How Competition Dynamics Drive Access to Shared Scavenging Opportunities Amongst a Group of Mesocarnivores in the Rocky Mountains of Alberta

by

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We acknowledge with respect the Lekwungen peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Abstract

Mesocarnivores occupy critical functional roles in regulating ecosystems and maintaining biodiversity. In the Canadian Rocky Mountains, mustelid species depend heavily on carrion as an important dietary contribution, particularly in winter when resources are scarce. In diverse mesocarnivore communities such as this, sympatric species must balance energetic resource acquisitions through scavenging with avoidance of costly competition dynamics, in a manner that optimizes energetic gain through risk aversion. We examined the nature of spatial-temporal interactions between wolverine (*Gulo gulo*), American marten (*Martes Americana*), and short-tailed weasel (*Mustela erminea*) in the Willmore Wilderness Park in western Alberta. Data were collected from camera traps (n = 59) baited with a simulated scavenging opportunity during winter months between 2006 to 2008. The spatial-temporal dimensions of intraguild competition were evaluated using a multi-model approach. Zero-inflated negative binomial (ZINB) or zero-inflated Poisson (ZIP) regression models were used to identify the competitive and environmental factors that affected (1) species presence/absence and (2) how intensely a species would spatiotemporally optimize a carrion site. A time-to-event analysis was used to quantify the directionality of fine-scale (hourly) reactionary behavioural responses of species to potential sources of competition. An extension of this group of models, the Cox proportional hazard (CPH) model was used to further reveal the relative influence of external environmental variables (i.e. diel period, landcover, and snow depth) on temporal spacing. Pairing CPH and ZINB/ZIP models enables us to recognize the relative contribution of fine-scale spatial and temporal behavioural responses to competitors in shaping coexistence strategies.

Our results suggest that facultative scavengers adopt different coexistence mechanisms based on the interspecific competitor and environmental conditions they encounter at carrion sites. We found that carrion use was impacted for all species by competition and snow depth. Marten scavenging behaviours were additionally impacted by habitat character. We also found evidence of fine-scale temporal attraction between marten and wolverine, thought to indicate a shared net-energetic gain at scavenging sites. Our results suggest that mesocarnivore scavengers are likely to adopt spatiotemporal mechanisms to facilitate carrion resource partitioning and adapt to conditions specific to carcass placement in a spatially complex environment. Given their vital ecological roles, it is important that we recognize the ability of individual mustelid species to exploit scavenging opportunities and identify the external factors that influence coexistence. Understanding the factors that drive access to these ephemeral resources will provide valuable information for anticipating impacts of climate change on facultative scavengers in the boreal forests of western Canada.

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1. Introduction

As the reaches of anthropogenic disturbance expand and carnivore populations continue to decline globally (Di Marco et al. 2019), the ability to conserve mammalian carnivore populations and thereby preserve their critical functional roles in regulating ecosystems and maintaining biodiversity, is made increasingly difficult. Most carnivores are capable of utilizing carrion (i.e. animal carcasses) as a dietary resource and it is believed that scavenging may represent a more substantial proportion of overall dietary contribution than had been previously recognized (DeVault & Rhodes 2002; DeVault 2003). Scavenging creates distinctive patterns of intraguild interactions and competitive structures at carcass sites that can have broad landscape-scale implications on carnivore distributions and population dynamics (Sivy et al. 2017). The nature of intraguild competitive interactions among carnivores is contingent on a competitor's ability to mitigate risk through the use of inherited co-existence mechanisms, which can often rely on accessing spatial or temporal areas of refuge (Ritchie & Johnson, 2009; Rota et al. 2016). Carrion sites represent unique, localized spatial-temporal regions of competitive risk exposure and energetic reward that may require sympatric carnivores to alter coexistence mechanisms in accordance (Selva et al. 2003). Mesocarnivores are increasingly understood to occupy unique roles in the structuring of ecosystems (Palomares & Caro, 1999), yet very little is known about the factors driving carrion acquisition by these species in the northern temperate forests of North America that experience prey-limited harsh cold winters.

The vital role of carrion in the structure and function of ecosystems and the transfer of energy and nutrients through food-webs is increasingly being recognized (DeVault et al. 2003; Wilson & Wolkovich, 2011). Anthropogenic changes to the foraging or movement behaviour of individual species can alter complex ecological interactions or modify carcasses availability in ecosystems and in turn initiate unpredictable ecosystem-level changes (Tucker et al. 2018). It is therefore vital that we come to recognize the ecological determinants of an individual's carrion use and the extrinsic factors that facilitate or impede the ability to scavenge.

Scavenging ecology considers the seasonal and spatial availability of carcasses (Pereira et al. 2014; Smith et al. 2017) within the ecosystem, the efficiency with which consumers utilize carcasses, and scavengers' access to the carcass based on behavioural ecology (DeVault, 2003). Most carnivores are facultative scavengers to some extent in that they opportunistically exploit carrion resources but are not restricted to scavenging as a mode of life; mammalian carnivores may shift foraging strategies between predation and scavenging subject to carrion availability (Moleón et al. 2014; Pereira et al. 2013). Yet, with marked exceptions (Klauder et al. 2021) there is a lack of research focusing on intraguild interaction factors that improve or constrain a carnivore's ability to scavenge at the level of the individual (DeVault, 2003). Moreover, investigations into mammalian scavenging ecology have frequently been aimed at deciphering the impacts of the largest predatory species that are frequently responsible for generating carcasses (Allen et al. 2015; van Dijk et al. 2008; Wikenros et al. 2013), and often negate interactions that occur among small and mid-sized carnivores, collectively referred to as mesocarnivores. This thesis will attempt to address this gap in knowledge by understanding the perceived costs of carrion feeding for a sub-group of mesocarnivores in a mountainous region of western Canada during winter when resource availability is scarce.

Carrion varies in its spatial and temporal deposition across heterogeneous landscapes and seasons (Pereira et al. 2014; Smith et al. 2017). In boreal mountain systems large ungulates are diverse (e.x. bighorn sheep (*Ovis canadiansis*), moose (*Alces alces*), elk (*Cervus canadensis*), mountain goats (*Oreamnos americanus*), mule deer (*Odocoileus hemionus*) and white tail deer

(*Odocoileus virginianus*)), and can die via disease, starvation, avalanches, falling from heights, direct predation, or remains from hunter harvesting (Wilkenros et al. 2013). Inside protected areas, different landscape characteristics can assume variability in ungulate vulnerability to legal recreational hunting (Plante et al. 2017). Alternatively, hunting activities and other forms of human activity can alter the spatial distributions of carnivores, in some cases displacing predators and serving as spatial refugia to prey species (Muhly et al. 2011; Wilkenros et al. 2013). The distribution of ungulate carcasses across available habitat is liable to be altered under both scenarios. Indeed, the kill sites of ungulates by large carnivores are often non-uniformly distributed across the landscape (Kohl et al. 2018), dependant on prey density or abundance, habitat structure, topography and the probability of predator hunting success that can further relate to microhabitat features (Podgórski et al. 2008). Moreover, Cortés-Avizanda et al. (2009) found that the spatial locations of carrion pulses negatively impacted herbivore spatial distributions likely as a consequence of increased probability of encountering predators at those locations.

1.2 Carrion and Intraguild Competition Dynamics

Carrion is a widely shared “ephemeral resource” (Barton et al. 2013), and carcass sites can alter intraguild interactions through trait-mediated direct and indirect effects of competition (Cortés-Avizanda et al. 2009). Cortés-Avizanda et al. (2009) observed localized increase in the number of facultative scavenger species at sites of large herbivore carcasses. Thus, for some species, scavenging is presumed to be a risky behaviour. Competing carnivores encounter a rise in probability of intraguild encounters at carcass sites and thus exposure to interference competition – defined by instances where one species affects the ability of another to acquire resources through direct acts of hostility (e.g. infanticide, harassment, kleptoparasitism and intraguild predation). Carrion foraging behaviours are ultimately shaped by individual trade-off decisions driven by aversion to risk and access to an energetic reward that optimize resource acquisition (i.e. net energetic gain) (Klauder et al. 2021). This may be especially important in boreal mountain environments where cold temperatures and snowpack incur very high metabolic costs compared to more temperate regions. Thus, we expect reward to be much more important here and hence the willingness to accept risk.

Mesocarnivores include mustelids, a diverse group of primarily solitary small to mid-sized carnivores and facultative scavenging is consistent among all species comprising the mustelid family. For example, the mustelid community in the Canadian region of the Rocky Mountains include wolverine (*Gulo gulo*), American marten (*Martes americana*), fisher (*Pekania pennanti*), and short-tailed weasels (*Mustela erminea*). These species vary in their habitat preferences and diel activity patterns with shifts in nocturnality observed for some species during winter (Clark et al. 1987). Mustelids are facultative scavengers that forage terrestrially on small mammals, birds, eggs and opportunistically fruits and carrion (Ruggiero et al. 1994). Mustelids also occasionally prey on one another (Banci, 1994). The proportional dietary contribution of shared prey can vary drastically, although dependence on carrion is not well understood since most diet analyses rely on stomach content analysis that often cannot distinguish acquired prey from scavenged meat (Aldous et al. 1942). Owing to the combined difficulty of identifying trends in carrion availability and quantifying proportional dietary contributions, the scavenged component of facultative scavenger diets is likely to be frequently overlooked or understated (DeVault et al. 2003). A noteworthy meta-analysis conducted by Prugh, Sivy & Sih (2020) estimated that scavenged ungulates comprise 30% of mesocarnivore diets, with a greater reliance on scavenging seen in larger mesocarnivores. Therefore, it is important to recognize how this dietary component is partitioned in the context of intraguild competition.

1.3 Carnivore Coexistence and Resource Partitioning

Niche differentiation can facilitate coexistence by reducing the effects of interspecific competition through some degree of spatial, temporal or dietary separation. Evolved behavioral (e.g. generalist versus specialist) and morphological (e.g. sensory abilities, physiology) species attributes that serve to minimize niche overlap are the evolutionary product of interwoven natural selection processes linked to competition (Creel, 2001; Schuette et al. 2013). Within a diverse carnivore community, the different mechanisms used to partition resources can have distinct ramifications for coexistence, sometimes resulting in competitive exclusion of subordinate competitors (Dröge et al. 2016; Swanson et al., 2014, 2016). On a more immediate scale, evolution has also armed organisms with sensory instruments and instinctive behavioural responses that track short-term signals of variation in temperature, threatening stimuli and resource availability (Tambling et al. 2015), which may depend on a spatiotemporally fluctuating relative margin of safety (Frid & Dill, 2002).

Increasingly, researchers have chosen to reconcile the inextricable linkage of space and time in estimating the direction and intensity of species interactions and carnivore community structures (Keim et al. 2019; Smith et al. 2019; Swanson et al 2016). The results of such investigations have highlighted that sympatric species can navigate space and time inversely to significantly reduce instances of spatiotemporal co-occurrence (de Satgé et al. 2017; Smith et al. 2019). Behavioural responses to spatial and temporal variation in the distribution of fitness risks versus resource acquisitions across the landscape result in visible coexistence strategies, which are subject to change in response to circumstance (Palmer et al. 2017; Smith et al. 2019; Pereira et al. 2013).

1.4. Project Significance and Contributions

In terrestrial forest communities, carrion is a "pulsed resource" that represents an important dietary contribution to an array of species, particularly in winter when energetic resources are scarce (Pereira et al. 2014; Stiegler et al. 2020). Estimating the nature of complex interactions in diverse carnivore communities requires an integrated approach that accounts for environmental habitat variables and the spatial and temporal distributions of species interactions. Still, while regulatory effects of large carnivores on ecosystems have been realized to some extent, relatively little remains known about the impacts of carrion resources on intraguild dynamics amongst mesocarnivores. This knowledge is particularly important in diverse carnivore communities that contain numerous co-occurring mesocarnivores undergoing dynamic influence over one another. Without accounting for how coexistence manifests amongst small and mid-sized carnivores at carcass sites and how these species are able to utilize these resources, we negate a crucial component process of scavenging ecology. The objective of this thesis is therefore to better understand the influences of scavenging behaviour for a group of facultative scavengers. To realize patterns of carrion usage, I implemented regression models and time-to-event analyses to evaluate the relative importance of fine-scale spatiotemporal and temporal reactionary responses to the external biotic and abiotic factors at carrion sites. Chapter 2 of this thesis presents this work in the format of a manuscript that will be submitted for publication at a later date. Chapter 3 presents some general conclusions from this study, discusses study limitations and constraints, and provides general recommendations for future work in this area.

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Chapter 2: Fine-scale competition dynamics of facultative scavengers during winter using a spatial-temporal analytic approach

2.1 Introduction

Scavenging ecology is an important ecosystem process represented by an intricate, complex network of energy acquisitions, shaped by interplay between environmental factors, predation and competition that perpetuate throughout food web linkages (Barton et al. 2013; Selva et al. 2005; Smith et al. 2017a, 2017b; Prugh & Sivy, 2020). Carrion, (i.e. the remains of dead animals) is a distinct form of detritus that generates a spatially and temporally distinct patch of rich energetic value and nutrient concentration to scavengers relative to its surrounding environment (Barton et al. 2013; Wilson & Wolkovich, 2011). Occurrences of large ungulate carrion in forest ecosystems exist as spatially distinctive "pulsed resources" that directly evoke behavioural responses by facultative scavengers and peripherally that of their associated prey (Cortés-Avizanda et al. 2009). In northern climate forest communities carrion represents a vital dietary component for many facultative scavengers, particularly in winter when energetic resources are scarce (Pereira et al. 2014; Stiegler et al. 2020). Vertebrate scavengers, not microbial decomposers, are frequently the dominant primary consumers of available carrion, thereby expanding the extent of energy and nutrient flows in food webs (DeVault et al. 2003). Among vertebrate scavengers, mesocarnivores (those represented by small to mid-sized carnivorous species) can account for most (>90%) of carrion consumption (DeVault et al. 2011). Carnivores frequently compete for carrion use (Klauder et al. 2021; Prugh & Sivy 2020) and the extent to which mesocarnivores are able to use these resources is contingent on intraguild competition as well as environmental conditions (Allen et al. 2015; Selva & Fortuna, 2007).

Most mesocarnivores are opportunistic facultative scavengers, and larger mesocarnivores in particular may rely heavily on carrion resources (Prugh et al. 2020; Mattison et al. 2011). In terrestrial systems, mesocarnivores frequently occupy unique roles as fundamentally important determinants of ecosystem structure and function (Roemer et al. 2009), for example facilitating changes to plant communities through altered patterns of seed dispersal and nutrient regimes (Steyaert et al. 2018). The regional availability and proportional dietary contribution of carrion to mesocarnivores is context specific and often not well understood, though recent estimates suggest that carrion represents >30% of mesocarnivore diets (DeVault et al. 2003; Prugh et al. 2020). Previous research has explored the concept of scavenger efficiency among taxa by attempting to understand how, for example, accessibility varies among mammals, avian species and microbes (DeVault 2003, Smith et al 2017a). For mammalian predatory species that are also facultative scavengers, carrion is unique in that it offers substantial energetic gains without the associative energy expenditure required to capture and overpower prey (Pereira et al. 2014).

