# Between a Risk and a Hard Place:
# Scavenging Patterns and Habitat Selection of Carnivores in the Subarctic

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## Abstract

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Animals must balance the need to acquire sufficient resources against the risk of being consumed by a predator. This challenge is faced by many species which, though predatory, are also subject to predation. The ecological relationship between top predators and these smaller "preydators" is a complex mix of competition, facilitation, and predation. Two arenas in which smaller predators must balance fitness needs with predation risk are at carcass sites, which represent a valuable but risky food source, and when making habitat use decisions in a landscape populated with top predators. In this thesis, I use photo data from carcass sites and location and survival data from sympatrically collared wolves (*Canis lupus*) and coyotes (*Canis latrans*) to examine the behavior and risk-mediation strategies of carnivores in an understudied environment: the subarctic. I found that carrion use was dominated by wolves and wolverines (*Gulo gulo*), with limited use by coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*). Risk-mediation while scavenging occurred primarily through alterations in use intensity rather than behavior. I show that coyotes do not universally avoid wolves, but instead demonstrate season--

specific responses to wolf risk. Specifically, although coyotes avoided wolf proximity under all circumstances, they switched from avoiding areas of long term wolf use in the summer to favoring them in the winter. These findings suggest that although inter-guild competition for carrion and space has strong effects, mesocarnivores use context-specific behavioral strategies to mediate the risk of apex carnivores. Future studies of carnivore population dynamics should account for these species-specific and context-dependent behaviors.

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# Chapter One: General Introduction

Risk of injury and death at the hands of other animals is one of the fundamental forces shaping animal distribution, ecology, behavior, and morphology. (Lima and Dill 1990; Lima and Bednekoff 1999; Ripple and Beschta 2004; Stankowich and Blumstein 2005; Thomson et al. 2006). Strategies to mediate predation risk include spatial and temporal partitioning, vigilance and monitoring behaviors, and physical mechanisms such as camouflage and toxins (Lima and Dill 1990; Lima and Bednekoff 1999; Ripple and Beschta 2004; Stankowich and Blumstein 2005; Thomson et al. 2006). Most of these efforts come at a fitness cost, forcing animals to make energy allocation trade-offs between risk-mediation and other biological and reproductive needs (Lima and Bednekoff 1999).

Because risk varies in time and space, at-risk individuals can use behavioral strategies to take advantage of spatial and temporal windows of reduced risk, thus better optimizing their ability to use important resources or save energy when possible (Lima and Bednekoff 1999; Valeix et al. 2009; Bischof et al. 2014; Stewart et al. 2016). Variable risk also means that individuals may have to modulate the level of risk they are willing to tolerate in order to meet other fitness needs (Lima and Bednekoff 1999; Valeix et al. 2009; Bischof et al. 2014; Stewart et al. 2016).

While response to risk of predation has primarily been studied for prey species, it applies to many predator species as well, who may be killed both as food items or as competitors (Polis et al. 1989; Polis and Holt 1992; Lourenço et al. 2014). Predators are connected through complex ecological pathways including direct and indirect competition for territory, prey, and carrion; intra-guild predation; provisioning; and facilitation (Linnell and Strand 2000; Ritchie and Johnson 2009; Moleón et al. 2014). Consequently, larger predators represent both risk and reward to smaller predators, a mixed dynamic that is not present in simpler predator-prey systems.

Terrestrial carnivores are one of the most widely-studied and prominently managed groups of predators. The hypothesis that top carnivores exert strong direct and indirect ecological effects which structure ecosystems and regulate the populations of mesocarnivores has received considerable scientific and public attention (Estes et al. 2011; Ripple et al. 2014; Sergio et al. 2014). Instances of apparent mesocarnivore release or suppression following changes in apex carnivore populations have been documented in several systems (Linnell and Strand 2000; Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2013). But despite continuing study of intra-guild population dynamics, the patterns and mechanisms of mesocarnivore suppression and release remain elusive, due in part to the mixed nature of the interactions between top carnivores and mesocarnivores (Elmhagen and Rushton 2007; Ford and Goheen 2015; Bergstr et al. 2017; B.L. Allen et al. 2017). While the phenomenon of large carnivores killing smaller carnivores is well-documented (Palomares and Caro 1999; Lourenço et al. 2014), its numerical effects have not always been sufficient to produce observed demographic changes, suggesting that indirect effects (sometimes called risk effects) of large carnivores may play a significant role in demographic patterns (Ritchie and Johnson 2009; Moll et al. 2017). Two possible mechanisms by which top carnivores might regulate or at least impact the populations of mesocarnivores are carrion provisioning and changes in habitat use of mesocarnivores driven by predation risk (Schmitz et al. 1997; Wilmers and Getz 2004; Ritchie and Johnson 2009; Khalil et al. 2014; Lourenço et al. 2014; Sivy et al. 2017).

The creation of carrion resources by top predators which are then utilized by other species has been termed "carrion provisioning," which carries connotations of a free lunch. However, since most predators, including top or apex predators, are also facultative scavengers, and because a large percentage of carrion comes from non-predation causes, carrion creation and utilization is unlikely to function discretely from predation dynamics and competition between predators (Wilson and Wolkovich 2011). Evaluating scavenging as a potential mechanism driving intra-guild population dynamics requires examination of risk-benefit trade-offs. According to the risk allocation hypothesis (Lima and Bednekoff 1999), if scavenging individuals are at high risk of injury or death from larger scavengers or conspecifics while feeding at a carcass site, they should seek to maximize the caloric reward of scavenging while minimizing the risk of agonistic encounter. While the risk allocation framework has been widely applied in foraging studies (Verdolin 2006; Luttbeg 2017), risk assessments of scavenging behaviors remain limited. Investigating the degree of risk carried by scavengers would thus help clarify the net effects of top carnivores by shedding light on whether carrion represents a "free lunch" enjoyed primarily by non-apex predators or a resource subject to guild-wide competition.

Because mesocarnivores may benefit from proximity to large carnivores by gaining access to carrion resources or by using large carnivore presence as a shield against competition and risk from other mesocarnivores (Switalski 2003; Khalil et al. 2014; Allen et al. 2015; M.L. Allen et al. 2017), the behavioral responses of mesocarnivores to large carnivores, as measured by habitat use, have not always demonstrated patterns of avoidance as is generally assumed (Ritchie and Johnson 2009; Swanson et al. 2014; Balme et al. 2017; Sivy et al. 2017). Instead, the tension between risk and reward, as well as the need to meet fitness needs despite predation risk, serves as an incentive for mesocarnivores to respond flexibly to large carnivore risk depending on the circumstances (Lima and Bednekoff 1999; Valeix et al. 2009; Bischof et al. 2014; Stewart et al. 2016). Additional research is needed to better document the spatial responses of mesocarnivores to large carnivores, and to identify contextual factors that influence resource use in the face of large carnivore risk.

Wolves (*Canis lupus*) are large, charismatic predators with a large global range and considerable cultural history, and are consequently one of the most extensively studied large carnivores. Their relationships with other widespread mesocarnivores such as coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) have also received considerable attention (B.L. Allen et al. 2017). Yet due to the complex nature of predator-predator dynamics, as well as the variety of shared habitats encompassed by these species, there are gaps in our understanding of how these species interact, as well as the effects of wolves on less-studied mesocarnivores such as the wolverine (*Gulo gulo*) (B.L. Allen et al. 2017). For example, it has been hypothesized that widespread extirpation of wolves in

North America facilitated the coyote's massive range expansion over the past two hundred years, yet coyotes also expanded their range into Canada and Alaska, regions with robust wolf populations (Thurber and Peterson 1991; Berger and Gese 2007; Berger et al. 2008; Gese et al. 2008; Ripple et al. 2013). This discrepancy demonstrates a need to better understand carnivore guild dynamics in these northern regions.

