel	2020	Null	1	189.76	0	0.23
Weasel	2020	Ground complexity	2	190.75	0.99	0.14
Weasel	2020	Average snow depth	3	191.21	1.46	0.11

Weasel	2020	CWD	4	191.23	1.47	0.11
Weasel	2020	Riparian	5	191.57	1.81	0.09
Weasel	2020	Mid-canopy	6	191.68	1.92	0.09
Weasel	2020	Average snow depth and distance to riparian	7	192.75	2.99	0.05
Weasel	2020	Mid-canopy+floor	8	192.86	3.1	0.05
Weasel	2020	Average snow depth and coarse woody debris	9	193.04	3.28	0.04
Weasel	2020	Mature forest	10	193.46	3.71	0.04
Weasel	2020	Riparian_area	11	195.07	5.32	0.02
Weasel	2020	Riparian_tree_type	12	195.69	5.93	0.01
Weasel	2020	Mature forest+tree_type	13	195.88	6.12	0.01
Weasel	2020	Vertical complexity	14	197.12	7.36	0.01
Weasel	2020	Full	15	203.87	14.11	0
Weasel	2021	Riparian	1	275.04	0	0.21
Weasel	2021	Riparian_tree_type	2	275.27	0.23	0.19
Weasel	2021	Null	3	276.22	1.17	0.12
Weasel	2021	Ground complexity	4	276.8	1.75	0.09
Weasel	2021	Average snow depth and distance to riparian	5	276.98	1.94	0.08
Weasel	2021	Mid-canopy	6	277.47	2.43	0.06
Weasel	2021	Average snow depth	7	278.05	3.01	0.05
Weasel	2021	Riparian_area	8	278.23	3.19	0.04
Weasel	2021	Mature forest+tree_type	9	278.32	3.27	0.04
Weasel	2021	Mid-canopy+floor	10	278.43	3.39	0.04
Weasel	2021	CWD	11	278.49	3.44	0.04
Weasel	2021	Mature forest	12	279.76	4.71	0.02
Weasel	2021	Average snow depth and coarse woody debris	13	280.4	5.35	0.01
Weasel	2021	Full	14	280.46	5.42	0.01
Weasel	2021	Vertical complexity	15	282.14	7.1	0.01
Weasel	2022	Full	1	369.91	0	0.28
Weasel	2022	Mid-canopy	2	370.76	0.85	0.18
Weasel	2022	Null	3	371.76	1.85	0.11
Weasel	2022	Mid-canopy+floor	4	372.4	2.5	0.08
Weasel	2022	Ground complexity	5	372.74	2.83	0.07
Weasel	2022	Riparian	6	372.81	2.9	0.07
Weasel	2022	Riparian_area	7	373.65	3.75	0.04
Weasel	2022	CWD	8	373.66	3.75	0.04
Weasel	2022	Average snow depth	9	373.81	3.9	0.04
Weasel	2022	Average snow depth and distance to riparian	10	374.84	4.93	0.02
Weasel	2022	Average snow depth and coarse woody debris	11	375.65	5.74	0.02
Weasel	2022	Mature forest	12	375.72	5.82	0.02

Weasel	2022	Vertical complexity	13	376.13	6.23	0.01
Weasel	2022	Riparian_tree_type	14	376.48	6.58	0.01
Weasel	2022	Mature forest+tree_type	15	377.39	7.49	0.01

Appendix 2 – Multi-species occupancy models ranked by AIC*c* for fisher (*Pekania pennanti*), American marten (*Martes americana*), American mink (*Neogale vison*), and short-tailed weasel (*Mustela erminea*) in 2015−2016 and 2020−2022 in the John Prince Research Forest, British Columbia, Canada.