However, carrion consumption can expose scavengers to an alternative set of risk factors such as infectious diseases (Selva et al. 2005), predation (Sivy et al. 2017) and competition with other carnivores that can result in energetic opportunity losses through direct antagonistic encounters or risk aversion (Wilkenros et al. 2013). Facultative scavengers are adapted to recognizing the associative costs and altering their behaviour such that energetic gains offset potential losses associated with scavenging and yet the nature of intraguild interactions at carcass sites has yet to be fully recognized as a unique and important component of scavenger ecology.

Competition for resources is the predominant driver for the extent of interference competition – defined by direct acts of aggression encompassing harassment non-consumptive or consumptive killing, kleptoparasitism and infanticide – observed among carnivores (Roemer et al. 2009). Past research has generated strong evidence that degree of competition is increased by taxonomic similarity (Prugh et al. 2020), comparable body-size (Leyequién et al. 2006) and dietary niche overlap (Merkle et al. 2017). Therefore, there is often specific interest in the interactions between predator pairs that are likely to exert especially strong competitive pressure on one another through these mechanisms (e.g. Fisher et al. 2013a). However, while differences in body size may indicate differentiation in dietary preferences and prey exploitation, which is thought to reduce competition, strong competitively-driven behaviours can exist even where direct competition for resources is limited (Swanson et al. 2014).

Such findings highlight that the motivation behind interference competition is not always clear. Moreover, potential outcomes of intraguild competition structures are not mutually exclusive; rather, they appear to be interwoven and highly complex (Prugh & Sivy, 2020; Selva & Fortuna, 2007). Large predators for example can dominate carcass sites thereby suppressing mesocarnivore access or alternatively, provide carrion provisions to smaller carnivores that are themselves unable to tackle large ungulate prey (Prugh & Sivy, 2020; Klauder et al. 2021). Moreover, the prevailing nature of large carnivore effects can oscillate seasonally to have a consolidated regulating effect on annual carrion abundance (Wilmers et al. 2003). Conversely, through generating localized feeding opportunities that serve as regions of intensified intraguild aggressions and heightened mortality rates for mesocarnivores, carcass sites can strengthen suppression by large carnivores – this concept is known as the Fatal Attraction Hypothesis (Prugh & Sivy, 2020; Sivy et al. 2017). While much research into carnivore scavenging ecology has existed through this lens of large carnivore regulation, less attention has been paid to carrion feeding behaviours and interactions amongst small to midsized carnivores.

Outcomes of scavenging community ecology play out through various mechanisms at two primary hierarchical scales: (1) the individual, relating to behavioural plasticity in foraging behaviour and carrion acquisition, (2) the population, which relates to species survival, fitness and ultimately abundance and distributions across the physical landscape. Thus, while the influence of scavenging manifests at the population level, acquisition to this vital resource is determined by a set of localized conditions encountered by the individual at carrion sites, which fluctuate in relation to scavenger community composition (Selva & Fortuna, 2007), physical landscape characteristics (e.g., landcover, topography), and environmental conditions (e.g. temperature, snow cover) (Selva et al. 2005; Smith et al. 2017; Stiegler et al. 2020; Pardo-Barquín & Mateo-Tomás, 2018).

At the level of the individual, mechanisms of coexistence between sympatric mesocarnivores can manifest through behavioural associations taking place over two interacting planes of coexistence: space and time. Inferences about the nature of species interactions is benefited by a combined approach that considers both of these planes of coexistence, to generate robust insights to species-specific attraction/avoidance tactics (Cusack et al. 2017; Karanth et al. 2017; Prat-Guitart et al. 2020; Swanson et al. 2016). At carcass sites, facultative scavengers can minimize costs associated with competition (i.e. energetic losses and risk associated with harassment and intraguild aggressions or risk of death) through selecting for carcasses located in spatial locations that involve less chance of competitive encounter, utilizing sites during temporal downtimes of co-occurring scavengers, or limiting the overall spatiotemporal extent of their carcass use.

This study focuses on intraguild interactions for a sub-group of cold-adapted mesocarnivores from the family Mustelidae: short-tailed weasels (hereafter weasel), American marten (hereafter marten) and wolverine, to examine species-specific scavenging behaviours during winter based on competition structures at scavenging opportunities. A large mesocarnivore and potential common threat to all mustelids under investigation, lynx, were also partially included in analyses to account for an additional competition factor at study sites. Carnivores must exploit various sources of food through the seasonal cycle (Pereira et al. 2014). During winter, all species in our study area are limited by food availability and exhibit some degree of dietary overlap with one another (Aldos & Manweiler, 1942; Banci, 1994; Clark et al. 1987).

Wolverines, the largest North American mustelid, are opportunistic predators capable of catching and subduing moose, elk, reindeer and caribou under favourable conditions (Banci, 1994). Large ungulates make up the largest proportion of wolverine diet, it is however likely that the relative contribution of this dietary component is highly reliant on uptake through scavenging (Dalerum et al. 2009; Mattisson et al. 2011). Large carnivores may be important suppliers of ungulate carcasses for wolverines to scavenge (Banci, 1994) and the considerable importance of large ungulate carrion to wolverine winter diet and survivability has been well established (Banci, 1994; van Dijk et al. 2008; Weaver et al. 1996). Wolverine fecundity has been linked to winter food availability (Persson et al. 2005) and indeed, the availability of ungulate carcasses appears to underlie wolverine reproductive success (Banci, 1994; van Dijk et al. 2008) in turn impacting population dynamics.

By comparison, principal prey species for American marten in winter has been identified as snowshoe hare (*Lepus americanus*), squirrels, mice and voles (Clark et al. 1987; Ruggiero et al. 1994). Carrion feeding has additionally been documented for marten (Clark et al. 1987), though little is known about overall dietary contribution during winter. Weasel winter diet similarly consists of birds and eggs, small mammals, the slightly larger snowshoe hare, and carrion (Aldous & Manweiler, 1942). Wolverine winter diet is subsidized with birds, snowshoe hare and other small mammals such as rodents and squirrels (spp. *Sciuridae*), where their diet overlaps with that of smaller mustelids (Aldous & Manweiler, 1942; Clark et al. 1987; Hargis & Mccullough, 1984). Moreover, American marten and short-tailed weasel have both been identified in wolverine diet analyses (Banci, 1994). These findings cannot distinguish among predation, direct killing related to interference competition or scavenging.

The focal species of this research are taxonomically similar, possess some degree of dietary overlap in addition to carrion and are subject to predatory as well as competitive linkages with one another. There is a need for improved understandings of the factors that foster or constrain a mesocarnivores ability to scavenge (Klauder et al. 2021; DeVault, 2003). To address this need, the overarching objective of this research was to determine those external factors that govern carrion acquisition by mesocarnivores and identify behavioural tactics used by focal species for minimizing interference competition, in a protected temperate forest of western Canada. More specifically, four foundational hypotheses guided this investigation, they are listed as as follows:

Hypothesis 1: We hypothesize that wolverine, the largest mustelid in this study with morphological adaptations for carcass segmentation and pronounced weaponry for competition, will show evidence of competitive dominance at carcass sites. This is expected to be supported by a lack of negative spatial or temporal influence by species interaction factors.

Hypothesis 2: Smaller mesocarnivores, which are agile and capable of arboreal and subnivean mobility are expected to navigate competitive factors at scavenging opportunities through fine-scale spatial-temporal behavioural patterns rather than spatial segregation or site exclusions. This form of conflict mitigation should manifest as competition variables having negative associations with the rate of site use with no associative effects on patterns of site occupancy.

Hypothesis 3: Large and small mesocarnivores will differ in their response to a potential common threat by a larger felid, Lynx. Wolverine benefit from ungulate carrion provisions by Eurasian lynx (Mattisson et al. 2011b). Under the assumption that tracking lynx may offer periodic energetic rewards to wolverine we hypothesize that wolverine in Alberta will demonstrate patterns of positive spatial association to Canada lynx. By contrast, lynx are proficient hunters of small to mid-sized mammals and are anticipated to evoke behavioural responses in smaller mustelids that is more akin to predator avoidance, more specifically spatial segregation at the site level.

Hypothesis 4: Differential habitat selection can impact site visitation and/or the nature of species interactions, we looked at whether habitat associations, competitive interactions, or an integrated habitat-competition approach best for determining mustelid spatial selection for scavenging sites in a heterogenous landscape and hypothesize that a combination of species interactions and site character will influence scavenger site use. Snow depth and landcover character (i.e. canopy closure) and daylight period were selected as external environmental attributes that might alter responses to an available scavenging opportunity.

The complexity of interwoven factors driving scavenging ecology calls for statistical approaches that can quantify carcass use in relationship to external environmental stimuli and tie together the spatial and temporal components of interreference competition. To accomplish these research objectives, a simulated scavenging opportunity was created and continuously replenished at remote camera traps. We adopted an integrated spatial-temporal framework using regression models and time-to-event analysis. Planes of avoidance (or attraction) behaviours were examined at fine spatial (point location) and temporal (hourly) scales and calibrated to take measure over the same temporal intervals. This investigation is thus situated at the level of the individual by exploring patterns of carrion feeding at the site-level as a function of species interactions and habitat relationships.

2.2. Methods

2.2.1 Study Site

The Willmore Wilderness Park (WWP) is a conservation area spanning approximately 4,600 km^2 in the Rocky Mountain region of Alberta, roughly 300 km northwest of Edmonton on the Alberta-BC border (Figure 2.1). The WWP is buffered from human disturbance by Kakwa Wildland Provincial Park and Protected Area (BC) and Kakwa Wildland Park (AB) in the north and Jasper National Park (AB) and Rock Lake-Solomon Creek Wildland Park (AB) in the south. The region is highly heterogeneous with regard to both landcover and elevation, which ranges between 1200m – 2400m above sea level.

At higher elevations, the vegetation in the WWP consists of alpine meadows transitioning to subalpine fir (*Abies lasiocarpa*) at approximately 2,000 meters (Alberta Parks, n.d.). Sub-alpine conifer forests dominate the WWP landscape, consisting predominantly of Engelmann spruce (*Picea engelmannii*), white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*) and balsam fir (*Abies balsamea*) with stands of black spruce (*Picea mariana*) at lower elevations and river valleys (ASLC, 2016; Fisher & Bradbury, 2014). Closed mixedwood and deciduous forest stands of trembling aspen (*Populus tremuloides*) and balsam popular (*Populus balsamifera*) are sparse throughout this site (ASLC, 2016). The area experiences naturally occurring seasonal forest fires, resulting in burn sites that create open regenerating forest patches – mainly in the southwest and northwest areas of the park.

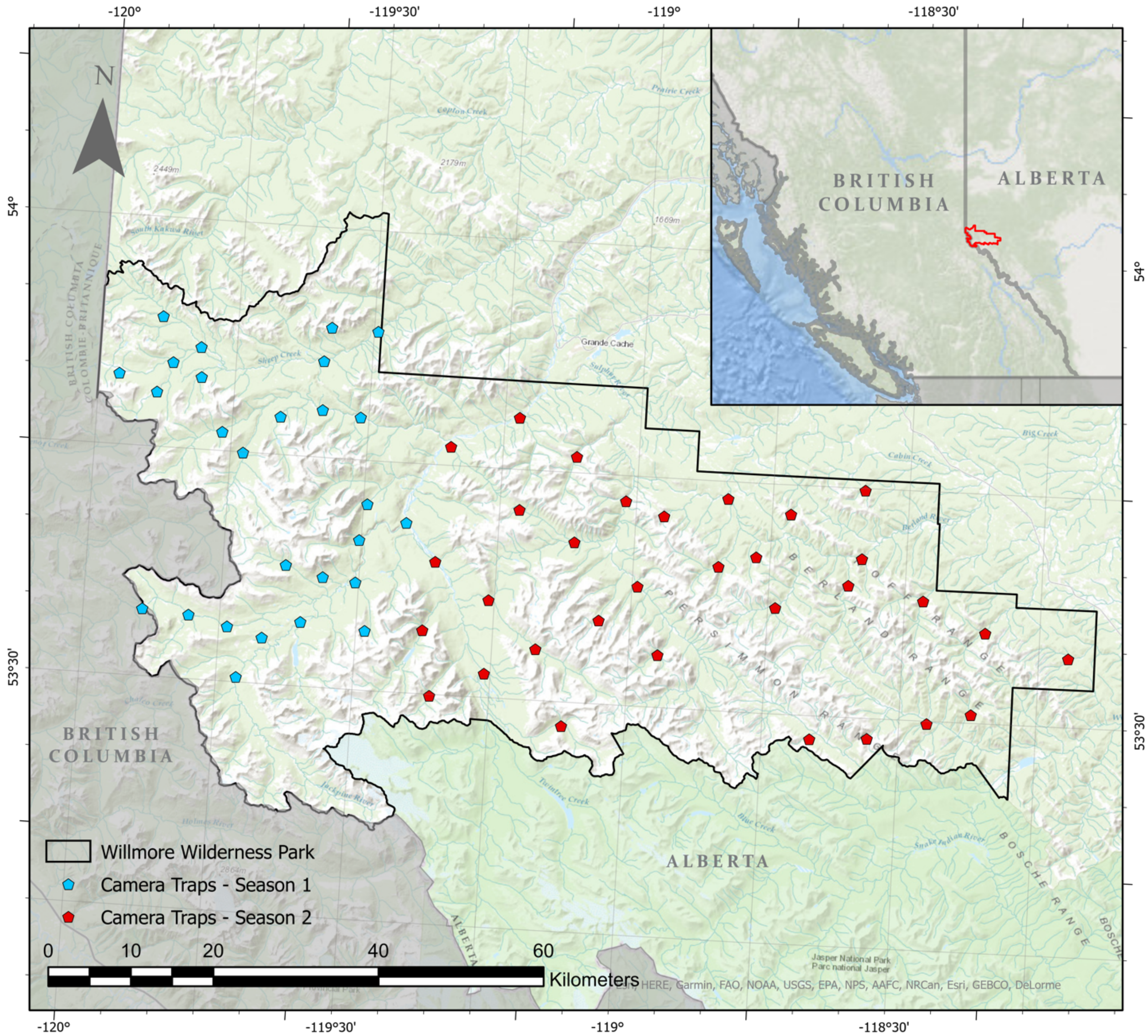


Figure 2.1: Willmore Wilderness Conservation Area, Alberta, Canada. Camera trap data were collected over two consecutive winter seasons during 2006/2007 (period 1, n=27, blue locations) and 2007/2008 (period 2, n=32, red locations).

WWP was established in 1959 and is managed under unique legislation of the Willmore Wilderness Parks Act (2002). The Act's mandate is to preserve the Willmore's expansive natural landscapes, conserve critical habitat for various wildlife inhabitants and minimalize visitor impacts. Anthropogenic disturbance inside the WWP is restricted to recreational activities, equestrian activities, hiking, snowshoeing, backcountry camping, hunting, trapping and fishing. Motorized vehicles are prohibited as are any industrial activities, as stated in section 2(4) c38 of the WWP Act (1995).