In this study, I examine scavenging dynamics and space use of a carnivore guild in the sub-arctic landscape of Denali National Park and Preserve, Alaska. Using photo data from trail cameras placed at carcass sites, I document wintertime carrion use and vigilance behavior of four carnivore species: wolves, wolverines, coyotes, and red foxes (Chapter 2). I investigate how carrion use and vigilance are affected by environmental and interspecific variables that might change the balance of risk or reward while scavenging. I also examine coyote space use, survival, and response to wolf risk using data from sympatric GPS-collared wolves and coyotes (Chapter 3). Specifically, I evaluate how coyotes gauge wolf risk by comparing their response to wolf proximity versus long term wolf use; I establish if their response to wolves is one of attraction or avoidance; and I determine whether that response varies by season and habitat.

Given the harsh environment and limited prey base in the wintertime sub-arctic, I predicted that carrion use would be similar for all species, but that smaller species (who are at a disadvantage in interspecific competition) would be at higher risk at carcass sites and therefore show more vigilance behavior and sensitivity to risk metrics (Palomares and Caro 1999; Switalski 2003; Selva et al. 2005; Dijk et al. 2008; Ritchie and Johnson 2009). Alternately, if scavenging is a low-risk high-reward activity (“provisioning”), I expected use of carcass sites to be unaffected by environmental factors or the threat of interspecific competition and simply decrease with time as the resource is consumed.

I predicted that coyotes would avoid nearby wolves but not be strongly avoidant of areas with high long-term wolf use, allowing them to otherwise optimize habitat selection and potentially take advantage of carrion in a harsh environment with limited prey base. I predicted that avoidance of wolves would be strongest in habitats with poor visibility, and in the summer when small prey are more readily available. I predicted that if coyotes did show attraction to wolves, it would be during the winter, when the potential rewards offered by carrion may be the most important. If instead coyotes selected habitat based only on habitat characteristics, with no response to wolf risk, it would indicate limited support for a potential spatial mechanism of mesocarnivore suppression/release.

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# Chapter Two

# Gifts of an Enemy: Scavenging Dynamics in the Presence of Wolves

## Abstract

Carrion represents a critical resource for many species, including many predators. Framing carrion as a resource "provisioned" by large carnivores does not account for guild-wide competition that occurs for carrion resources. Examining scavenging in a risk-reward framework allows for a better understanding of how predator guilds compete for and benefit from carrion. We used trail camera data to compare wintertime carrion use and vigilance behavior of four carnivores in Denali National Park and Preserve and examined how use and behavior were affected by environmental factors. We found that carrion use was dominated by wolves (*Canis lupus*) and wolverines (*Gulo gulo*), with limited use by coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*). Risk-mediation occurred primarily through alterations in use intensity, with some evidence of behavioral risk-mediation at high-use sites. Scavenging use and behavior were influenced by the origin of the carcass, the age of the site, and the long-term intensity of wolf use in the area. These findings document a top carnivore (wolves) as a "top scavenger," and suggest that inter-guild competition for carrion strongly affects the extent to which different species benefit from carrion resources.

## Introduction

> "To them it seemed that the gifts of an enemy were to be dreaded."
>
> Voltaire, *Henriade*, Chapter II

Scavenging is increasingly recognized as an influential force within ecosystems and a critical food component for even presumed "facultative" scavengers (DeVault et al. 2003; Wilson and

Wolkovich 2011; Moleón 2015). The creation of carrion resources by top predators which are then utilized by other species has been termed "carrion provisioning," which carries connotations of a free lunch. However, most predators, including top or apex predators, are also facultative scavengers. Furthermore, a large percentage of carrion comes from sources other than predators and is not automatically exploited by a particular predator, as is the case with a kill. Therefore carrion creation and utilization is unlikely to function discretely from predation dynamics and inter-guild competition (Wilson and Wolkovich 2011). Carnivores compete directly and sometimes lethally with one another, thus carrion is unlikely to be a resource which can be utilized without risk (Palomares and Caro 1999). Given that carrion resources could be critical for scavenging species, but acquiring them requires direct competition with other predators and may therefore be risky, scavenging deserves further attention as an important pathway of behavioral and ecological interactions in carnivore guilds.

Evaluating scavenging as a potential mechanism driving intra-guild population dynamics requires examination of risk-benefit trade-offs. According to the risk allocation hypothesis (Lima and Bednekoff 1999), if scavenging individuals are at high risk of injury or death from larger scavengers or conspecifics while feeding at a carcass site, they should seek to maximize the caloric reward of scavenging while minimizing the risk of agonistic encounter. Scavengers can mediate risk in several ways, all of which limit potential caloric intake: by reducing the amount of time spent at a carcass, by increasing their level of vigilance while present, by selecting less-risky periods of time in which to scavenge, or through some combination of the above. In contrast, if scavengers are not at risk they should follow optimal foraging strategies that maximize caloric reward gained from scavenging (Charnov 1976). While the risk allocation framework has been widely applied in foraging studies (Verdolin 2006; Luttbeg 2017), risk assessments of scavenging behaviors remain limited.

The hypothesis that top carnivores exert strong direct and indirect ecological effects which structure ecosystems and regulate the populations of mesocarnivores has received considerable scientific and public attention (Estes et al. 2011; Ripple et al. 2014; Sergio et al. 2014), and instances of apparent mesocarnivore release or suppression following changes in top carnivore populations have been documented in several systems (Linnell and Strand 2000; Ritchie and Johnson 2009; Ripple et al. 2013). However the mechanism(s) of suppression and release have remained elusive, even for heavily-studied species such as wolves (*Canis lupus*) (Wilmers, Crabtree, et al. 2003; Schmitz et al. 2004; Borer et al. 2005; Ford and Goheen 2015). Carrion provisioning is a possible mechanism by which top carnivores might regulate or at least impact the populations of mesocarnivores (Wilmers and Getz 2004; Khalil et al. 2014; Sivy et al. 2017); but the contrasting roles of large carnivores as provisioners and competitors have made it difficult to fully assess this hypothesis. Investigating the degree of risk carried by scavengers would help clarify the net effects of top carnivores by shedding light on whether carrion represents a "free lunch" enjoyed primarily by non-apex predators or a resource subject to guild-wide competition. If the benefits or risks of scavenging vary widely among scavenger species, a more nuanced view of the trickle-down effects of top carnivore carrion creation and use may be necessary.

Wolves occur in multiple ecological systems around the globe, and are thus a key element in multiple guilds of carnviores (Mech 1974; Ripple et al. 2014; Winnie and Creel 2017). Wolves' continuing range expansion in North America and Europe, and the complex political and social tensions they generate, make it particularly important to understand their ecological effects. Though wolf scavenging, on both their own kills and other carcasses, is a broadly-acknowledged phenomenon (Metz et al. 2011), it remains poorly quantified in North America. Effects of group size and kill site characteristics on wolf scavenging rates have not been investigated, leaving much unknown about the extent to which wolves use carrion resources and the resulting threat they pose to other scavengers. We define scavenging by wolves as including returning to feed on their own kills after the initial abandonment of the kill. While some authors do not classify such visits as scavenging, several factors indicate that returning to kills should be considered as behaviorally and energetically distinct from feeding immediately post-kill. There is a large decrease in both quality and quantity of food available after initial abandonment, and the amount of food remaining at old kills is unpredictable (Wilmers, Crabtree, et al. 2003). Thus caloric intake is not comparable between the two scenarios, and we would not expect similar decision making processes to govern the use of fresh kills versus old kills (McNamara and Houstoun 1992). This functional non-equivalency is supported by evidence that wolves who are more easily able to make new kills are less likely to return to their old kills (Wikenros et al. 2013).