Year	Species	model	rank	K	AIC*c*	ΔAIC*c*	AIC*c* ω_i
2015-2016	Marten + Mink	ρ(.)ρ(.) ψ(cc3-10)	1	8	819.11	0	0.81
2015-2016	Marten + Mink	ρ(.)ρ(.) ψ(cc0-3)	2	8	822.13	3.02	0.18
2015-2016	Marten + Mink	ρ(.)ρ(.) ψ(cc10+cc0-3)	3	11	828.37	9.26	0.01
2015-2016	Marten + Mink	ρ(.)ρ(.) ψ(.) (fit 1)	4	5	830.39	11.27	0
2015-2016	Marten + Mink	ρ(.)ρ(.) ψ(.) (fit 2)	5	4	830.83	11.72	0
2015-2016	Marten + Mink	ρ(.)ρ(.) ψ(distance_to_riparian)	6	8	831.65	12.53	0
2015-2016	Marten + Mink	ρ(.)ρ(.) ψ(cc10)	7	8	833.74	14.63	0
2015-2016	Marten + Weasel	ρ(.)ρ(.) ψ(cc3-10)	1	8	854.82	0	1
2015-2016	Marten + Weasel	ρ(.)ρ(.) ψ(.) (fit 1)	2	4	868.4	13.59	0
2015-2016	Marten + Weasel	ρ(.)ρ(.) ψ(.) (fit 2)	3	5	870.28	15.46	0
2015-2016	Marten + Weasel	ρ(.)ρ(.) ψ(distance_to_riparian)	4	8	875.32	20.51	0
2015-2016	Marten + Weasel	ρ(.)ρ(.) ψ(cc0-3)	5	10	1080.73	225.91	0
2015-2016	Marten + Weasel	ρ(.)ρ(.) ψ(cc3-10+cc0-3)	6	13	1088.49	233.68	0
2015-2016	Mink + Weasel	ρ(.)ρ(.) ψ(cc3-10)	1	8	594.82	0	0.64
2015-2016	Mink + Weasel	ρ(.)ρ(.) ψ(.) (fit 1)	2	4	597.6	2.78	0.16
2015-2016	Mink + Weasel	ρ(.)ρ(.) ψ(distance_to_riparian)	3	8	598.02	3.19	0.13
2015-2016	Mink + Weasel	ρ(.)ρ(.) ψ(.) (fit 2)	4	5	599.1	4.28	0.08
2015-2016	Mink + Weasel	ρ(.)ρ(.) ψ(cc0-3)	5	10	1080.73	485.9	0
2020-2022	Fisher + Mink	ρ(.)ρ(.) ψ(distance_to_riparian)	1	8	717.68	0	0.99
2020-2022	Fisher + Mink	ρ(.)ρ(.) ψ(.) (fit 1)	2	4	727.48	9.81	0.01
2020-2022	Fisher + Mink	ρ(.)ρ(.) ψ(.) (fit 2)	3	5	729.82	12.14	0
2020-2022	Fisher + Mink	ρ(.)ρ(.) ψ(cc3-10)	4	8	736.24	18.56	0
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(cc3-10)	1	9	1316.76	0	0.94
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(snow_depth)	2	9	1323.79	7.04	0.03
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(cc0-3)	3	9	1324.84	8.08	0.02
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(cc10+cc3-10+cc0-3)	4	15	1326.32	9.56	0.01
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(distance_to_riparian)	5	9	1327.17	10.41	0.01
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(cc10)	6	9	1328.45	11.69	0
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(.) (fit 2)	7	5	1331.91	15.15	0
2020-2022	Fisher + Marten	ρ(.)ρ(.) ψ(.) (fit 1)	8	4	1337.25	20.5	0
2020-2022	Mink + Marten	ρ(.)ρ(.) ψ(cc3-10)	1	8	1164.73	0	0.5
2020-2022	Mink + Marten	ρ(.)ρ(.) ψ(distance_to_riparian)	2	8	1165.03	0.29	0.43
2020-2022	Mink + Marten	ρ(.)ρ(.) ψ(.) (fit 1)	3	4	1169.13	4.4	0.06

2020-2022	Mink + Marten	ρ(.)ρ(.) ψ(.) (fit 2)	4	5	1171.31	6.58	0.02
2020-2022	Marten + Weasel	ρ(.)ρ(.) ψ(cc3-10)	1	10	1771.12	0	1
2020-2022	Marten + Weasel	ρ(.)ρ(.) ψ(snow_depth)	2	10	1784.17	13.05	0
2020-2022	Marten + Weasel	ρ(.)ρ(.) ψ(cc10)	3	10	1785.41	14.3	0
2020-2022	Marten + Weasel	ρ(.)ρ(.) ψ(cc10+cc0-3)	4	13	1793.13	22.01	0
2020-2022	Marten + Weasel	ρ(.)ρ(.) ψ(distance_to_riparian)	5	10	1819.12	48	0
2020-2022	Marten + Weasel	ρ(.)ρ(.) ψ(.) (fit 1)	6	4	1835.54	64.42	0
2020-2022	Marten + Weasel	ρ(.)ρ(.) ψ(.) (fit 2)	7	5	1837.81	66.69	0
2020-2022	Fisher + Weasel	ρ(.)ρ(.) ψ(cc10)	1	9	1351.93	0	0.99
2020-2022	Fisher + Weasel	ρ(.)ρ(.) ψ(distance_to_riparian)	2	9	1360.59	8.66	0.01
2020-2022	Fisher + Weasel	ρ(.)ρ(.) ψ(.) (fit 1)	3	4	1393.89	41.96	0
2020-2022	Fisher + Weasel	ρ(.)ρ(.) ψ(.) (fit 2)	4	5	1396.09	44.16	0
2020-2022	Fisher + Weasel	ρ(.)ρ(.) ψ(cc3-10)	5	8	1398.6	46.67	0
2020-2022	Mink + Weasel	ρ(.)ρ(.) ψ(distance_to_riparian)	1	10	1173.89	0	0.99
2020-2022	Mink + Weasel	ρ(.)ρ(.) ψ(cc3-10)	2	10	1184.16	10.27	0.01
2020-2022	Mink + Weasel	ρ(.)ρ(.) ψ(snow_depth)	3	10	1186.71	12.82	0
2020-2022	Mink + Weasel	ρ(.)ρ(.) ψ(cc10)	4	10	1187.32	13.43	0
2020-2022	Mink + Weasel	ρ(.)ρ(.) ψ(cc10+cc0-3)	5	13	1193.73	19.83	0
2020-2022	Mink + Weasel	ρ(.)ρ(.) ψ(.) (fit 1)	6	4	1225.77	51.88	0
2020-2022	Mink + Weasel	ρ(.)ρ(.) ψ(.) (fit 2)	7	5	1226.44	52.55	0