Figure 2.2: Camera trap images of marten (left, 22-02-2008) and wolverine (right, 03-03-2008) in the Wilmore Wilderness Park, AB. Beaver carcass serving as a carrion scavenging opportunity is visible. Barbed wire at baited trap sites extracted DNA samples for wolverine as part of a study independent of this one.

The Park supports a diverse community of carnivores, including one of the highest densities of grizzly bear (*Ursus arctos horribilis*) in the province (Fisher et al. 2014). Other large predators include black bear (*Ursus americanus*), grey wolf (*Canis lupus*) and cougar (*Puma concolor*). The mesocarnivore community is comprised of lynx (*Lynx canadensis*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), fisher (*Pekania pennanti*), American marten (*Martes* *americana*), short-tailed weasel (*Mustela erminea*) and red fox (*Vulpes vulpes*). Wolverines represent the only focal species currently of conservation concern in Canada. The species is described as "may be at risk" by the province, though detailed status is data deficient (Mowat, 2001), and is listed as Special Concern nationally (COSEWIC, 2014).

2.2.2 Data

This study utilizes camera trap data collected from a systematic sampling array (n=66) deployed in the WWP. Photographic data for this research were provided by the Applied Conservation Macro Ecology Laboratory (ACME Lab) at the University of Victoria and have been repurposed from initial studies focused on wolverine spatial ecology (Fisher et al. 2011, 2013b). Reconyx infrared camera models PM30 and PM85 (Reconyx, Holman, WI, USA) were baited with beaver carcasses (Figure 2.2) and placed approximately 5.73 km apart.. Data were collected between late-December to early-March over two consecutive winters in 2006/2007 (period 1, n=30) and 2007/2008 (period 2, n=36) (see complete details: Fisher et al. 2011, 2013). Fifty-nine sites of the initial array were successfully surveyed, while the other seven were removed owing to mechanical failures. The study period covers a period during which all camera traps were consistently operational, totalling 70 days respectively for winter season 1 (2006-12-28 to 2007-03-08) and season 2 (2007-12-29 to 2008-03-08). The two seasons were combined to a single period by Julian date in order to evaluate the behavioural ecology of mesocarnivores during winter over the entire wilderness area.

2.2.3 Analysis

Multiple lines of evidence were used to probe different key aspects of the fundamental research objectives. Each of these approaches are described in detail in the preceding sections but as a general overview, for a given point location (i.e. scavenging opportunity):

> **(1) A ZINB binomial process**, representing distinct spatial segregation of species, is performed to address the question: Is mustelid site occupancy (i.e., species presence/absence defined as at least one site visit over a 5-day interval) influenced by occupancy by heterospecifics?
>
> **(2) A ZINB count process**, representing spatial co-occurrence related to the fluctuating rate of site use per unit time, provides insight into the inquiry: Does the intensity of site use by one species influence that of another?
>
> **(3) A Temporal Spacing Analysis,** provides a means to answer: Do species with intersecting spatial and diel temporal niches react to one another through more immediate, reactionary temporal avoidance?
>
> **(4) Finally, a Cox Proportional Hazard Model,** is developed to ask: Do habitat characteristics play a role in shaping patterns of temporal interaction occurrences (time spacing analysis)?

2.2.3a ZINB regression models: estimating resource partitioning

To examine the relationship between the intensity of site usage by competing mustelids, we used zero-inflated negative binomial (ZINB). ZINB models are a two-tiered process that estimate the degree of influence of causal factors at camera sites on species presence/absence and on the rate at which sites are utilized. The response variable is the photographic rate (PGR) of capture for focal species at each trap location over consecutive 5-day periods spanning the duration of the study period (n=826 individual intervals). Weasels were detected in the second winter season only, therefore PGR data represent the 2007/2008 winter for this species alone (n= 392). Large carnivores, wolves and cougar, were captured by camera traps very infrequently during winter in the WWP (cougar n= 67, wolves n=31). However, Canadian lynx did occupy carcass sites with moderate relative frequency (n=165). We therefore included lynx as a potential competition variable in ZINB models in addition to sympatric mustelids. This allowed us to determine whether periodic site visitation by another large mesocarnivore would influence mustelid feeding behaviours and improve model performance.

To ensure data represented independent capture events of unmarked species, we removed successive captures of the same species occurring within 10 minutes, similar to procedures followed in other camera trap data analyses (Keim et al. 2018). Repeat captures of the same species exceeding 10 minutes were considered to be indictive of either prolonged site usage by the same individual, or the appearance of a different individual, both circumstances that are relevant to measuring the relative intensity with which a species utilizes a spatial location. When multiple individuals were captured during a single capture event, each occurrence considered an independent data point.

We looked to overall CR of scavengers at baited traps and chose 5-day sampling occasion lengths to derive meaningful trends in species presence and intensity of site usage (i.e. CR). Similar to assessments by previous camera trap surveys, this duration provided adequate sample sizes to measure the effects of covariates while at the same time reducing the number of zero-count data for species presence (Naidoo & Burton, 2020). Species occurrence (presence/absence) data using this modeling framework are sufficiently resolved to be interpreted as fine-scale spatial-temporal processes. Since the objective of this investigation is to better understand species interactions as a function of external stimuli at the site level, 5-day occasion lengths were further assumed to control for spatial independence across camera locations. However, because the cut-off time for each successive sampling occasion is effectively arbitrary, we could not ensure temporal independence of adjoined intervals. As a result, data points contributing to the overall CR for a given mustelid at the beginning of a sampling occasion could relate to a set of circumstances – for instance a period of intense usage by a competitor – which occurred in the occasion before it. We were unable to account for the lack of temporal independence between repeated 5-day observations within sites, or that species temporal reactions to one another may involve a lag period but acknowledge that such possibilities could affect model estimates.

We assessed CR data for zero-inflation and overdispersion to select the most suitable modelling design for analyzing count data and strengthen ecological inferences (Blasco-Moreno et al. 2018). Despite the fact that attractants typically increase carnivore detections at trap sites, thereby reducing the severity of zero-inflation (Holinda et al. 2020), zeros arise from any 5-day occasion where a focal species is not captured and are common in camera survey species count data.

Mustelid CR datasets were tested for overdispersion using the Pearson dispersion statistic (Payne et al. 2018). Inspection into the zero-inflation of count data was performed by the Vuong test that has been commonly used to look for zero-inflation by comparing non-nested NB-GLM with their ZINB counterpart having the same predictor variables (Desmarais & Harden, 2013), though this approach has been met with some criticisms (Wilson, 2015). Zero-inflated negative binomial models are well suited to count data which is both overdispersed and zero-inflated and adoption of a ZINB modelling approach was justified in the case of two mustelids (see Results section 2.3.1).

ZINB regression models use a hierarchical approach to account for zero inflation by classifying zeros into either excess ("structural") zeros *or* circumstantial ("random") zeros that are related to sampling variability in the observation process (Blasco-Moreno et al. 2018). These models assume that excess zeros (representing species presence/absence) result through a separate ecological process, independent of that driving the count process (representing intensity of site use). ZINB is a mixture model comprised of two distributions that are analyzed using (1) a binomial logistic regression that accounts for the excess zeros, and (2) a Poisson or negative binomial count process that examines the rate of capture. For each focal species, we considered a ZINB model with the same basic set of four explanatory covariates for the binomial and count processes: three competitive interaction variables – the presence/absence (binomial process) or PGR (count process) of sympatric scavengers, and two environmental factors – snow depth and landcover. Odds ratios (i.e. the exponentiated regression coefficients, Table 1) offer a measure of the strength of association between the predictor and outcome.

Scavenger community structure at the landscape scale as well as the ability of species to locate and acquire carrion at the site-level are driven by a combination of differential selection for habitat characteristics and competitive intraguild interactions (Gompper et al. 2016; Pardo-Barquin & Mateo-Tomas, 2020; Smith et al. 2017). To examine the role of habitat vegetative cover on frequency of site use, landcover at camera sites was designated as either open (e.g. herbaceous areas, wetlands, grassy meadows) or closed (e.g. conifer or mixedwood forest) canopy (Table S1). Among all camera trap sites, only two (sites 8 and 66) fell under shrub classifications, specifically, open upland shrub and shrubby wetland. Since both of these are relatively open shrub dominated habitats, we included these in the open classification. Landcover classifications were derived from the Alberta Satellite Land Cover (ASLC) raster that is produced by the Government of Alberta (ASLC, 2018).

Deep snow can alter metabolic rates and influence movements of mustelids (Martin et al. 2020). Snow cover is vital to short-tail weasel ecology as they can easily navigate the subnivean space (region between the snow cover and the ground created by rising water vapor), which provides concealment and foraging opportunities (Frey & Calkins, 2014). Persistent spring snow cover and snow depths have also been linked to wolverine distributions and reproductive den sites (Inman et al. 2012; Jokien et al. 2019; Magoun & Copeland, 1998). Owing to the observed influence of snow depth on mustelid distributions, movement, and foraging behaviour, we examined daily snow depth as a predictor of scavenging behaviours. As snow depth is dynamic with respect to time, this factor further allowed us to account for seasonal differences between the two study seasons. Snow cover is persistent across much of the WWP during the winter months with variability in depth correlating with elevation, terrain ruggedness and seasonal climate variability. Daily snow depth analysis measures were performed by Brown and Brasnett (2010) using a combination of in-situ observations and a snow accumulation and melt model.

To assess the relative strength of environmental habitat character against the influence of competitive interactions among facultative scavengers, we evaluated a set of three candidate models that included: environmental factors exclusively, intraguild interactions exclusively, and a combined model that incorporated both sets of parameters (Appendix Table S2). Akaike's Information Criterion (AICc) scores and normalized AIC weights were used to rank candidate models (*sensu* Burnham and Anderson, 2002, 2011), and best-fit models were selected based on the lowest AIC score (highest AIC weight).

2.2.3.b Cox proportional hazard model: external influences on fine-scale temporal interactions

To assess the role that habitat characteristics play in shaping patterns of fine-scale temporal interactions, we employed a time-to-event model, frequently referred to as survival analysis for their extensive use in medical research and clinical trials (Zwiener et al. 2011), which looks to the time that it takes for some event to occur to evaluate the influence of external factors on whether the event of interest takes place. For our purposes, an event is characterized as the photographic capture of a focal species hereafter referred to as species B (SpB) following the capture of a given competitor designated species A (SpA), at a specified spatial location. It follows then that the capture time of the SpA serves as a reference point with respect to time ($t = 0$). Mustelids are equipped with sensory capacities for detecting the recent presence of species that represent a predatory or competitive threat (Chaudhry, 2007). To examine the behaviours of focal species in response to the immediate threat of competitive interactions as a function of habitat character, we employed a regression method - the Cox proportional hazard model (CPH) – for time-to-event data.

The CPH (Cox, 1972) regression model focuses on the concept of *hazard*, which in the context of its initial applications refers to human survivorship where the event of interest is death and the reference point is some treatment of a life-threatening condition. More broadly, hazard refers to the rate of event occurrence. The CPH model describes the hazard function h(t), which represents the instantaneous probability of an event occurring at a given point in time as determined by a collection of predictive factors. The model is expressed as:

$$h(t) = h_0(t) * \exp\left(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k\right) \qquad \text{Eq. 1}$$

Where, t = time since the reference capture (t_o), h(t) = the hazard function (or rate), x_k are the explanatory variables, β_k are the explanatory variable coefficients, exp(β_1) = the hazard ratio (HR), and h_0 = the baseline hazard. The baseline hazard calculates the value of the hazard when all values of x are equal to zero. CPH is a semi-parametric approach because the baseline hazard is allowed to vary over time (i.e., its value is not specified), while the covariates are the linear components of the model.

As introduced in Eq.1, the CPH model provides an estimate of the hazard ratios. HR's can be interpreted as the hazard (event rate) ratios for predictor variable groups relative to a given reference group. For example, for the habitat variable landcover canopy closure, the CPH model summary may give the HR for open relative to closed landcover (reference group). It is important however to note that HRs do not provide any information on the duration of time until the event took place as they have been commonly mistaken to infer (Spruance et al. 2004).

Cox regression is considered a *proportional* hazards model owing to the fact that the HR is independent of time and therefore assumed to be consistent over the observed study duration. In addition to following the same basic assumptions of other linear models, the assumption of proportional hazards is a critical caveat of the CPH model with associative implications for the interpretation of outputs. We used a common test for hazard proportionality that correlates the scaled Schoenfeld residuals for each covariate with time in order to check for independence. The associated significance level for all covariates, as well as a global test for the entire model, was not significant ($p > 0.05$); we were therefore able to assume proportional hazards.

CPH model outputs can offer a number of valuable insights. The beta coefficient (β) is the event rate relative to the reference group, or put another way, is the estimated logarithm of the HR, where if β = x, then exp(β) = e^x = HR. A negative value for β therefore represents a lower rate relative to the reference group. HRs are commonly taken to represent the effect size of the covariates and can be interpreted as follows: HR>1 represents positive association with event occurrence or a relative increase in probability of an event; HR<1 indicates a negative association with event occurrence or a relative decrease in the probability of an event; and an HR equal to 1 represents no effect on event outcome. For example, when β equal to – 0.36, with a HR equal to 0.697 for the variable diel period: day relative to night, suggests that the rate of site visits are lower in the day than they are at night (β = - 0.36) and that the rate is reduced by a factor of roughly 0.70 or alternatively, about 30%.

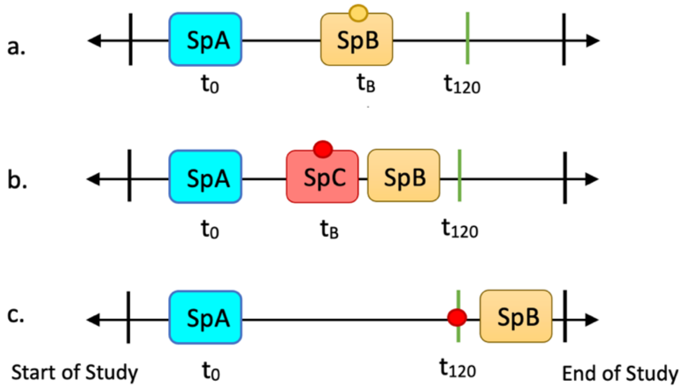


Figure 2.3: Cox proportional hazard model data points designated as censored (red dots) or true events (yellow dots). True events are defined as having occurred within 120h (5-day) interval following the reference detection (case a). Censored data can arise through an intermittent site visit by SpC (case b) or in cases where a SpB eventually visited the site subsequent to SpA but where the time-to-event measured greater than the specified 120-hour time interval (case c).