In this study, we used trail cameras to document wintertime carrion use and vigilance behavior of four carnivores in Denali National Park and Preserve (DNPP), located in interior Alaska. DNPP provides an ideal study system for investigating carnivore interactions, as it contains a full suite of large and midsize carnivores in a relatively undisturbed landscape. Previous work in this system indicates that mesocarnivores are positively associated with wolves at a local scale, despite regional and global evidence that wolf presence reduces mesocarnivore density and abundance (Ritchie and Johnson 2009; Sivy, Pozzanghera, Grace, et al. 2017). This pattern of association suggests that scavenging at carrion may be leading to a positive association and may be an important interaction pathway that could increase risk of conflict or death.

We compared overall carrion use, vigilance levels, and temporal patterns of scavenging among four species: wolves, wolverines (*Gulo gulo*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*). We also examined how carrion use and vigilance were affected by environmental and interspecific variables that might change the balance of risk or reward while scavenging. Previous studies indicate that wolverines, coyotes, and foxes commonly scavenge (Switalski 2003; Selva et al. 2005; Dijk, Andersen, et al. 2008), thus we predicted use of carcass sites by these species would be roughly equal, and differences in risk sensitivity would manifest primarily through vigilance behavior. Because body size is a strong predictor of dominance in interspecific competition (Palomares and Caro 1999; Ritchie and Johnson 2009), we predicted that a species' sensitivity to risk at scavenging sites would increase as body size decreased. Therefore, we predicted that scavenging would be a low-risk activity for wolves, and their scavenging activity would be driven primarily by caloric reward. We expected all three mesocarnivore species to be sensitive to caloric reward and to the risk posed by wolves and by other mesocarnivores, with risk sensitivity and vigilance increasing as body size decreased. Alternately, if scavenging is a low-risk high-reward activity ("provisioning"), we expected use of carcass sites to be unaffected by environmental factors or the threat of interspecific competition and simply decrease with time as the resource is consumed.

## Methods

### *Study area*

Our study area comprised the northeast corner of Denali National Park and Preserve (DNPP), as well as adjacent state lands (Figure 2-1). The area experiences a subarctic climate with long cold winters and short summers. It is comprised of steep mountain ranges bisected by broad glacial river valleys. The primary vegetative communities are boreal forest (spruce [Picea] and aspen [Populus] species), taiga (willow [Salix] and dwarf birch [Betula nana] deciduous shrub with scattered spruces), and alpine tundra. Average annual precipitation is 38 cm, with average winter and summer temperatures of -15°C and 12°C respectively (Sousanes 2016). Average snow depth during study period (December-March 2014-2017) was 35cm (L Prugh unpublished data). Harvest of game and fur-bearing species is allowed on the state lands; however this has been shown to not significantly affect wolf density (Borg et al. 2015). Data are limited for other furbearers but the scope and intensity of harvest are not likely to significantly reduce populations within the study area. Available ungulate prey species are moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall sheep (*Ovis dalli dalli*).

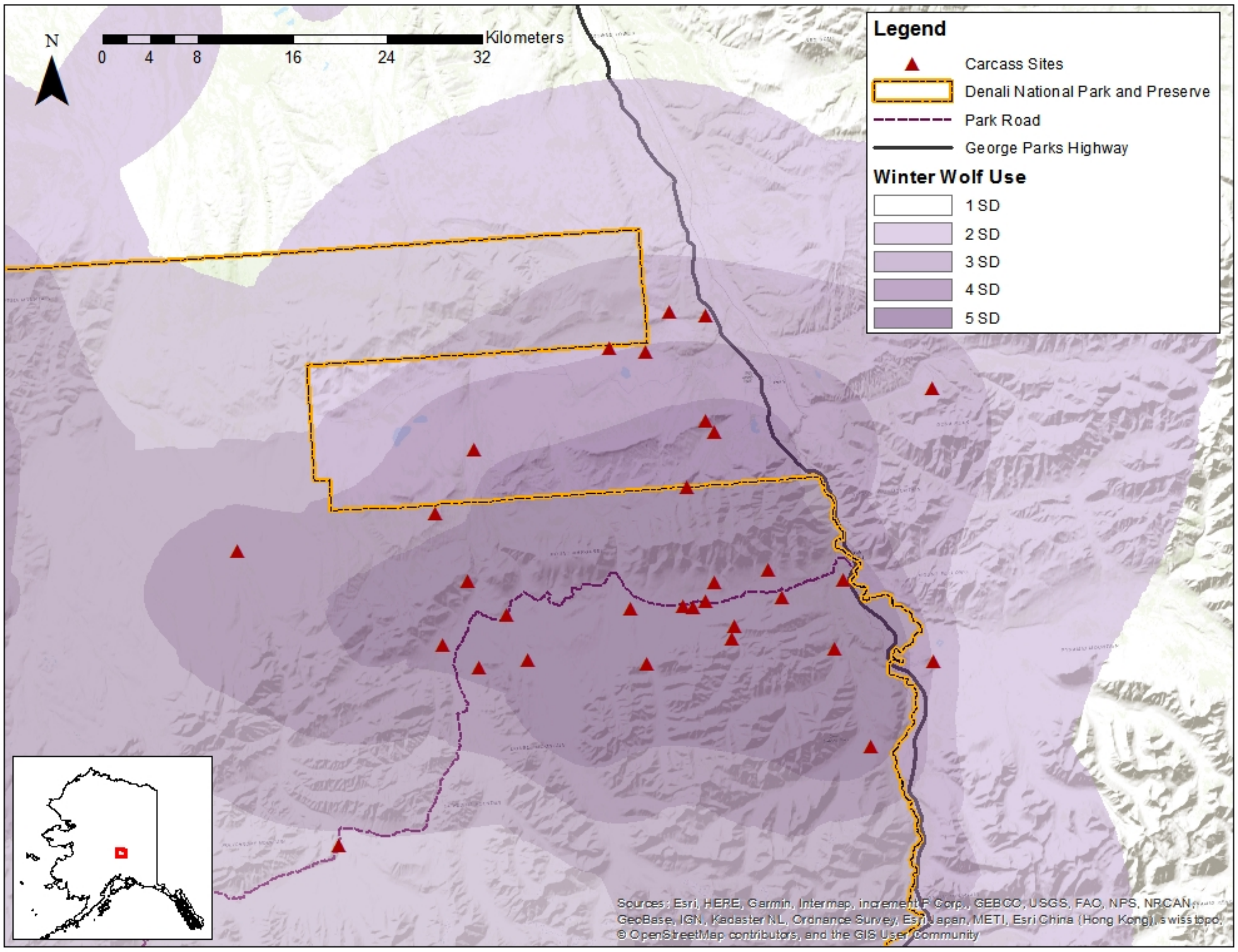


Figure 2-1. Map of study area showing border of Denali National Park and Preserve (yellow dashed line), carcass sites (triangles), roads, and average winter wolf use intensity as calculated from combined utilization distributions (purple shading, with each shade representing an increase of one standard deviation of use intensity, lowest standard deviation shown without color for clarity). Inset shows location of study area within the state of Alaska.