A unique advantage of CPH models is that they utilize all available information, which includes instances where the site is visited by SpB after the endpoint of the study or when localized site conditions are altered between the reference capture and the event. This is done through the inclusion of censored data points. Censored data represent a subset of capture data where the event time is either unknown or has become unreliable. In the context of intraguild interactions, this can be because (1) the capture event occurred after the endpoint of the time-since interval, or (2) a different event takes place before the event of interest occurs rendering the relationship between the true event and the reference point indiscriminate – in our case SpB site use in relationship to SpA. For example, a site visit by a common predator (i.e., wolf, cougar, lynx, human) occurring between a wolverine reference capture and subsequent marten-event disrupts the ability to associate the marten-event with the presence of the wolverine. In this case, marten site occupancy is very likely to be related to the more recent spatiotemporal presence of the third-party site inhabitant, hereafter referred to as SpC. We can, however, include the time-since measure of the alternative event as a censored observation, thereby indicating to the model that the true event time was at least t = time of SpC capture. The statistical power of the model is improved when uses data from all eventual events at every time-since value (i.e. the number of events that have occurred versus not yet occurred) to calculate hazard rates. As such, under this scenario the model can use the information "no event yet" for all times up to SpC(t) (Figure 2.3). The CPH model recognizes that time-since measures for censored observations inherently underestimate the timing of true events. For this study, we considered events occurring within 5-days (120h) of a reference capture. With this allotted time-since interval, a marten capture at, say 130h would be censored at 120h following the reference point. In combination with the SpC situation described above (Figure 2.3), this creates a combined dataset of true events and censored datapoints (Figure 2.4).

In summary, through censoring, CPH models provide a method to include captures that occur following the end of the observed study interval and those that cannot be considered beyond the moment that the site character undergoes change with respect to the degree of threat or energetic gain offered at a point location. Alternatively choosing to exclude those data that adhere to one of these scenarios could serve to introduce bias since data generated prior to censor times are relevant to improving the validity of the analysis.

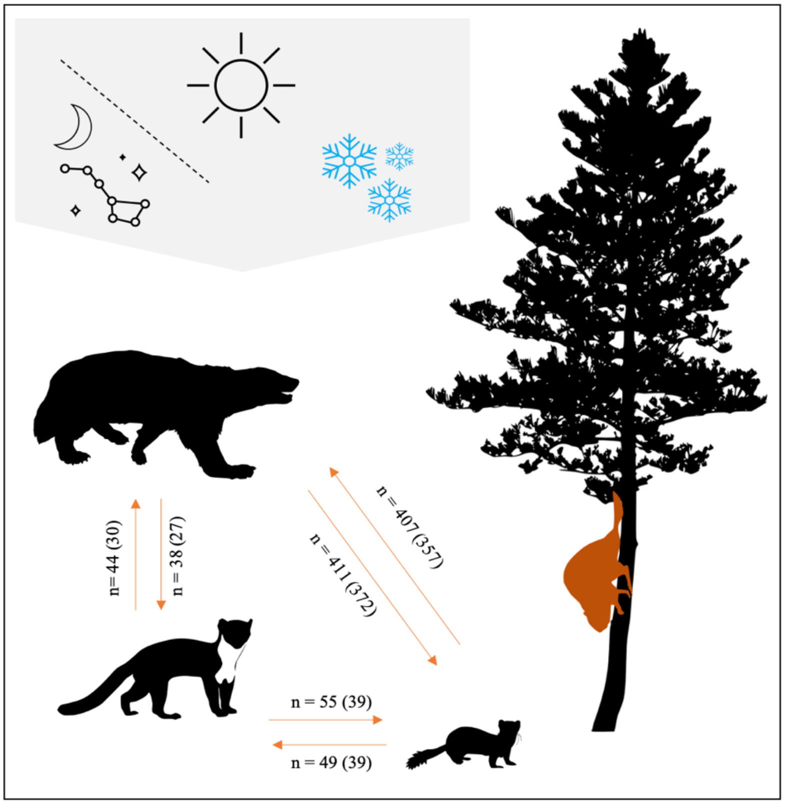


Figure 2.4: Time-to-Event model visualization, for wolverine (8.5 – 10 kg), marten (0.5 – 1.4 kg), and short-tailed weasel (0.03 – 0.45 kg) in the Willmore Wilderness Park, AB (Banci, 1994; Sandell 1989). Arrow direction goes from species A to species B. Event sample size for each SpA-SpB pair are indicated including right-censored events, number of 'true events' is indicated in parentheses. Environmental predictors include diel period and snow depth.

In instances where multiple successive captures of the same species occurred, time-to-event was calculated by observing the time difference between the last capture of the first species and the first capture of second species. We assumed that direct interactive processes were likely to occur inside of this timeframe, as avoidance or attraction occurring over broader (e.g. monthly) temporal scales is more likely to be related to niche partitioning processes (Fisher & Bradbury, 2014) than immediate perceived threat. Some sympatric carnivores have been shown to coexist by practicing fine-scale spatiotemporal avoidance, thereby avoiding suppression at the habitat or landscape scale (Swanson et al. 2014). The study interval chosen is designed to align with the duration of sampling occasion used in the ZINB analysis so that we might draw comparisons on the manner in which the mechanisms of coexistence operate.

To account for the potential influence of daylight, we included diel period as a covariate in addition to landcover and snow depth environmental covariates used in the ZINB models. Marten and weasels have frequently been found to exhibit nocturnality in the winter months in North America (Frey et al. 2020; Zielinski, 2000). Some nocturnal animals are evolved to have sensory capacity for foraging and movement in dark light conditions. Species with heightened sensory capacity for night may be able to respond more quickly to threatening stimuli or, by contrast, darkness can offer concealment from predators or competitors allowing for differences in the degree of spatial avoidance exercised (Haswell et al. 2020). We categorically defined diel periods as either day or night. This distinction was made according to sunrise and sunset using the date and geographic locations of each camera trap to retrieve solar event data. We generated daily activity pattern density functions using the "Overlap" package in R (Ridout & Linkie, 2009; Meredith & Ridout 2014). Activity pattern analysis provides capture densities across a diel (24-hour) timescale. Nouvellet et al. (2012) established that using sun time over clock time significantly improves efficiency for deciphering meaningful ecological signals associated with animal behaviours related to particular times of day. This is caused by changing sun cycles over extended study periods or where study sites are dispersed over a relatively large area. We transformed clock time to solar time using the "suntime" function (Nouvellet et al. 2012; Frey et al. 2020) to account for variability in day length within and across study seasons.

We classified diel periods into either day or night by partitioning captures on either side of sunrise and sunset (Appendix Figure S1).

2.2.3.c Temporal Spacing Analysis

To test whether fine-scale temporal partitioning patterns at camera sites differed from what would be expected under random occurrences of mustelid encounters, we randomized capture data for each focal species for 1000 iterations. To accomplish this, we randomly selected a spatial location by choosing a unique camera trap location where the species of interest had been observed at least once over the entire study period. Next, we selected a new capture date at random from the survey period, where if the camera ID number identified in step 1 fell between 1 – 30, we selected dates from winter season 1 (2016/2017). Alternatively, if the camera ID was between 31 – 66, we selected from the date ranges for winter season 2 (2017/2018). We then select a new time by sampling the activity pattern probability density function of the corresponding focal species, following the same procedure as noted in the CPH for generating activity pattern densities. The new random capture data was integrated with the observed data for the reference point, and we then calculated the TTE between species pairs as per the CPH model procedure. In this case, we removed any events that exceeded 120 hours (5-days). In the observed TTE (TTE_{obs}) distributions, if a third-party animal with potential to influence the behaviour of focal species arrived between the reference point and the event thereby possibly altering the timing of the event, those event data points were removed. Under this scenario, as time increases so too does the possibility of an intermittent site visit by another animal.

By examining the time-to-event data used in the CPH model, we observed that between 68% and 91% of events recorded for species pairs were represented by “true events” (no intermittent species occurrence), with an average of 78%. To emulate this aspect of TTE data, we applied a probability density function with exponential decay to the new TTE_r, such that the probability of selecting an event decreased with increased time-since measure, then randomly chose 80% of those data without replacement to generate the final TTE_r. Finally, we compared mean values of the TTE_r and TTE_{obs} datasets using a two-sample Mann-Whitney U test, a standard test for exploring differences between two groups with skewed distributions. Where the p-value of the test is less than the significance level alpha = 0.05, we are able to conclude that the average TTE_{obs} is significantly different from that of the TTE_r.

2.3. Results

During the monitoring of 70 camera trap days over two winter seasons between 2006 and 2008, independent photographic detections for species of interest totalled: 305 lynx, 1080 wolverine, 342 weasels and 12,599 martens (the most photographed focal species in our study area).

2.3.1 ZINB/NB-GLM models: spatial interactions and habitat use

Dispersion statistical tests were performed to assess whether count data was overdispersed, in the case of weasel count data (winter season 2007/2008) the negative binomial general linear model resulted in a comparable dispersion statistic to that of the ZINB model. Weasel count data had a very high proportion of zeros however this attribute alone does not imply zero-inflation (Figure S2). The Vuong statistic (AIC) revealed that the GLM-NB performed better for weasel count data. Therefore, we determined that the more parsimonious NB-GLM was a more suitable model for weasel. ZINB models were most appropriate for marten and wolverine datasets based on overdispersion and zero-inflation model assessment (Appendix, Table S5).

Table 2.1: Zero inflated negative binomial model outputs for photographic rates of (a) wolverine, (b) American marten and (c) short-tailed weasel. Table values include regression coefficients estimate (β), exponentiated regression coefficients (exp(β)) that represent the odds ratio., standard deviation (SD) and p-value (significance level = 0.05, indicated with '*').

(a) ZINB Model M3: Wolverine Zero-inflation model coefficients (binomial with logit link)	Estimate	exp (β)	SE	p
(Intercept)	1.52	4.58	0.341	< 0.001 *
Marten	- 0.582	0.559	0.265	0.0148 *
Weasel	- 0.218	0.804	0.365	0.115
Lynx	- 9.439	7.96 e-05	82.9	0.0297 *
Landcover (Open)	0.0698	1.072	0.309	0.765
Snow Depth	- 0.0114	0.989	0.00354	< 0.001 *
Count model coefficients (negative binomial with log link)				
(Intercept)	1.55	4.73	0.273	< 0.001 *
Marten (CR)	0.00974	1.0098	0.00399	0.0280 *
Weasel (CR)	0.190	1.21	0.120	0.550
Lynx (CR)	- 0.119	0.888	0.0546	0.909
Landcover (Open)	0.0724	1.08	0.243	0.822
Snow Depth	- 0.00866	0.991	0.00221	0.00124 *

(b) ZINB Model M3: Marten Zero-inflation model coefficients (binomial with logit link)	Estimate	exp (β)	SE	p
(Intercept)	1.90	6.67	0.341	< 0.001 *
Wolverine	- 0.504	0.604	0.253	0.0466 *
Weasel	0.275	1.32	0.324	0.396
Lynx	0.964	2.62	0.502	0.0547
Landcover (Open)	- 1.526	0.217	0.406	0.000172 *
Snow Depth	- 0.0320	0.968	0.00444	< 0.001 *
Count model coefficients (negative binomial with log link)				
(Intercept)	2.18	8.88	0.154	< 0.001 *
Wolverine (CR)	0.0201	1.02	0.0139	0.148
Weasel (CR)	-0.0369	0.964	0.0487	0.449
Lynx (CR)	- 0.137	0.872	0.0556	0.0134 *
Landcover (Open)	- 0.163	0.850	0.126	0.195
Snow Depth	0.00796	1.01	0.00128	< 0.001 *

(c) GLM-NB M3: Weasel	Estimate	exp (β)	SE	p
(Intercept)	3.30	27.0	0.622	1.18 e-07 *
Marten	-0.0593	1.06	0.0180	0.000959 *
Wolverine	0.0306	1.03	0.0417	0.463
Lynx	0.0215	1.02	0.0327	0.510
Snow Depth	-0.0614	0.94	0.0103	2.92 e-09 *
Landcover (Open)	0.165	1.18	0.390	0.673

Mustelid spatial patterns were best supported by a combined model that included both habitat and competition predictor variables (Appendix Table S2). The results of the best supported models are presented in Table 1. Recall for ZINB models that the binomial process reflects species presence/absence, while the count process evaluates the strength of relationship between species photographic capture rates (CR) and predictor variables.

Wolverine were detected across 53 camera trap locations (total of 1080 independent captures). Presence of wolverine was significantly reduced by that of marten (p = 0.015, β = -0.582) or lynx (p = 0.03, β = - 9.43). The likelihood of wolverine presence over 5- day periods was 66% more probable at sites that lacked marten and, notably, nearly 8 times more likely at sites where lynx was absent (Table 1a). By contrast, the CR of marten slightly increased with wolverine CR (p= 0.028, β = 0.00974), whereas rate of lynx site use showed no association.

Wolverine presence was highest at sites with low relative snow depth (p <0.001, β= -0.01143). This pattern continued for the rate at which wolverine utilized a scavenge opportunity, where CR of wolverine was reduced by 1% for every 1cm rise in snow depth. Daily snow depth across all study sites over the entire study period in the WWP ranged from roughly 20 cm to 200 cm. Landcover type did not impact wolverine spatiotemporal distributions or CR (Table 1a).

Marten appeared over 51 spatial trap locations, the most captured mesocarnivore at carcass sites by an appreciable margin (total of 12599 independent captures). The presence of marten was highest in closed forest habitats (p<0.001, β = - 1.53) with low relative snow depth (p<0.001, β= - 0.0320). Habitat type in particular was highly influential in determining marten presence/absence, where marten presence decreased by 88% in open sites relative to closed forest canopy (Table 1b). Landcover type did not alter marten CR to a significant degree. Rising snow depths increased marten CR by 1% for every 1cm rise in snow depth (p<0.001, β= 0.00796). Competitive interactions appeared to negatively influence both marten occurrence and rate of site utilization. Marten presence was approximately 40% lower at sites that had been occupied by wolverine inside the same 5-day period. Lynx exerted pressure through intensity of site use, reducing marten capture rate by a factor of 0.87 or about 22% (Table 1b).