*Fieldwork*

We conducted fieldwork during the winters (November to April) of 2014-2017. During this time the National Park Service maintained GPS collars on at least one member of each of the four packs within the study area, with collars scheduled to record locations every eight hours. Carcass sites were located primarily by searching wolf GPS collar clusters (three or more points within ~400m), as well as from reports of others in the field, and from field sign and backtracking. At a carcass, prey species was noted and sites were assessed to determine likely cause of death based on sign such as presence of chase trail, evidence of hemorrhaging, degree of disarticulation, and orientation of carcass. Causes of death were categorized as wolf kill, natural, or unknown. Animals not killed by wolves were presumed to have died of causes such as starvation or disease, as there are no other predators active in winter capable of killing large ungulates. No road-killed ungulates were detected or included in this study. Percent shrub and tree cover within a ten meter radius were visually estimated, and distance to nearest cover was measured. Cover was defined as the nearest object that could provide substantial visual cover for an animal of coyote size. Examples include mature spruce trees, ravines, and dense thickets. When possible, GPS collar data was used to determine date of death, with first wolf location within 300m of the carcass site presumed to represent date of death. Remaining sites were aged based on amount of the carcass consumed and level of degradation of the remaining tissue. Reconxy PC900 game cameras (Reconyx, Holmen, WI, USA) were mounted one to ten meters from site center on trees, at heights ranging from from 0.5 to 1.5 meters off the ground. The cameras were set either in default mode (a burst of three photos at a rate of one/second when triggered, followed by a one-second recovery), or in near-video mode (continuous photos at a rate of one/second while sensing movement). This difference was not relevant for the calculation of results. Any dispersed carcass pieces were aggregated in the target zone of the camera. In all but one case, camera deployment occurred after initial abandonment by wolves.

As part of the long-term wolf monitoring procedure, DNPP staff deployed and maintained 1-3 GPS collars on wolves in each wolf pack that occurred in the study area, generally on breeding animals. Wolves were darted from helicopters, immobilized with Telazol, and fitted with Telonics GPS collars (Telonics, Inc, Mesa, AZ, multiple models; see Meier et al. 2009 for protocol details). Wolf collar fix intervals varied between four and 24 hours. Capture and handling procedures for wolves and coyotes were approved under National Park Service (NPS) IACUC protocol "AKR_YUCH and DENA_Burch_Wolves_2013." These data were used to generate wolf utilization distributions (see below).

*Photo coding*

Each photo was coded for species and number of individuals present using Timelapse2 Image Analyzer software (Greenberg & Godin, 2015, available at http://saul.cpsc.ucalgary.ca/timelapse/.). Because group size varies among packs and may affect risk levels at carcass sites, we distinguish wolf groups (more than one individual) from lone wolves. We use the term "group" rather than "pack" because "pack" refers to the entire social assemblage, but pack members often split off into sub-groups which travel separately from the main body and many such sub-groups were recorded on camera (Benson & Patterson, 2015; Metz et al., 2011). Behavior of each individual was coded as “feeding,” “vigilant,” or “other.” “Feeding” was defined as having any food in the mouth, biting or chewing on the carcass, or being positioned in such a way as to be immediately able to do so (head down, mouth at carcass). “Vigilant” was defined as having the head up, ears erect, and gaze directed outward or upward (Atwood and Gese 2008). “Other” covered all other behavior, including moving around the general area, interacting with conspecifics, or indeterminate. Photos were grouped into "visits," which we defined as beginning when a carnivore appeared on camera and ending at the last photo of that carnivore which was followed either by the subsequent appearance of a different species, or by a gap of 60 minutes or greater until the appearance of the same species. A given visit thus could contain gaps in time when the animal was not on camera, provided that the gaps did not exceed 60 minutes. Sixty minutes was chosen to help ensure independence of visits, and is typical compared to other camera-trap studies of carnivores (Burton et al. 2015). Both wolves and wolverines are known to remain near carcasses even when not actively foraging (Wright and Ernst 2004; Mech 2011); 60 minutes should represent sufficient time for these species to have engaged in some alternate behavior state (sleeping, caching, traveling) before returning to feed again. Because we were unable to deploy cameras at fresh carcasses in the summer due to limited access and the presence of bears on the landscape, we truncated data to be used for analysis at May 1st of the year, the median date of bear appearance on camera.

*Analyses*

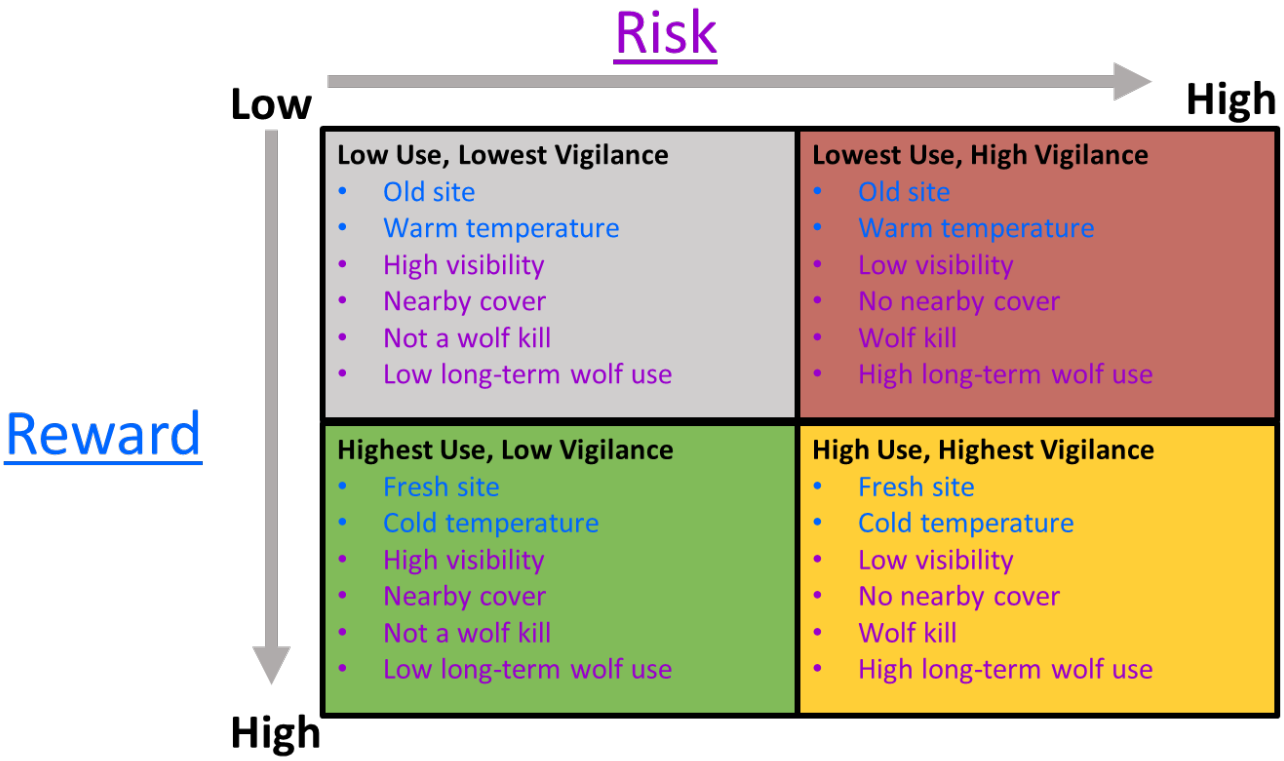
We decomposed the concept of carcass use into three measurable response variables: (1) presence or absence at a site, (2) number of visits made to a site, (3) duration of visits at a site. Duration of a visit was calculated as the total time in minutes of the visit, with visits of less than one minute rounded to one. We measured vigilance as the proportion of time an animal exhibited vigilance behavior while on camera, with each photo representing one second of time. In the case of multiple animals on camera, behavior proportions were calculated out of total animal-seconds. For example, a photo of three wolves in which two were feeding and one was vigilant contributed three animal-seconds to the total, two of which were classified as feeding and one of which was classified as vigilant.