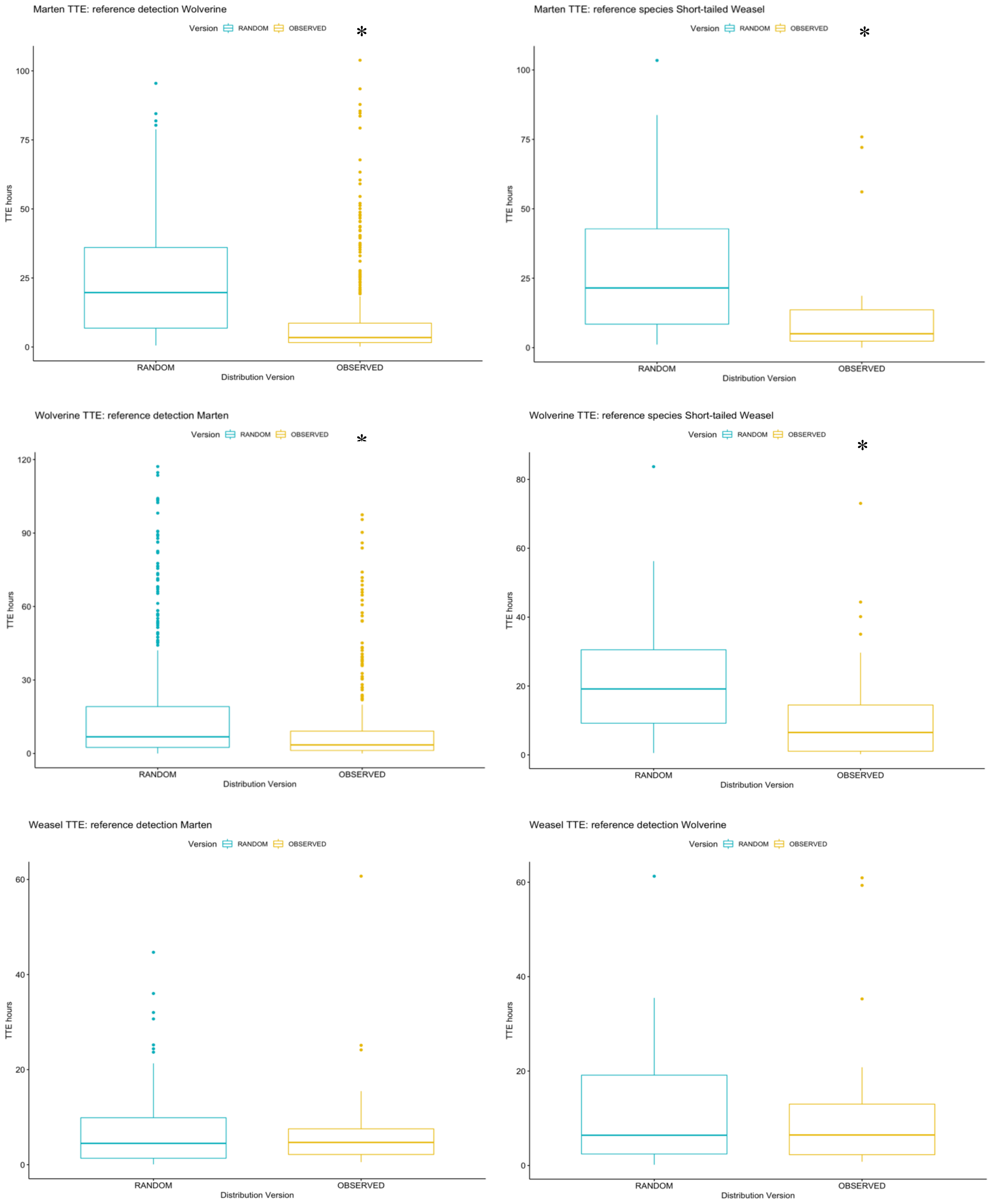
Weasel occurred at 15 trap locations (total of 342 independent captures). The relative frequency of weasel feeding events decreased with increased snow depth by approximately 1% for every 1cm increase in depth ($p<0.001$, β = - 0.06135). Weasel CR was also sensitive to the frequency of site use by competitors, declining with increasing counts of marten ($p < 0.001$, β= - 0.0593). Weasel CR was not associated with canopy closure (Table 1c).

2.3.2 Temporal spacing analysis

Wolverine did not show random patterns of temporal spacing from martens or weasels ($p<0.001$ and $p=0.002$ respectively), appearing at carrion sites following smaller mustelid species in lesser time on average than was predicted (Figure 5, Table S3). Expected mean time-to-event of wolverine following weasel (mean = 22.2 hours) was nearly double the observed time (mean = 12.3 hours) after accounting for patterns in wolverine diel activity.

We observed similar patterns of apparent temporal attraction by martens, which visited carrion sites subsequent to co-occurring mustelids: wolverine ($p <0.001$) or weasel ($p<0.001$) (Figure 5). In both cases, marten appeared at a site, on average, within 12 hours of a potential competitor, less than half the anticipated amount of separation time for wolverine (mean = 24.9 hours) and weasels (mean = 29.4 hours).

Weasels neither avoided nor showed evidence of attraction towards wolverine (Figure 5). Average time until weasel appearance was not found to differ significantly from expected values when they followed larger mesocarnivores, wolverine (p-value = 0.96) or marten (p-value = 0.75).


Marten TTE: reference detection Wolverine

Marten TTE: reference species Short-tailed Weasel

Wolverine TTE: reference detection Marten

Wolverine TTE: reference species Short-tailed Weasel

Weasel TTE: reference detection Marten

Weasel TTE: reference detection Wolverine

Figure 2.5: Temporal spacing box plots representing results of Wilcoxon rank sum test for 2-group comparison of average temporal spacing according to random (TTE_r) and observed (TTE_{obs}) time-since distributions, following a competitive threat for all focal species pairs. Reference detections represent the competitor that visited the resource first. Median time-since measures for TTE_{obs} that were found to be significantly different from TTE_r where $p\text{-value} < 0.05$ (Table S2), are indicated with an asterisk.

2.3.3 CPH models

Model selection for CPH models indicated that inclusion of habitat type did not improve explanatory power for all species pairs (Table S3). As such we evaluated a model that included time-dependant environmental variables associated with trap sites: diel period (sunlight) and daily snow depth.

Diel period did not influence the rate of marten capture for any time-since wolverine (p=0.221) or weasel (p=0.688). Non-linear trends for snow depth did alter marten temporal avoidance/attraction behaviour at sites recently occupied by wolverine (p-value = 0.016, Figure 2.6a). Similarly, the relationship between snow depth and the rate of marten events following weasels was non-linear (p-value = 0.014, Figure 2.6b). Daily snow depth measures varied between 21.8 cm to 203.50 cm and 23.6 cm to 92.2 cm for sites shared by marten-wolverine and marten-weasel respectively

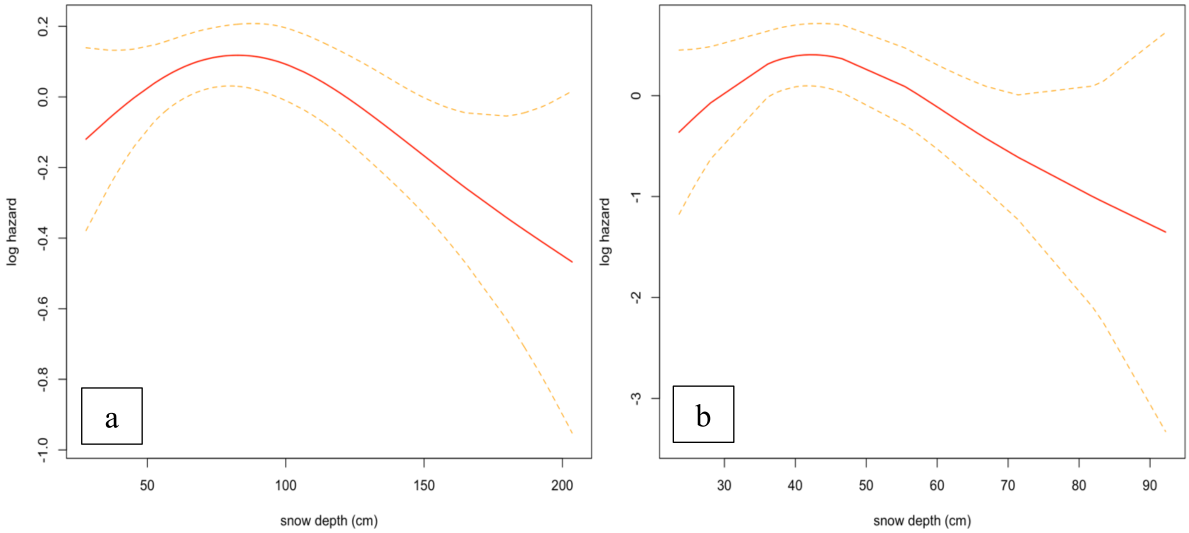


Figure 2.6: Relative log hazard ratio associated with non-linear snow depth (red line, df = 2) for marten following wolverine (a) (p-value = 0.016) and short-tailed weasel (b) (p-value = 0.014) in the Willmore Wilderness Park during winter (2006/2007 and 2007/2008). Orange dotted lines represent standard error (Table 2.2).

Table 2.2: Results of Cox proportional hazard model time-to-event analysis for mustelids following a sympatric competitor as a function of environmental covariates. SpB capture events that occurred within 5-days (120 hours) of a SpA reference capture were considered, events beyond this time were right censored. Results were considered significant where p-value equals <0.05, as indicated by an asterisk.

Wolverine (SpA = Marten)
n= 411, number of events = 372
Likelihood ratio test = 20.79 on 2 df, p = 3.065 e-05*

(Day = 195, Night = 216)	**coef**	**exp (coef)**	**se(coef)**	**p-value**
Diel Period (Day)	-0.339	0.713	0.105	0.00128 *
Snow Depth (linear)	-0.00336	0.997	0.00122	0.00569 *

Wolverine (SpA = Weasel)
n= 44, number of events = 30
Likelihood ratio test = 8 on 3.05 df, p = 0.05

(Day =14, Night = 30)	**coef**	**exp (coef)**	**se(coef)**	**DF**	**Chisq**	**p-value**
Diel Period (Day)	- 1.0004	0.368	0.4438	1.0	5.081	0.024 *
Snow Depth (linear, df = 2)	0.0233	1.024	0.0135	1.0	2.96	0.085
Snow Depth (non-linear, df = 2)	n/a	n/a	n/a	1.06	1.06	0.321

Marten (SpA = Wolverine)
n= 407, number of events = 357
Likelihood ratio test=12.2 on 3.04 df, p=0.007*

(Day n = 131, Night n = 276)	**coef**	**exp (coef)**	**se(coef)**	**DF**	**Chisq**	**p-value**
Diel Period (Day)	- 0.141	0.986	0.444	1.0	1.50	0.221
Snow Depth (linear, df = 2)	- 0.00189	0.998	0.0135	1.0	2.34	0.126
Snow Depth (non-linear, df = 2)	n/a	n/a	n/a	1.04	5.92	0.016 *

Marten (SpA = Weasel)
n= 55, number of events = 39
Likelihood ratio test=11.1 on 3.05 df, p=0.01*

(Day n = 17, Night n = 38)	**coef**	**exp (coef)**	**se(coef)**	**DF**	**Chisq**	**p-value**
Diel Period (Day)	0.137	1.15	0.339	1.0	0.162	0.688
Snow Depth (linear, df = 2)	- 0.0135	0.987	0.0115	1.0	0.0114	0.241
Snow Depth (non-linear, df = 2)	n/a	n/a	n/a	1.06	5.90	0.017 *

Weasel (SpA = Marten)
n= 49, number of events = 39
Likelihood ratio test=2.57 on 3.08 df, p=0.5

(Day n = 8, Night n= 41)	**coef**	**exp (coef)**	**se(coef)**	**DF**	**Chisq**	**p-value**
Diel Period (Day)	- 0.272	0.761	0.429	1.0	0.405	0.52
Snow Depth (linear, df = 2)	- 0.00825	0.992	0.0105	1.0	0.617	0.43
Snow Depth (non-linear, df = 2)	n/a	n/a	n/a	1.1	0.927	0.37

Weasel (SpA = Wolverine)
n= 38, number of events = 27
Likelihood ratio test=2.89 on 3.09 df, p=0.4

(Day n = 8, Night n= 41)	**coef**	**exp (coef)**	**se(coef)**	**DF**	**Chisq**	**p-value**
Diel Period (Day)	- 0.382	0.683	0.505	1.0	0.572	0.45
Snow Depth (linear, df = 2)	- 0.0125	0.988	0.0118	1.0	1.12	0.24
Snow Depth (non-linear, df = 2)	n/a	n/a	n/a	1.1	0.456	0.58

Wolverine were significantly more likely to appear at a carrion site following a marten during the night, where the probability of a wolverine event was 71% greater for any given time-since marten, relative to daylight hours (β = - 0.338968, HR = 0.71, p = 0.00128). Increasing snow depths negatively influenced the likelihood of wolverine site visits where marten had recently been present (p-value = 0.00569). The effect size given for snow depth (HR=0.996643), reflects that for every one-unit (1 cm) increase in snow depth the probability of wolverine capture increases by 1% (Table 2.2).

Likelihood ratio tests for overall model performance revealed that predictive factors used in Cox regression models for weasel (SpA = wolverine), weasel (SpA = marten) and wolverine (SpA = weasel) did not significantly explain variability in the data and were overall poor predictors of the rate at which mustelids utilized carrion sites in the presence of a possible competitive threat (Table S4). We therefore omit those models from the subsequent discussion.

2.4. Discussion

Winter carrion consumption is a vital dietary component for many facultative scavengers that can serve to stabilize annual diet (Wilkenros et al. 2013). Scavenging is a pathway for behavioural interactions and competition for resources is the predominant driver of the extent of interference competition observed among carnivores (Roemer et al. 2009). It follows then, that carnivores frequently engage in various forms of interference competition with heterospecifics at carcass sites. In multi-carnivore communities, interference competition is widespread often manifesting in altered foraging behaviour, habitat use changes or exclusions, it is a principal process in structuring ecological communities (Ritchie & Johnson, 2009; Swanson et al. 2014, 2016). At the level of the individual, carrion feeding decisions are based on outcomes of energetic cost-benefit analyses (Klauder et al. 2021), that are subject to influence by external environmental conditions (Smith et al. 2017; Selva & Fortuna, 2007; Selva et al. 2003). Individuals can mitigate the adverse effects of interference competition at scavenging sites through reducing their intensity of site use (time spent at carcass or frequency of site visits) or choosing to feed during temporal periods or at carcass locations that carry lesser risk of intraguild encounters. Competitive dominance is shown by a lack of evidence for negative site use in relation to the spatial-temporal distribution of competitors (Vanak et al 2013). Whereas spatiotemporal aggregation can point to positive interactions between sympatric species such as facilitation of dietary resources (Wilmers et al. 2003), which may serve to promote coexistence (Hass & Dragoo, 2017). Through this investigation of fine-scale spatiotemporal interactions among four mesocarnivores, we uncovered mechanisms by which facultative scavengers share in benefitting from a valuable winter resource. Mustelids in the WWP utilized these pulsed resources through site-level habitat use to facilitate sympatry (i.e. minimize costs associated with competition) and reactionary temporal avoidance to maximize energetic rewards.

2.4.1 Facultative Scavenger Species Interactions

Feeding decisions by wolverine were influenced by interspecific interactions. After accounting for differences in response to habitat type and snow depths, both lynx and marten presence negatively influenced patterns of wolverine presence. Lynx site occupancy exerted a particularly strong effect on wolverine spatiotemporal presence, resulting in a nearly 7-fold decrease in the likelihood of a wolverine feeding event. Somewhat conversely, Mattisson et al. (2011b) found that wolverine scavenged a high proportion of Eurasian lynx (*Lynx lynx*) reindeer kills (68%), almost half of which remained occupied by a lynx on the arrival of wolverine.

Associated research, however, found no spatial or temporal evidence of attraction or avoidance between these two species (Mattisson et al. 2011a). Canadian lynx is a specialized predator of snowshoe hare (Krebs et al. 2001; Mowat & Slough, 2003), a species abundant in the study area and also preyed upon by wolverine (Banci, 1987). It is possible that in the absence of sufficient potential for ungulate carrion provisions, lynx in the northern Rocky Mountains exist predominately as a competitive threat to wolverine. Our findings therefore challenge the widely held assumption that wolverine track and scavenge ungulate kills by Canadian lynx (Abramov, 2016) and suggest that wolverine actively avoid lynx in the WWP. Moreover, the degree of aversion to lynx presence presents evidence of spatial-temporal segregation consistent with behaviours of avoidance related to more severe forms of interference such as kleptoparasitism and interspecific killing.

Spatial exclusion at this scale did not translate to adverse reactionary behavioural mechanisms playing out over finer spatial or temporal scales. This was exhibited by findings that, where wolverine and lynx presence overlapped spatially (9 camera locations), wolverines were able to navigate the degree of time spent at carcasses by lynx without altering their own rate of scavenging. Thus, our results suggest that wolverine primarily reduced their risk of exposure to lynx encounters via spatial avoidance but not by reducing their use of carrion. This is consistent with the observed tendencies for wolverine to dominate activity at carrion sites even in the presence of competitive superiors (Klauder et al. 2021). Divergent foraging strategies are believed to partially mitigate competitive encounters between lynx and wolverine, as lynx is a specialist obligate predator while wolverine is a generalist predator-facultative scavenger (Banci, 1994; Mowat & Slough, 2003). Wolverine higher dependence on carrion likely incentivizes emboldened behaviour at carcass sites. These findings corroborate work by Klauder et al. 2021 indicating wolverine do not regard any co-occurring carnivores as consequential threats at scavenging opportunities, regardless of their competitive dominance or intensity of use, as evidenced by extensive site use and lack of vigilance behaviours.

Despite the supported prediction that wolverine dominate carcasses and supress smaller mesocarnivore usage (Klauder et al. 2021), marten spatiotemporal distribution negatively impacted wolverine presence and, marten followed a similar trend in relationship to wolverine 5-day site occupancy. Murrell and Law (2003) describe the concept of heteromyopia, a circumstance in which competition between heterospecifics plays out over shorter distances relative to competition occurring between individuals of the same species. The strong extent of intraspecific competition taking place among individuals of the more abundant species then reduces the density of that species thereby creating spatial openings that are then taken up by the less common interspecific competitor (Amarasekare, 2003). Coexistence achieved via heteromyopia would require that wolverine and marten compete at shorter distances than the distance over which they sense and compete with conspecifics (Murrell & Law, 2013). This study utilized data for unmarked mustelids and did non measure intraspecific competition indicators, nor did the spatial extent chosen for this investigation allow us to make inferences about broader patterns of species spatial segregation at the landscape scale. However, heteromyopia may help to reconcile conflicting findings that while wolverine and marten segregate spatially at a local spatial scale, while at fine spatial-temporal scales where they do co-occur these species were observed to promote the appearance of one another through temporal tracking and/or increased rate of occurrence. In heterogenous environments, heteromyopia can manifest as apparent segregation between sympatric species at a localized scale and higher average densities (i.e. aggregation) of the more common competitor relative to the more rare one

(Amarasekare, 2003; Murrell & Law, 2013; Fisher et al. 2013a). Marten was by far the most highly detected mustelid species in this survey, with independent captures surpassing wolverine by more than ten-fold (Appendix, Table S6). Moreover, Fisher et al. (2013a) found evidence to support that marten aggregate where they do occur inside the Willmore landscape. Thus, we observed partial evidence of such a process here, although more extensive multi-scaled analysis would be required to substantiate this relationship. Recall also that interactions with other large and meso-carnivores were not taken under consideration and the reciprocal negative influence of site occupancy (presence/absence) observed for marten and wolverine could also reflect relationships to other conspecific scavengers in the Willmore.

The extent of wolverine site use (i.e. prolonged feeding or frequent recurrences) increased with marten intensity of use and wolverine often arrived at carcass sites while a marten was either very recently or remained present (10% of all wolverine events occurred less than 30 min following a marten). Wolverine further tracked marten temporally (Figure 2.5).

Almost all mustelids use scent signaling to communicate information about habitat features and olfactory cues from prey are important determinants of foraging efforts (Price & Banks, 2016). We interpreted the heightened wolverine activity at carrion sites in relationship to marten as being motivated by the potential for kleptoparasitism, in that wolverine may exploit martens by tracking their scent markings to locate carcass sites already discovered by the smaller mustelid. Baited camera traps in the WWP simulate a naturally occurring scavenging site. Temporal attraction inferences are therefore inextricably linked to the lure of a valuable resource and by design, will alter the behaviour of species in their periphery either as an attractant or a repellant via the secondary effects of carrion sites (Rocha et al. 2016). Temporal spacing indices are therefore indictive of carrion feeding incentivization outweighing the potential threat of encountering interspecific competitors and have been interpreted as such here.

The rate of wolverine carrion visitation in the time-since a marten used the site decreased in the day and with rising snow depth. Deepening snow also reduced the probability of wolverine presence at carrion sites and their intensity of site usage (Table 1a). This corresponds to previous research that observed snow depth as a limiting factor for habitat utility of wolverines in the boreal forest of Alberta and British Columbia, where wolverine optimized forest stands that offered a buffering effect over ground snow depths (Wright & Ernst, 2004). Wolverine in the WWP utilized all available carrion sites across open and closed habitats indiscriminately (Table 1), we infer that they are able to exploit closed stands for improved mobility and open areas for carrion foraging based on availability.

Marten maximized their access to carcasses through adaptive competitor-specific behavioural tactics. Martens generally avoided sites with wolverine presence (Table 1) but did not alter their rate of site usage in accordance with that of wolverine. Marten also frequently used sites in the same day as wolverine, showed evidence of temporal attraction (Figure 5) and therefore appeared to perceive carrion feeding as having a net energetic gain after despite the immediate threat of a wolverine confrontation. Wolverine possesses physiological adaptations for feeding on bone and frozen carcasses (Banci, 1994). Carcass openness has been described as a highly important determinant of carcasses utilization time and accessibility to scavengers (Selva et al. 2003). Selva et al. (2003) found that wolves played a vital role in altering bison carcasses to facilitate feeding accessibility by other carnivores through progressively opening previously inaccessible regions such as for example, the viscera enclosed within the thoracic cage. Wolverine may offer a similar service to marten in the WWP, hence the close proximal temporal tracking displayed by marten following a wolverine visit.

Rather than avoiding locations used by lynx, marten reduced their rate of scavenging in lynx high-use areas. Lynx is occasional predator of marten, and although predation is not thought to be substantial enough to impact marten populations (Clark et al. 1987), our findings suggest that they may limit the rate at which marten are able to utilize a shared resource. Interestingly, although a marginally insignificant predictor ($p = 0.055$), marten spatial-temporal distribution was by contrast positively related to the presence of lynx, in that marten presence was far more likely (262%) at sites lynx had occupied in the same period. This finding may be of some significance in an ecological context. Prugh et al (2020), found other large felids to be "equal opportunity" killers at carrion sites, likely able to limit access by a broader taxonomic demographic of mesocarnivores but with lesser overall intensity relative to the high degree of hostilities (i.e. intraguild killing) observed *within* families. In addition to this hypothesis, competitive encounters and the degree of competitive pressure between sympatric carnivores has strong positive association with similarity in body size (Leyequién et al. 2006; Palomares & Caro, 1999; Ritchie & Johnson, 2009). As previously discussed, lynx limited the spatial-temporal extent of wolverine, a species having comparable body mass (lynx 5 – 18 kg and wolverine 8 – 18 kg). By contrast, Marten (0.5 – 1.4kg) and weasels (0.03 – 0.45 kg) are a fraction of the body size of wolverine or lynx and may represent less conspicuous competitors to lynx (Banci, 1994; Sandell 1989). It is possible then that by displacing wolverine, lynx provide marten with spatial-temporal behavioural refugia from wolverine. Similar to mesopredator release, a theory associated with population dynamics of subordinate predators being contingent on top-down effects of dominant species (Prugh et al. 2009), spatiotemporal behavioural release (or suppression) has cascading effects through the carnivore guild and correspondingly, the greater ecological community. Wang et al. (2015) for example, found that the direction and degree of coyote influence on smaller mesocarnivores was dependant on cougar occupancy. Marten may therefore maximize their access to a valued resource through reducing encounters with lynx by reactively responding to lynx feeding patterns through reduction of intensity of site use. This strategy may provide occasional provisions from lynx and incur the secondary benefit of providing refuge or reduced intensity of interference competition by wolverine.

The likelihood of marten presence across carrion sites decreased with deeper snow, whereas the rate of marten site usage increased slightly as the snow accumulated. Martens have been observed to navigate the surface of the snow and penetrate the subnivean space at access points to capture prey (Corn and Raphael 1992). Under conditions of deep snow accumulation, marten also use subnivean cavities as rest sites to reduce heat loss (Taylor & Buskirk, 1994). Therefore, the apparent reduction in marten presence in this study is likely to reflect increased thermoregulatory periods beneath the snow surface with unaffected or marginally increased rates of feeding occurring during above-snow ventures in the interim.

Moreover, the relative rate of marten occurrences in the time-since a wolverine or weasel increased moderately with snow depth before declining significantly (Figure 6a and & 6b), though the depth thresholds differed at approximately 80 cm and 43 cm snow depth following wolverine and weasel respectively. In winter, most prey of marten are captured below the surface of the snow (Banci, 1994); thus, the observed difference in response to wolverine and weasels in relation to snow depth could reflect predatory tracking of weasels, an occasional food source (COSEWIC, 2014), as both species are able to move and forage efficiently in the subnivean environment. The move towards occupying subnivean space may be driven by the intersection of three separate energetic considerations: behavioural thermoregulation during severe winter conditions (i.e. snow depth, wind, temperatures), availability of forage beneath the snow and a cost-benefit analysis of energetic resource acquisition at the snows surface.

Winter foraging is expected to be a costly behaviour for martens. Taylor and Buskirk (1994) suggest that energy conserved via thermoregulation should serve to minimize time required for foraging, at the same time elevating the associative threat of being exposed to predation. It is therefore possible that martens seek refuge from competition and advantageously shift to predatory feeding behaviour or resting beneath the snow in harsh winter conditions owing to the thermal efficiencies of these environments.

Weasels reduced encounters with marten through avoiding scavenging during periods of intensified usage by marten and wolverine, potentially to reduce the chances of a direct encounter. The extent of weasel activity at camera sites at the surface of the snow decreased slightly as snow depth rose. Weasels are proficient at subnivean mobility and may prefer habitats having deep snow for their ability to evade larger competitors by retreating beneath the snow when needed.

The rate of weasel activity at carrion sites was not significantly different in open relative to closed habitats. This is inconsistent with previous assessments of site-level and habitat-scale winter habitat associations of weasel, showing preference for open forest stands with incomplete canopy closure, edge habitats adjacent to forested areas or grass-dominated riparian zones (Mowat & Poole, 2005; Mowat, Shurgot & Poole, 2000). Predatory birds have been found to scavenge more often in open clearings (Selva et al. 2003). The potential of increased exposure to avian or mammalian predation at carrion in open habitats appeared to have altered typical habitat preferences in the vicinity of beaver carcasses.

2.4.2 Habitat Influence on Scavenger Behaviour

Open habitats appear to foster competition among carnivores across an array of ecosystems possibly because carcasses are more readily discovered (Creel, 2001). Scent of carrion is expected to travel more quickly and be more easily detected in open areas (Spencer et al. 2021) and mustelids are likely able to locate these sites more quickly. In keeping with this idea, Selva et al. (2003) discovered that carcasses during winter in forested areas were depleted by scavengers over a longer time relative to those in open habitats. Mesopredators also appear first at carrion sites nearby open meadows (Stiegler et al. 2020) and mustelids are generally efficient at finding food remains (Willebrand et al. 2017). Wolverines, a large mesocarnivore with well-equipped weaponry, may exploit this advantage at open carrion sites because while their habitat preferences have been linked to an array of topographical, anthropogenic (Fisher et al. 2013b), and landcover characteristics, it has largely been attributed to food availability (Banci, 1994).

Unlike wolverines, martens principally avoided open clearings in the WWP, concurrent with previous findings that marten show aversion to habitats that lack forest cover such as meadows and clear-cuts (Banci, 1994; Fisher et al. 2013a), and have been observed to even reduce their hunting during winter in openings slightly wider than 100m particularly in deep snow periods (Clark et al. 1987). Instead, martens appear to be more specialized to mature conifer forests (Clark et al. 1987; Fisher et al. 2013a), which make up the majority of landcover in the WWP. These enclosed habitats offer heavy woody debris that provide protection from predation by wolves, increased hunting efficiency (Andruskiw et al. 2008), access sites to subnivean spaces (Corn and Raphael, 1992) and improved concealment from competitive threats.

At the site level, marten showed higher habitat selectivity, whereas wolverine and weasel used carrion sites in open or closed habitats more generally or may have been more influenced by scavenging potential causing them to break with typical patterns of habitat usage. Differences in habitat use and functional environmental tolerances can serve to foster mustelid co-existence at carrion sites, evidence here suggests that interactions could be intensified by breaking down habitat differentiation niche partitioning.

2.4.3 Study Limitations

It is likely that some variability in mustelid site use went unexplained since we were unable to account for the influence of all intraguild competitors. Owing to a lack of data, we omitted cougar, wolves, red fox and fishers from this investigation, which could potentially hinder our interpretations of mustelid scavenging strategies in relation to competition. For instance, martens and fishers spatially partitioned themselves at the landscape scale in the study area (Fisher et al. 2012). In addition, wolverine have been known to track wolves due to opportunities for carrion provisions (Klauder et al. 2021), as such considering fishers or wolves may have improved our overall understanding of fine-scale mustelid spatial-temporal distributions.

Cox regression models stood out as being relatively uninformative except to confirm that snow depth appears to play a role in fine scale temporal interactions. Site attributes such as extent of woody debris (e.g. fallen logs) – which provide access to subnivean areas (Corn & Raphael, 1992) – or other measures of site complexity that could facilitate escape – may have been more relevant than habitat closure for examining fine-scale interactions between small to mid-sized carnivores. The state of the carcass (i.e. phase of consumption/decomposition), has previously been found alter carcass use by scavengers (Selva et al. 2005) and is likely also an important determinant of immediate decisions to scavenge in relation to competition at this scale of investigation. Including the recorded dates of when bait rewards were replenished at camera sites could have buffered against bias resulting from a fluctuating degree of energetic payoff at carrion sites.

Data constraints also precluded inclusion of interaction terms for competition predictor variables, however previous research by Prugh & Sivy (2020) found mortality of mesocarnivores resulting from intraguild predation by larger carnivores to be in some cases superadditive. Furthermore, as carnivore diversity increases, the directionality and intensity of competitive pressures placed on mesocarnivores may interact with one another (Roemer et al. 2009; Rota et al. 2016). In relation to this, the correlations between mustelid species observed herein does not necessarily exist as evidence of ecological interactions (Blanchet et al. 2020). Inferences regarding causation of scavenging behaviour variability is even more vulnerable to confounding factors considering the taxonomic scope of this investigation. Ideally, researchers should strive to adopt a guild-level approach to examining carrion feeding ecology of facultative scavengers, especially in landscapes diverse predator assemblages.