We then created four general linear models to examine how characteristics of the carcass site affected each of the three carcass use metrics and vigilance behavior. We grouped these attributes into three categories: (A) caloric need and reward (with temperature as a proxy for caloric need), (B) visual obstruction and escape ability, and (C) factors which might affect the probability of encountering another carnivore (Table 2-1). Wolf utilization distributions (one element of probability of encounter) were generated using the *kernelUD* function from the package adehabitat (Calenge 2007). Kernels were generated for each pack using the adhoc method for determining reference bandwidth, and a bivariate normal distribution. If a site had a non-zero UD value from multiple packs, the values were summed.

Figure 2-2 outlines the expected effects of our predictor variables on carcass use and vigilance levels in a risk-reward balance framework.

Table 2-1. Description of predictor variables used in models of scavenging activity and vigilance at carcass sites. Mean values, with the range of values in parentheses, are shown for each variable.

| **Predictor Variables** | **Mean (Range) of Values** | **Description** |
|---|---|---|
| *Caloric Need and Reward* | | |
| Age at deployment | 18 (1-103) days | Age of the kill in days (day 0 being day of the kill) on the first day the camera was deployed. Measure of site freshness at deployment and thus of the time window captured by the camera. |
| Site age | 46 (1-169) days | Age of the kill in days (day 0 being day of the kill) on the day of the visit by an animal. Measure of site freshness during each visit. |
| Temperature | -11 (-24 – 5) °C | Lowest temperature for the date of visit, degrees Celsius, as recorded at the NOAA weather station at DNPP Headquarters. A proxy for caloric need. (https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00505778/detail) |
| *Visual Obstruction & Escape Ability* | | |
| Vegetation | 61 (0-115) % | The sum of percent shrub cover and percent tree cover within a 10m radius of the kill site. Proxy for visual obstruction. |
| Distance to cover | 6 (0-30) m | Distance (m) to nearest object that could provide substantial visual cover for an animal of coyote size. |
| *Encounter Risk* | | |
| Origin of carcass | - | Cause of death of ungulate (wolf kill, natural death, unknown) |
| Long-Term Wolf Use | 8.7e-10 (0-3.0e-09) | Value of wolf utilization distribution for the carcass site, generated for the winter season (Oct – April) of that year, summed across packs where applicable. |
| Duration of visit | 32 (1-477) | Duration (minutes) of the visit. This variable was included only in the model of vigilance proportion while on camera. |



| | |
|---|---|
| **Low Use, Lowest Vigilance**<br>• Old site<br>• Warm temperature<br>• High visibility<br>• Nearby cover<br>• Not a wolf kill<br>• Low long-term wolf use | **Lowest Use, High Vigilance**<br>• Old site<br>• Warm temperature<br>• Low visibility<br>• No nearby cover<br>• Wolf kill<br>• High long-term wolf use |
| **Highest Use, Low Vigilance**<br>• Fresh site<br>• Cold temperature<br>• High visibility<br>• Nearby cover<br>• Not a wolf kill<br>• Low long-term wolf use | **High Use, Highest Vigilance**<br>• Fresh site<br>• Cold temperature<br>• Low visibility<br>• No nearby cover<br>• Wolf kill<br>• High long-term wolf use |

Figure 2-2. Expected relationship between environmental factors dictating risk (shown in purple) and reward (shown in blue) at carcass sites, and the associated use intensity and vigilance behavior of scavengers.

To test for evidence of temporal risk mediation, we compared the gap time between visits of different species in two ways: across species pairs and by the log-ratio of the body-weight of the two species. The average body mass of each species was calculated from capture records of wolves and coyotes in DNPP and published estimates from Alaska when available (Table S2-1). We restricted this analysis to gaps of less than 48 hours because we assumed the second species was most likely able to detect the presence of the first species during this time window. To examine temporal risk mediation over the diel cycle, we calculated the degree of temporal overlap between each species using the methods described in Ridout & Linkie (2009), as implemented by the *overlapEst* function in the R package *overlap* (Meredith and Ridout 2017). We used the scavenging visit as the unit, defined by time at beginning of the visit. We used the estimator Dhat1 as indicated for small sample sizes. We calculated bootstrapped confidence intervals for the coefficient of overlap with 10000 samples. In interpreting the coefficient of overlap we follow Linkie and Ridout (2011) and Lynam et al. (2013) in considering "high" overlap to be values ≥0.8, and we consider values ≤ 0.4 to be "low," with the intervening range considered "moderate." Finally, we calculated the average and coefficient of variation of return intervals (time between visits) for each species to estimate how frequently each species returned to carcasses and how predictable their visits were (i.e., if variation in return intervals was low or high).

We used generalized linear models (GLMs) for all analyses other than time overlap (Table 2-2). We initially fit each as a mixed model with carcass site as a random effect, then checked the intraclass correlation coefficient (ICC, Koch, 2004) to determine if the random effect was necessary. In all cases ICC values were at or extremely near zero, which indicated that samples from within sites were no more similar than samples between sites, so we proceeded with a fixed-effect modeling framework. Camera duration (the number of days that the camera was out and functioning) was included as a fixed effect in the model of species presence and included as an offset in the model of number of visits to account for differing lengths of camera deployment. Species was included as a four-level categorical predictor in the three carcass use models and the vigilance model, and interaction terms between "species" and the other variables, excluding camera duration, were included to examine species-specific responses. Wolf group and wolf kill were set as the reference levels for species and origin of the carcass because they were generally the most abundant. Continuous variables were scaled to a mean of zero and standard deviation of one to assist in model convergence.

Proportional data, such as our vigilance measures, can be difficult to model, particularly when the data include zeroes and ones (Bolker et al. 2009). Following Warton and Hui (2011), we adjusted values of zero to 0.006, which corresponded to the smallest non-zero proportion in our data, and values of one were correspondingly adjusted to 0.994. This adjustment may bias coefficient values slightly towards no effect (Warton and Hui 2011), so our vigilance model should be viewed as conservative. We present complete model specifications in Table 2-2. Adequacy of model fit was assessed using Q-Q plots, examining plotted residuals, and R-squared values. Analyses were done in program R (ver. 3.4.3) using packages lme4 and glmmTMB (Bates et al. 2015; Brooks et al. 2017; R Core Team 2017).