2.4.4. Conclusions

Improved insight into carrion use by facultative scavengers and the associative factors that shape carrion acquisition for those species will deepen our understanding of broader ecosystem processes and energy transfers in food webs. Intraguild competition at scavenging opportunities can influence adjoining trophic levels resulting in cascading effects on the greater ecosystem. Competition may be more pronounced at large mammal carcass sites in boreal forests and mountainous landscapes in western Canada, especially in winter when resources become more limited. The interplay between intraguild competition and habitat features for spatial-temporal analysis suggest that mustelids manage resource acquisition through a mixture of spatial and behavioural tactics that changed with site conditions. Key findings reveal that reactionary temporal responses to intraguild competitors at carrion sites is dynamic and subject to localized site conditions.

Microhabitat composition and differences in attraction/avoidance techniques of mustelids in the WWP appeared to alter site visitation behaviours and may govern accessibility to carrion in a multi-carnivore landscape. Differences in mechanisms of competitive interactions of species within the same guild can translate to differences in species abilities to coexist or vulnerability to competitive exclusions (Swanson et al. 2014). Findings from this research further highlight the importance of exploring bilateral species influences in multi-carnivore systems in contrast to making assumptions of hierarchical competitive dominance and applying unidirectional structure to exploring those relationships. This work aligns with the growing body of literature highlighting improved understandings of how intraguild competition dynamics, in addition to habitat composition and traditional predator-prey structures, exist as an important predictor of habitat selection and foraging behaviour of sympatric carnivore species.

Climate Change threatens to modify existing structures of scavenging community composition and dynamics globally (Wilson and Wolkovich, 2011). It is estimated that the availability of carrion in terrestrial systems could decrease by 20–40% over the next century (Beasley et al. 2012). Scavengers which are limited by competition or depend heavily on carrion resources may experience disproportionate impacts from such declines. Understanding the factors that drive access to these ephemeral resources can further provide valuable information for anticipating impacts of climate change on facultative scavengers in the boreal forests of western Canada.

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Chapter 3: Conclusion

Scavenging is prevalent in terrestrial ecosystems and yet remains relatively understudied despite the essential role that it plays in increasing scavenger fitness and the transfer of energy and nutrients in the food web of many ecosystems. Most carnivores are facultative scavengers to some extent (DeVault et al 2003; van Dijk et al. 2008), and through consumption of carrion these species play critical functional roles within ecosystems. Carrion feeding patterns and efficiency of individual species is determined by a set of highly complex and integrative factors that include competition, characteristics of the carcass, and habitat composition (Selva & Fortuna, 2007). The nature of facultative scavenger foraging strategies (i.e. hunting versus scavenging) is dynamic and sensitive to change in response to immediate spatiotemporal conditions (Pereira et al. 2014). This thesis contributes to scavenging ecology through improved understanding of how carrion resources are partitioned during winter among a group of taxonomically similar species with variation in body size and in their strategies and adaptations for scavenging. The following chapter sections provide general conclusions and considerations for future research in this area.

3.2 Carrion acquisition and patterns of connectivity

In seasonal forests, winter facultative scavenging is an essential adaptation for survival for a number of carnivore species. The number of ungulate carcasses that emerge through predation, disease, starvation or other means varies seasonally; therefore, carnivores must adjust to seasonal trends in carrion availability (Pereira et al. 2013). When carrion is scarce, facultative scavengers can switch to exploiting small mammals (Pereira et al. 2013). As a result, carrion shortages are likely to increase the degree of dietary overlap among small and mid-sized carnivores and could place disproportionate energetic strain on competitive subordinates. Furthermore, through examining site-level interactions at locations that mimic conditions of a naturally occurring scavenging opportunity during the cold season, this study found evidence that access to carcasses appears to be the result of interactions among multiple sympatric carnivores. Similar to trends observed by Allen et al. (2015) we observed evidence that carnivores that assert dominance over carcasses may negatively alter feeding patterns by one competitor and associatively increase the extent of feeding behaviours of another in what appears to represent a cascading pattern of intraguild suppression and behavioural releases. Recognizing patterns of connectivity in carrion acquisition by sympatric species is important for anticipating the effects of changes to annual trends in carcass temporal and spatial availability on ecosystem processes (DeVault et al. 2003).

3.3 Niche overlap and planes of coexistence

This work exemplifies the importance of simultaneously evaluating spatial and temporal planes of interactions to uncover mechanisms of attraction and avoidance. For example, mustelids in this study employed opposing tactics to avoid lynx likely driven by morphological differences. These tactical differences resulted in distinct limitations to carrion feeding, where navigating moment-to-moment lynx usage appeared to provide improved access to carrion resources. These processes could only be detected through a spatial-temporal framework. Existing efforts to estimate carnivore community structures (Jiménez et al. 2016; Richie & Johnson, 2009) and understand behavioral mechanisms driving coexistence (Rota et al. 2016; Swanson et al. 2014, 2016; Vanak et al. 2013) have provided much needed knowledge into the structure and function of carnivore community ecologies. Much of this work has examined how carnivores can reduce undesirable encounters with competitors on one of two planes of segregation: (1) spatially through altered habitat use (Durant, 2000; Foster et al. 2010; Rota et al 2016; Wereszczuk &

Zalewski, 2015), or (2) temporally through either activity pattern partitioning (Caravaggi et al. 2018; Frey et al. 2020; Ridout & Linkie, 2009; Marinho et al. 2020) or adoption of fine scale temporal evasion tactics (Swanson et al. 2016). While informative, the methodologies used in these examinations have tended to focus exclusively on a single plane of interaction (spatial *or* temporal), and as a result have sometimes fallen short in their ability to discern a comprehensive picture of coexistence mechanisms. There is an emergent trend in behavioural ecology of considering species interactions in space and time as unified construct (Naidoo & Burton, 2020; Swanson et al. 2016; Wang et al. 2015; Kohl et al. 2018; Palmer et al. 2017; Keim et al. 2018). Past literature has contributed valuable insights into how sympatric mesocarnivores partition along ecological niches spatially (Fisher et al. 2013a) and temporally (Frey et al. 2020) in the study area. This investigation follows those paths of inquiry that test for patterns of species co-occurrence and niche intersection by resolving how species traits dictate carnivore interactions at ephemeral resource patches following a behavioural approach based on attraction-avoidance indices at simulated carrion sites. Ideally, ecologists should seek to explore competitive coexistence at multiple planes and scales to derive robust conclusions as to the behavioural adaptations and processes at play (Amarasekare, 2003).

3.4 Fine scale species-scapes: integrating habitat selection and species interactions

The role of habitat in partitioning scavengers in relation to carcass sites has been identified in numerous past studies (Selva et al. 2005; Stiegler et al. 2020). Carrion is a pulsed resource, though the spatial and temporal aspects of carcass deposition is itself a non-random process that can initiate lasting changes to ecosystem community dynamics and structure (Selva & Fortuna, 2007). Seasonality in habitat structure and utility is inextricably linked to scavenging ecology, ungulates for example die of starvation typically later in the winter and carcasses generated through predation are likely to arise more frequently in habitats that incur advantageous hunting conditions for large predators. In a broad context, evaluating habitat selection and competition in conjunction strengthens the ability to decipher whether resource acquisitions are controlled by responses to competitive risk aversion or relates to some other aspect of overall habitat quality (Gompper et al. 2015), or to evaluate the effect that habitat composition has on the nature of species interactions. At the landscape level, the notion of "species-scapes" describes an interwoven habitat-interspecific interaction framework to explaining species distributions (Fisher et al. 2013a). This integrated approach calibrated to the site-level highlights the importance of unique behavioural adaptations for foraging and capacity for concealment or mobility provided by micro-habitat features in a species decision to scavenge.

As evidenced by our findings, environmental in addition to competition factors govern the use of carrion by facultative scavengers in the WWP. Moreover, carcass decomposition occurs at different rates dependant on habitat structure and carcass exposure (Creel et al. 2001; Selva et al. 2003). This has a twofold influence on the mammalian scavengers. First, rapid decomposition associated with higher temperatures and open areas omit odors more readily and olfactory cues appear to be the primary signal for carrion detection (DeVault & Rhodes, 2002), thus carcasses are located or removed by scavengers more quickly under these conditions (Stiegler et al. 2020). Secondly, the battle for carrion resources against microbes is intensified with expediated decomposition, thus a smaller window may exist wherein carrion is available to mammalian carnivores before risks of disease transmission predominates (Selva et al. 2002). Therefore, habitat structure in the context of scavenging relates directly to carnivore habitat selection and utility and alters the carcass condition such that it changes the probability it will be discovered and the availability or efficiency by which it can be consumed.

3.5 Winter habitats: the importance of snow and ambient temperature at fine scales

It is apparent that intraguild interactions transpiring at carcass sites are susceptible to climatic variability at fine spatial resolutions, where animal behaviour is represented by foraging and daily movements. Our findings related to the influence of snow depth at carrion sites is consistent with previous work that identified weather conditions (i.e. snow cover and ambient temperature) as having influence over carrion availability for scavengers in northern climates (DeVault & Rhodes, 2002; Selva et al. 2005). Microhabitats in seasonal environments can alter the behaviour of carnivores owing to differentiation in their structural complexity resulting in variation in thermoregulatory (Taylor & Buskirk, 1994) and hunting (Andruskiw et al. 2008; Klecka & Boukal 2014; Willebrand et al. 2017) efficiencies. Similarly, facultative scavenger foraging and feeding behaviours are also impacted by weather conditions. Seasonally, carcass visitation occurrences tend to increase during winter (Stiegler et al. 2020) however, at finer temporal resolutions during the cold season, daily ambient temperature has been positively correlated with the rate of small carcass removal (DeVault & Rhodes, 2002) and negatively linked to scavenger visitation frequency at large carcasses for a multitude of species (Selva et al. 2005). Habitat differentiation is a hierarchical process (Mcloughlin et al. 2004), for example where Canada lynx and bobcat experience range overlap, the species were spatially segregated at the landscape scale but showed markedly similar patterns of habitat use in relation to snow depth, prey availability and landcover at the microhabitat level (Morin et al. 2020). Hence, small and mesocarnivore habitat differentiation and coexistence mechanisms at ephemeral resource patches can exhibit different trends than those observed for the habitat scale. Our findings that snow depth could impede or facilitate spatiotemporal access to beaver carcasses in a different manner than it impacted frequency of site visitation by the same species adheres to this logic. We thereby acknowledge and contribute to mounting evidence that weather impacts scavenging dynamics at the site level and suggest that future work considering intraguild interactions and foraging strategies of small and mid-sized facultative scavengers can be improved by looking to the importance of weather-related factors such as wind, temperature and precipitation on differential micro-habitat usage at carrion sites.

3.6 Scavenging community dynamics: directionality and hierarchies

We found that interactions amongst scavengers did not follow a straightforward hierarchical pattern, highlighting how in diverse carnivore communities, assessments of intraguild interactions can benefit by considering multiple species interactions (Burger et al. 2019; Caravaggi et al. 2018; Ritchie & Johnson, 2009). In a general context, carnivore community ecology has been dominated by unidirectional investigations of the impacts of large carnivores on mesocarnivores and the suppressive forces that drive community structure (Ritchie & Johnson, 2009; Wang et al. 2015). In the realm of scavenging ecology, intraguild interference competition or predation between species pairs can occur unilaterally at carcass sites where a single species both dominates scavenging potential and threatens mortality to the subordinate competitor (strictly negative impacts to subordinate) or alternatively, the dominant species allocates scavenging provisions to a competitive subordinate (positive-negative paradigm) (Creel, 2001; Sivy et al. 2017). Recent studies have increasingly revealed the importance of impartial intraguild interactions and facilitative processes as determinants of scavenger community structure (Klauder et al. 2021; Selva & Fortuna, 2007).

In diverse carnivore communities a research framework that extends to a multitude of intraguild competitors and uses a bilateral approach to identifying the nature of those interactions, can offer improved understandings of facultative scavenger dynamics, avoid confounding research outcomes, and uncover cascading or interconnected community interactions (Prugh & Sivy, 2020; Selva & Fortuna, 2007). Guild-level and multi-species approaches to understanding habitat use by carnivores aligns with a growing trend in conservation of transitioning away from species-specific protection strategies to more wholistic notions that consider ecological community-level protections (Burger et al. 2018; Heim et al. 2019). A challenge within behavioural ecology research is that it often involves isolating a limited number of focal species under investigation, as was the case in the research performed here, which knowingly results in a partial view of wholistic guild or community level dynamics. Where data are constrained, carnivore species assemblages selected for research initiatives should not be restricted to the unidirectional influence of top predators on smaller carnivores. Focal species herein were chosen based partially on taxonomic similarity and to represent an array of body sizes and foraging strategies, but with some degree of dietary overlap in addition to carrion feeding. This research has revealed the complexity of interactions in a sub-set of facultative scavengers, ranging in body size from small to large mesocarnivores, and in doing so has revealed additional scavenger community linkages in need of investigation.

3.7 Final Thoughts

The potential outcomes of intraguild competition are not mutually exclusive, rather, they are interwoven and highly complex (Prugh & Sivy, 2020; Selva & Fortuna, 2007). Examining carnivore interactions at carrion sites as a function of habitat attributes using a fine scale spatial-temporal framework offers for an improved understanding of the external cues that determine a mustelid’s ability to scavenge. Examining mesocarnivore community structure through the lens of scavenging potential can provide new insights into interspecific processes and food web connectivity. Understanding the factors governing carrion accessibility is a logical first step in piecing together broader effects of these resources on ecosystem functionality. For example, in relationship to foraging pathways such as direct predation and herbivory, carrion consumption has received comparatively little attention with respect to cross-tier food web energy transfers (Wilson and Wolkovich, 2011).

Changes to population dynamics of mammalian scavengers can perpetuate large scale community responses (Olson et al. 2012). Small to mid-sized carnivores that are also facultative scavengers serve critical functional roles within ecosystems as seed dispersers (Steyaert et al. 2018), facilitators of prey populations, and prey species themselves. Wolverine and marten are both undergoing localized declines with habitat fragmentation due to industrial activities such as logging and oil exploration (Adamov, 2016; Helgen & Reid 2016). Wolverine have further been designated as a species of special concern according to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2014), owing to data deficient population estimates and trends nationwide. It is therefore critical that we unravel the constraints and facilitating factors presiding over scavenging dynamics.

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Appendix

Table S1: Habitat character classifications for examination of mesocarnivore space use in the Willmore Wilderness Area, derived from the ASLC dataset (ASLC, 2016). Resulting raster resolution equal to 25m.