Table 2-2. Model specifications for models of scavenging use, behavior while scavenging, and gap time between visits. All models were generalized linear models.

| **Response variable** | **N** | **Distribution family** | **Link** | **Predictor variables** |
|---|---|---|---|---|
| Presence/ absence | 155* | Binomial | logit | camera duration + species*carcass age + species*vegetation + species*origin of carcass + species*long-term wolf use |
| Number of visits | 84** | Negative Binomial | log | Offset(log(camera duration)) + species*carcass age + species*vegetation + species*origin of carcass + species*long-term wolf use |
| Duration of visits | 407 | Negative Binomial | log | species*site day + species*temperature + species*vegetation + species*distance to cover + species*origin of carcass + species*long-term wolf use |
| Proportion time vigilant on camera | 407 | Beta | logit | species*site day + species*temperature + species*vegetation + species*distance to cover + species*origin of carcass + species*long-term wolf use + species*duration of visit |
| Gap time between visits | 95 | Gamma | log | A: species pairing<br>B: log-ratio body size |

*5 species categories by 31 sites. **For this analysis, number of visits was tabulated only for those species which had appeared at a site.

## Results

We collected 50,881 photos of the four carnivore species (wolves, wolverines, coyotes, and red foxes) over 1,472 camera-days from 31 carcass sites, comprising 17 wolf kills, six natural deaths, and eight sites with unknown cause of death. At no time were two species of carnivore present in the same photo. Carcasses were primarily moose ($n$ = 27) with the remainder caribou ($n$ = 3) and Dall sheep ($n$ = 1) (see Table S2-2 for carcass site summaries). Wolf killed carcasses were estimated to have an average of 13%(SD = 24%) biomass remaining at camera deployment; natural death carcasses 37%(SD= 28%), and unknown origin 0.5%(SD = 0.5%). Lynx (*Lynx canadensis*) were captured on camera only 4 times and did not appear to be scavenging; thus they were excluded from analysis. Grizzly bears (*Ursus arctos*) only appeared in the late spring and were not active during the majority of camera deployments and thus were excluded from analysis. Avian scavengers including ravens (*Corvus corax*), gray jays (*Perisoreus canadensis*), and American black-billed magpies (*Pica hudsonia*) were recorded scavenging; however their group sizes were small (typically only one to three birds at a time), unlike reports from lower latitudes (eg Kaczensky, Hayes, & Proberger, 2005; Stahler, Heinrich, & Smith, 2002; Vucetich, Peterson, & Waite, 2004). Because their effect as competitors to mammalian scavengers was relatively minimal and their risk-reward balance likely differs substantially due to their ability to fly, they were also excluded. We identified one outlier: a fox made 34 visits to one site, ten higher than the next highest number in the dataset and roughly five times higher than the grand mean, which obscured the ability to examine general trends. To avoid having to exclude the entire site, we changed this value to the mean number of visits made by foxes as calculated without the outlier (six visits) when modeling number of visits. Complete model results, including results with the outlier included, are presented in supplementary material (Tables S2.3-S2.7).

### *Utilization of Carcass Sites Across Species*

Wolves and wolverines were approximately twice as likely as coyotes and foxes to use a carcass site at least once (Figure 2-3, Table S2-3). At visited sites, wolverines made approximately twice as many visits to carcass sites as wolves and foxes, and over three times as many as coyotes (Figure 2-3, Table S2-4). Duration of visits were longest for wolf groups, and shortest for coyotes (Figure 2-3, Table S2-6). Wolverines dedicated roughly one-third less time to vigilance than the other species (Figure 2-3, Table S2-7). Although percent of time feeding was variable, on average wolf groups dedicated the most time to feeding (41%, SD = 26%), followed by wolverines (34%, SD = 31%), lone wolves (23%, SD = 30%), coyotes (18%, SD = 28%), and foxes (16%, SD = 24%).

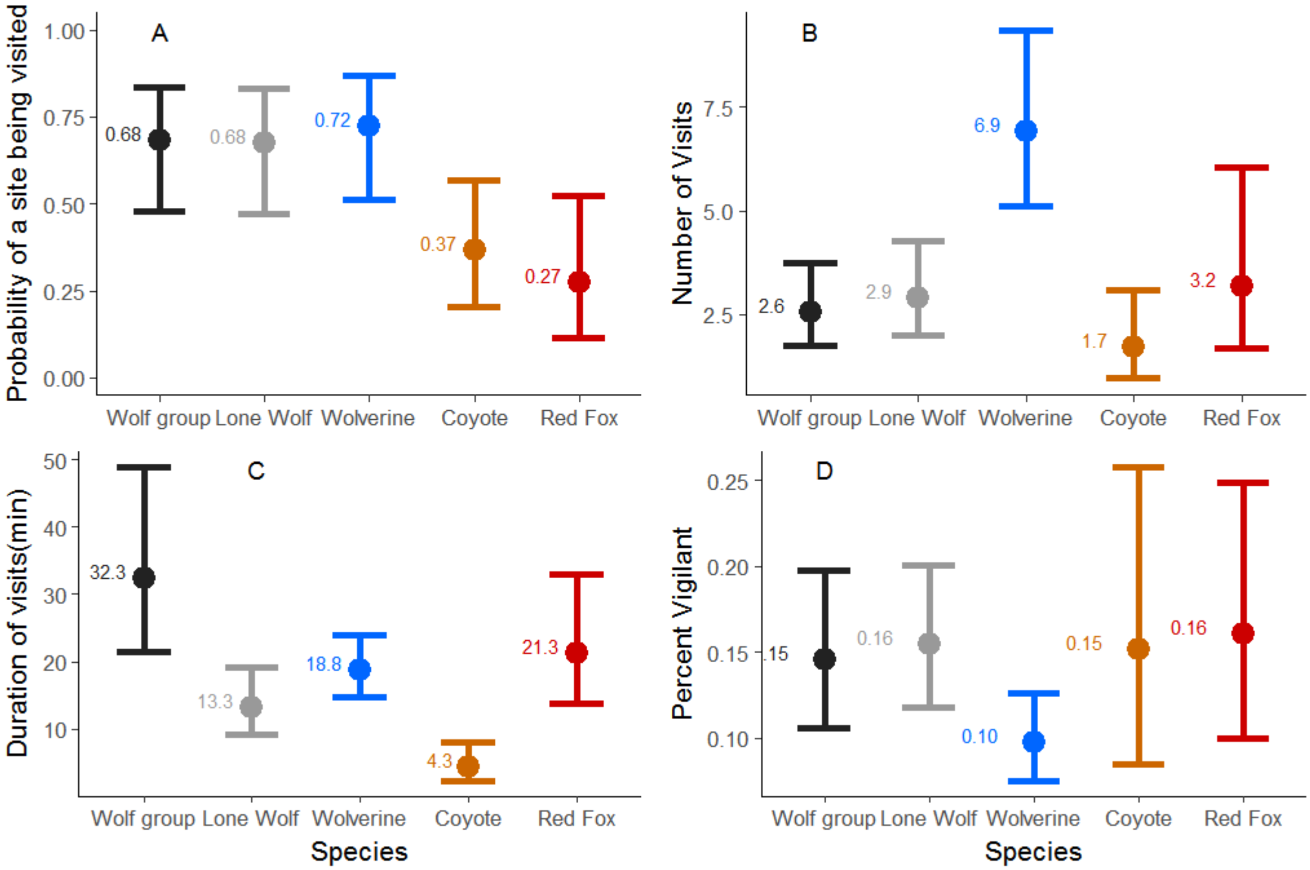


Figure 2-3. Estimates of three metrics of carcass use and of vigilance behavior across four species of scavengers (wolves split by group size) at wintertime carcass sites in Denali National Park, Alaska, derived from generalized linear models incorporating information about the carcass sites (see

Methods; Tables S2-3 – S2-7). (A) probability of a site being visited; (B) number of scavenging visits; (C) duration of scavenging visits; (D) percent of time vigilant. Error bars show 95% CI.

### *Effect of Site Characteristics on Use and Vigilance*

Origin of the carcass had strong effects on use, with natural death carcass sites having the highest number of visits, duration of visits, and vigilance behavior for most species (Figure 2-4). Long-term wolf use also had strong effects that varied by species (Figure 2-5). Most of the instances of mesocarnivore scavenging were observed in the lower 50% of long-term wolf use values. Increases in age of the carcass site and temperature generally decreased carcass use or had no effect. Vegetation around the site mostly had no effect on use, with some instances of decreasing use with increasing cover (Tables S2.1-S2.7). Distance to cover also had generally no effect on use, with some instances of increasing use as distance increased (Tables S2.1-S2.7). Vegetation and distance to cover overall had the weakest and most inconsistent effects on carcass use and vigilance (Tables S2.1-S2.7).

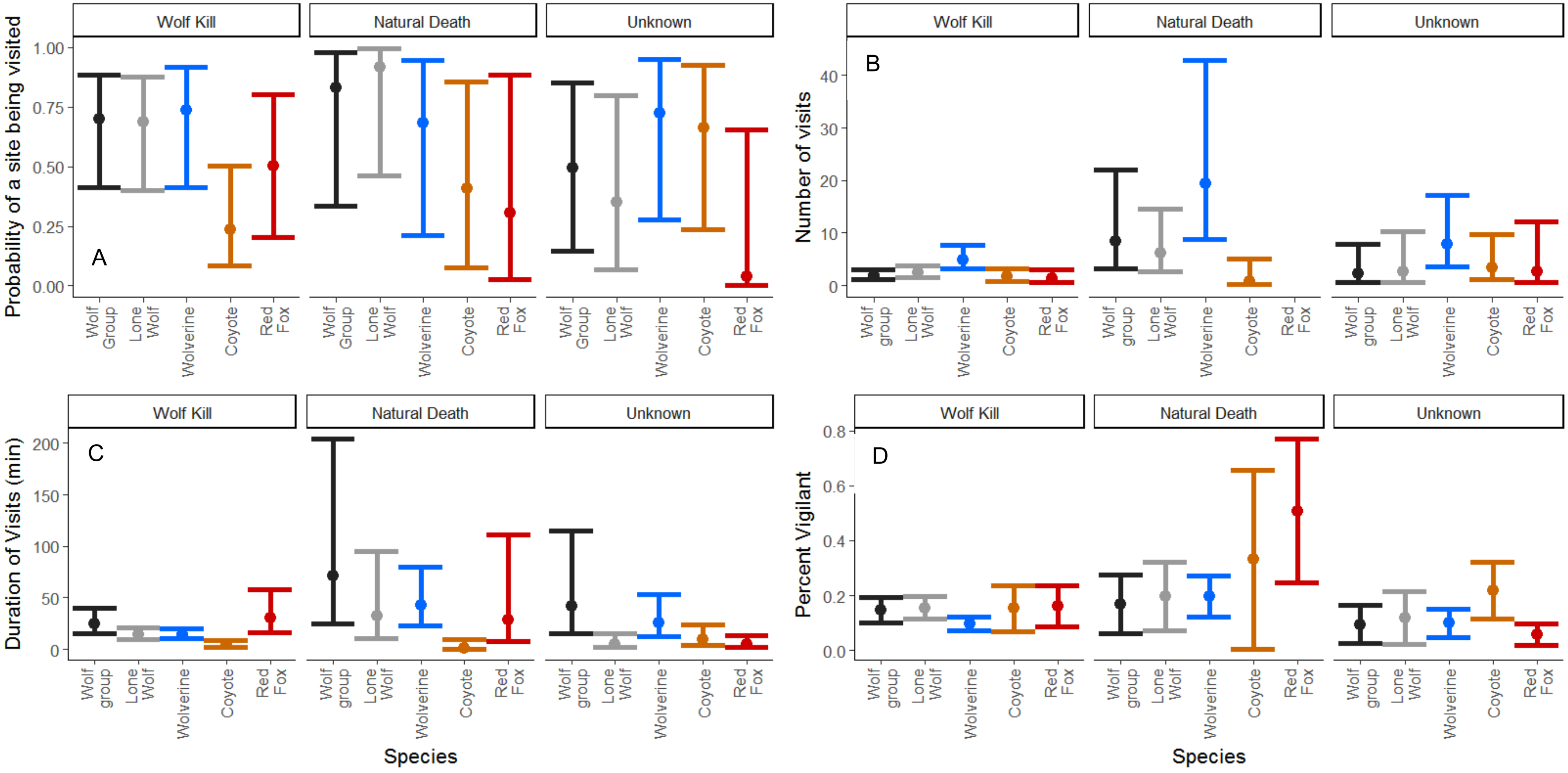


Figure 2-4. Effect of origin of carcass site on three measures of carrion use and vigilance behavior for four scavenging species at wintertime carcass sites in Denali National Park, Alaska, derived from generalized linear models incorporating information about the carcass sites (see Methods; Tables S2.3 – S2.7). (A) probability of a site being visited; (B) number of scavenging visits; (C) duration of scavenging visits; (D) percent of time vigilant. Error bars show 95% CI. Because red foxes visited only a single natural death carcass site, the variability

of the estimate for number of visits at that site type was an order of magnitude higher than for any other species, leading us to omit that estimate as unreliable.