Habitat Character	Alberta Satellite landcover classifications
Open	Open fir, open black spruce, open pine, open Engelmann/white spruce, open undifferentiated coniferous, tree dominated clear cut, fescue grassland, closed upland shrub, open upland shrub, Emergent wetland, Graminoid wetland, Shrubby wetland, Undifferentiated wetland, Black spruce bog, water (lakes), Permanent ice and snow, no Data, cloud/haze blocking, undifferentiated burn
Closed Forest	closed black spruce, closed pine, closed fir, closed Engelmann/White spruce, closed undifferentiated coniferous, Fir dominated coniferous, Black Spruce Dominated coniferous, Pine dominated coniferous, White spruce dominated coniferous, closed aspen/balsam popular/birch, closed deciduous dominated mixedwood, closed mixedwood

Table S2: ZINB/NB-GLM model selection for wolverine, American marten, and short-tailed weasel spatial distributions during winter in the Willmore Wilderness Park, Alberta. ZINB/NB-GLM models are ranked according to model weight associated with AICc values. Parameters are designed to create representational models for: habitat character factors (M1), competition related factors (M2) and a full model consisting of combined habitat-competition factors.

Model number	Predictor Variables
M1	mustelid no.1 + mustelid no.2 + Lynx
M2	Landcover + Snow Depth
M3	mustelid no.1 + mustelid no.2 + Lynx + Landcover + Snow Depth

(A) Wolverine Model Rank	AICc	delta	weight
M3	2083.1	0.00	0.997
M1	2095.6	12.47	0.002
M2	2096.5	13.39	0.001

(B) Marten Model Rank	AICc	delta	weight
M3	5302.4	0.00	0.981
M2	5310.3	7.93	0.019
M1	5461.2	158.83	0.000

(C) Weasel Model Rank	AICc	delta	weight
M3	751.9	0.00	0.856
M2	755.4	3.56	0.144
M1	778.3	26.40	0.000

Table S3: Summary statistics for TTE_r and TTE_{obs} distributions for all species pairings (minimum, 1^{st} quantile, median, mean 3^{rd} quantile and maximum values). Results of the Wilcoxon rank sum test are given where, alternative hypothesis: true time-to-event is not equal to what would be expected at random. The p-value of the test is less than the significance level alpha = 0.05.

Species Pair: SpA (SpB)		
Random TTE distribution (TTE_r)	Observed TTE distribution (TTE_{obs})	Mann–Whitney U test
(A) Wolverine (Marten): TTE_r n = 475.2, TTE_{obs} n = 372		
Min. 1st Qu. Median Mean 3rd Qu. Max. 0.000 2.483 6.792 15.904 19.133 117.150	Min. 1st Qu. Median. Mean 3^{rd} Qu. Max. 0.000 1.233 3.492 9.799 9.125 97.450	W = 136618, p-value = 5.897412e-10
(B) Wolverine (Weasel): TTE_r n = 44.8, TTE_{obs} n = 30		
Min. 1st Qu. Median. Mean 3rd Qu. Max. 0.55 9.20 19.15 22.18 30.53 83.70	Min. 1st Qu. Median. Mean 3rd Qu. Max. 0.200 1.071 6.517 12.339 14.496 73.033	W = 962, p-value = 0.001945
(C) Marten (Wolverine): TTE_r n = 144, TTE_{obs} n = 357		
Min. 1st Qu. Median. Mean 3rd Qu. Max. 0.550 6.825 19.717 24.875 36.033 95.483	Min. 1st Qu. Median. Mean 3rd Qu. Max. 0.150 1.600 3.433 10.182 8.633 103.850	W = 40038, p-value = 1.459266e-22
(D) Marten (Weasel): TTE_r, n = 27.2, TTE_{obs} n = 39		
Min. 1st Qu. Median. Mean. 3rd Qu. Max. 1.100 8.458 21.500 29.427 42.783 103.433	Min. 1st Qu. Median. Mean. 3rd Qu. Max. 0.000 2.342 5.017 12.053 13.633 75.900	W = 780, p-value = 0.000755014
(E) Weasel (Marten): TTE_r n = 173.6, TTE_{obs} n = 39		
Min. 1st Qu. Median. Mean 3rd Qu. Max. 0.067 1.350 4.483 6.895 9.879 44.683	Min. 1st Qu. Median. Mean 3^{rd} Qu. Max. 0.533 2.142 4.683 7.464 7.542 60.700	W = 3282, p-value = 0.7508
(F) Weasel (Wolverine): TTE_r n = 66.4, TTE_{obs} n = 27		
Min. 1st Qu. Median Mean 3rd Qu. Max. 0.167 2.438 6.408 11.312 19.138 61.267	Min. 1st Qu. Median. Mean 3rd Qu. Max. 0.800 2.292 6.467 11.701 13.000 60.933	W = 884.5, p-value = 0.9595

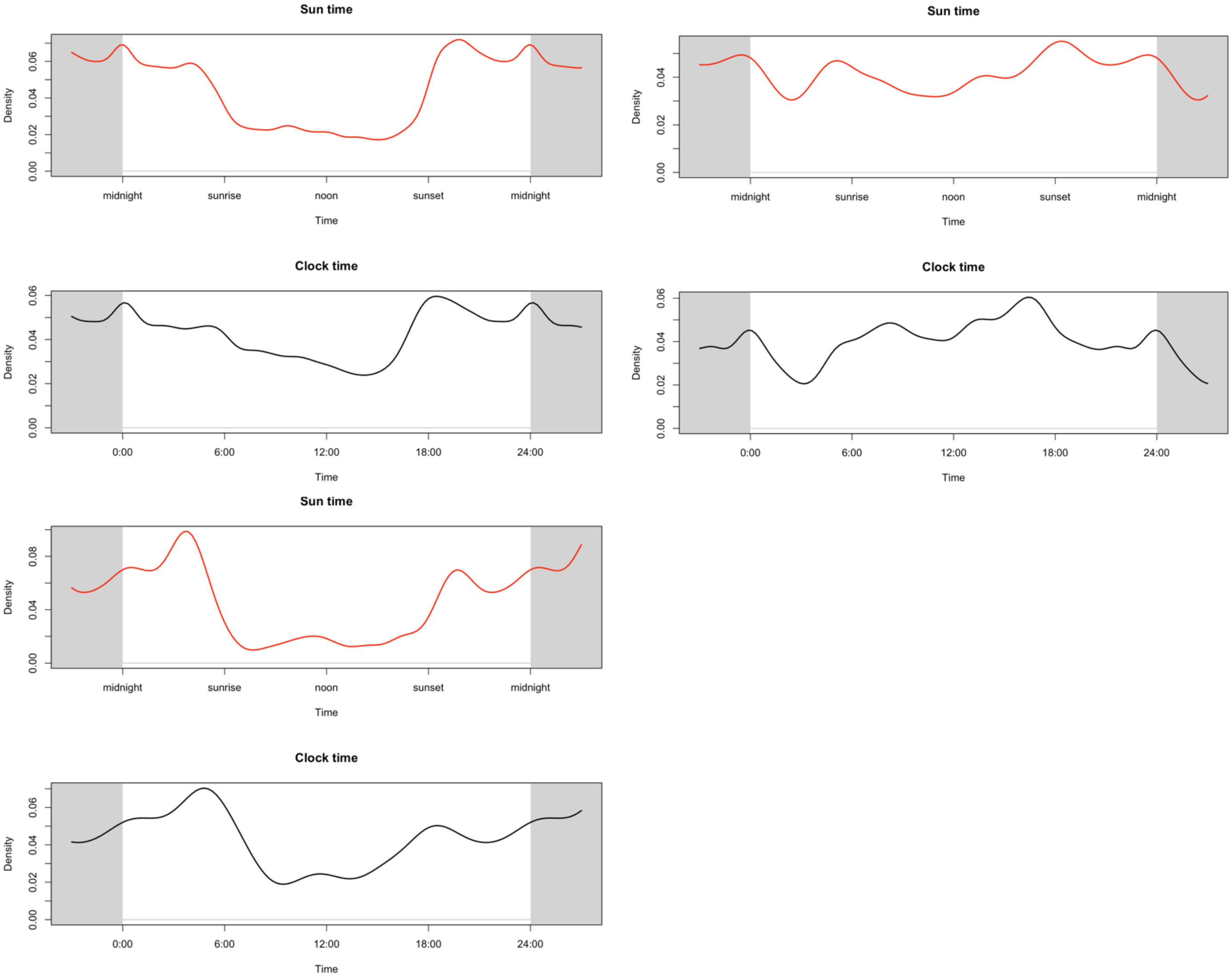

Figure S1: Comparison of clock time (black) to sun time (red) activity pattern curves from mustelids in the Willmore Wilderness Park to demonstrate the marked effect of calibrating daylight cycles from various sites and dates. Nocturnality of weasels (n = 342, bottom left) and marten (n = 12599, top left) is more clearly defined for sun time APA graphs. Wolverines (n = 1080) appear cathemeral (top right).

Table S4: Model Selection Tables for Cox Proportional Hazard Models. Format: Species B (Species A), showing AICc, delta (AICc) and model weight ranked for each species pair from highest ranked model to least. Models with the highest weight were selected as the best models for describing factors influencing time separation between mustelids in the WWP.

Model Number	Predictor Variables
M1	diel period + landcover + daily snow depth
M2	diel + daily snow depth

(A) Wolverine (Marten)	AICc	delta	weight
M2	3809.8	0.00	0.559
M1	3810.3	0.48	0.441
(B) Wolverine (Weasel)	AICc	delta	weight
M2	187.8	0.00	0.712
M1	189.6	1.81	0.288
(C) Marten (Wolverine)	AICc	delta	weight
M2	3809.8	0.00	0.728
M1	3810.3	1.81	0.272
(D) Marten (Weasel)	AICc	delta	weight
M2	249.6	0.00	0.767
M1	252.0	2.38	0.233
(E) Weasel (Wolverine)	AICc	delta	weight
M2	167.8	0.00	0.788
M1	170.5	2.62	0.212
(F) Weasel (Marten)	AICc	delta	weight
M2	245.8	0.00	0.713
M1	247.6	1.82	0.084

Table S5: Model selection for mustelid count data regression models based on Pearson's dispersion statistic for overdispersion and Vuong test statistic to assess zero-inflation. ZINB were found to be the best suited models for marten and wolverine datasets, whereas a NB-GLM was more suitable for the weasel distribution.

Focal Species	**Model Structure**	**Pearson's Dispersion Statistic**	**Vuong Non-Nested Test Statistic (VS)**
Weasel (82%)	GLM-P	7.016	AIC-corrected VS:1.68 GLM-NB > ZINB p-value 0.0463
	GLM-NB	0.919	
	ZIP	1.55	
	ZINB	0.967	
Marten (34%)	GLM-P	31.73	AIC-corrected VS: - 5.88 ZINB > GLM-NB p-value 2.061 e-09
	GLM-NB	0.837	
	ZIP	5.812	
	ZINB	0.999	
Wolverine (96%)	GLM-P	8.91	AIC-corrected VS: - 2.13 ZINB > GLM-NB p-value 0.0167
	GLM-NB	0.926	
	ZIP	1.901	
	ZINB	0.958	

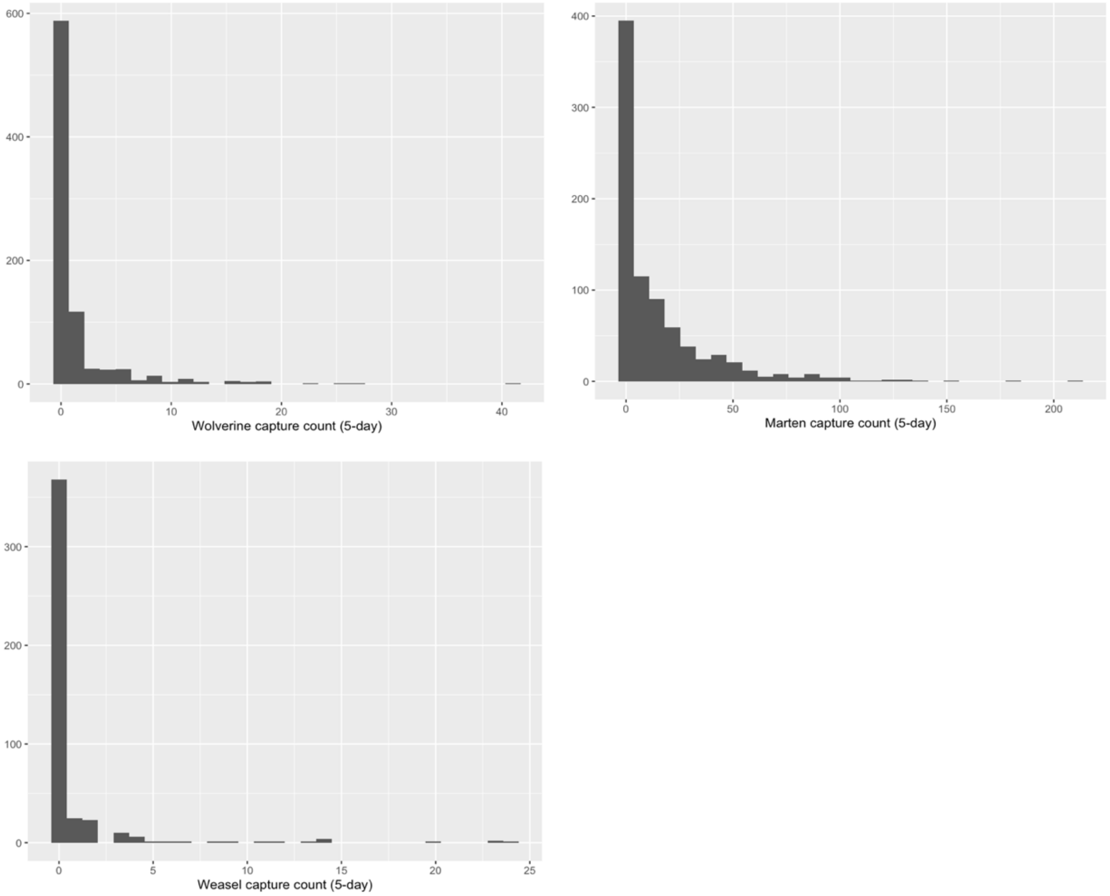

Figure S2: Species capture count values over 5-day intervals: wolverine, marten (2006-2008 n=4130) and weasel (2007-2008, n=2240) in the WWP. Percent total sampling occasions that resulted in a zero are: wolverine (71.19 %), marten (34.14 %) and weasel (82.14 %).

Table S6: Dataset summaries for wolverine, marten, weasel, and lynx detected in the Willmore Wilderness Area, AB during winter. Data includes the number of sampling occasions when species was present versus absent and total number of independent captures occurring over the 70-day sampling period for all camera locations.

Species	Total independent captures	Times present (versus absent) for all sampling occasions	Number of unique camera locations for species
Lynx	305	32	11
Wolverine	1080	238	51
Marten	12599	544	53
Weasel *	342	80	15

* Presence data is out of a total of 4130 sampling occasions (unique camera sites n = 59) for all species except weasel having 2240 sampling occasions (unique camera sites n = 32).