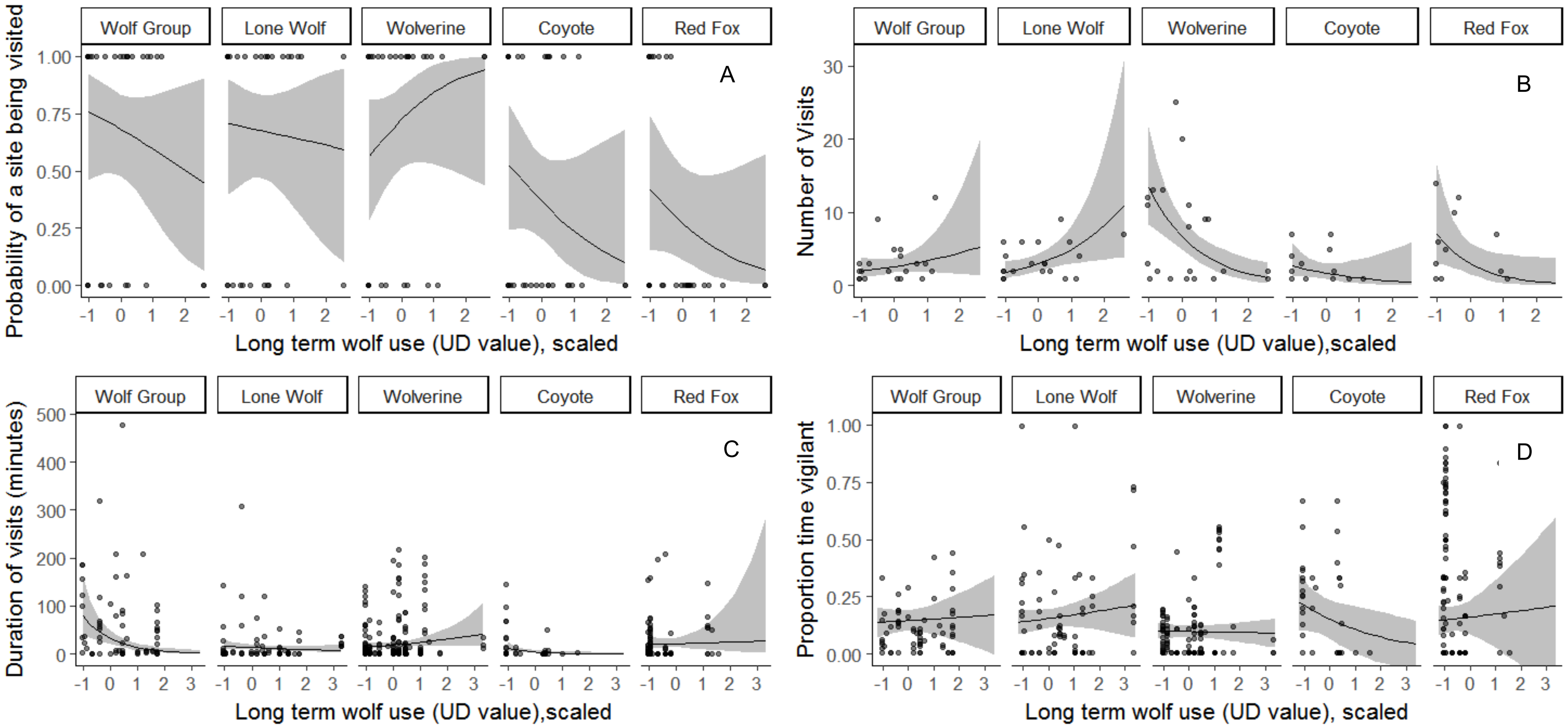


Figure 2-5. Effect of long-term wolf use at carcass location (measured as a value of the combined utilization distribution of multiple packs, scaled) on three measures of carrion use and vigilance behavior, for four scavenging species at wintertime carcass sites in Denali National Park, Alaska, derived from generalized linear models incorporating information about the carcass sites (see Methods; Tables S2.3 – S2.7). (A) probability of a site being visited; (B) number of scavenging visits; (C) duration of scavenging visits; (D) percent of time vigilant. Shading represents 95% CI.

### *Temporal Risk Mediation*

A comparison of gap time between visits of different species showed no differences by species pairing, by size ranking of the species in the pair, or by the log-ratio of body size. (Figure 2-6, Tables S2.8, S2.9, Figure S2-2).

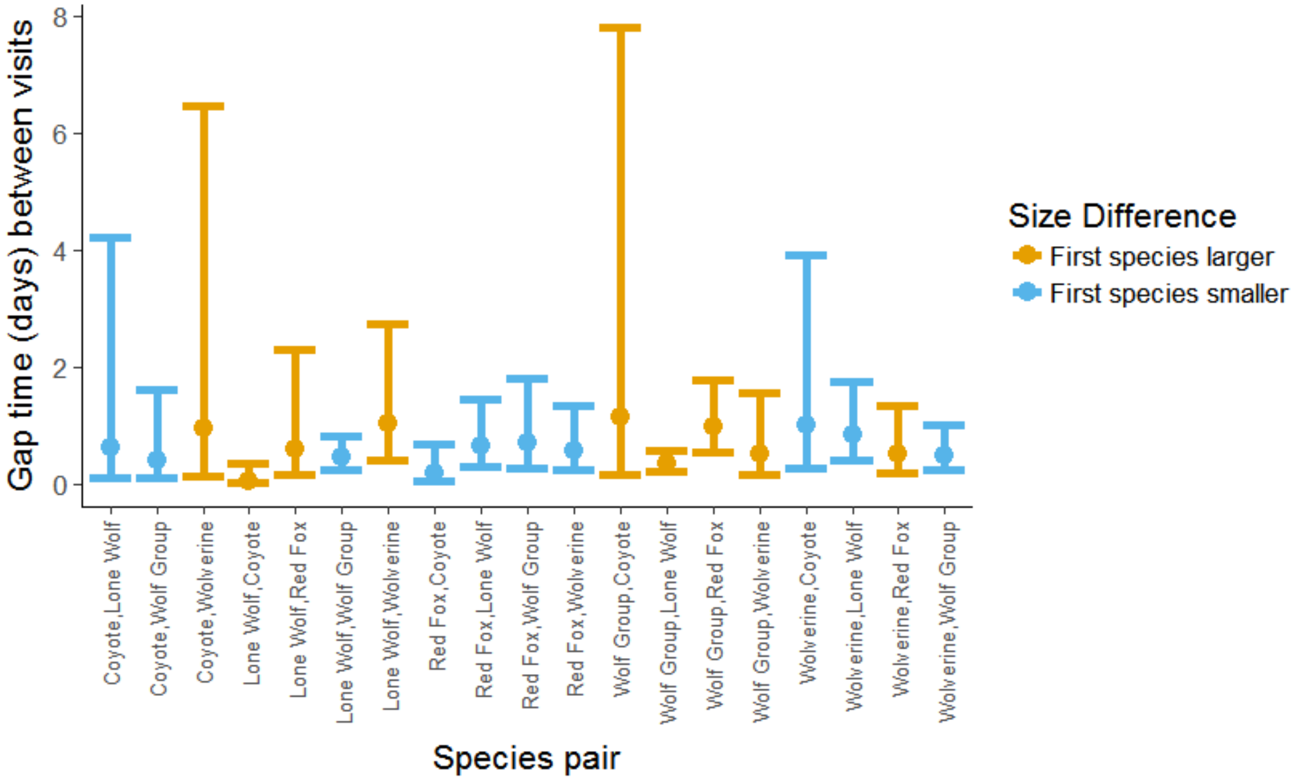


Figure 2-6. The gap time in days between subsequent visits of different scavenging species to the same carcass. Analysis was restricted to gaps of less than 48 hours. Species body mass was taken from published records and Denali National Park and Preserve capture records. Error bars show 95% CIs.

All species showed a high or moderate degree of temporal overlap with one another (Table 2-3). The highest overlap was between wolverines and wolves, alone or in groups. Coyotes and red foxes showed noticeably lower overlap than any other pair, but their overlap was still moderate (Figure 2-8). Red foxes showed the strongest diel pattern, appearing to be almost entirely crepuscular/nocturnal, and all species except coyotes showed a dip in activity between approximately 12:00 and 18:00 (Figure 2-7). A post-hoc comparison between coefficient of overlap and log-ratio of body size showed no significant relationship (linear model, $p = 0.79$, $R^2 = 0.009$, $n = 10$).

Table 2-3. Temporal overlap values, 95% CIs, and overlap classification for pairs of scavenging species.

| Species Combination | Coefficient of overlap | 95% CI | Degree of Overlap |
|---|---|---|---|
| Coyote - Red Fox | 0.56 | 0.41-0.71 | moderate |
| Lone Wolf - Red Fox | 0.72 | 0.60-0.83 | moderate |
| Wolf Group - Red Fox | 0.72 | 0.60-0.84 | moderate |
| Wolverine - Red Fox | 0.74 | 0.64-0.84 | moderate |
| Wolverine - Coyote | 0.78 | 0.65-0.90 | moderate |
| Lone Wolf - Coyote | 0.79 | 0.65-0.91 | moderate |
| Wolf Group - Coyote | 0.82 | 0.67-0.94 | high |
| Wolf Group - Lone Wolf | 0.87 | 0.77-0.96 | high |
| Wolf Group - Wolverine | 0.91 | 0.83-0.99 | high |
| Lone Wolf - Wolverine | 0.93 | 0.85-1.0 | high |

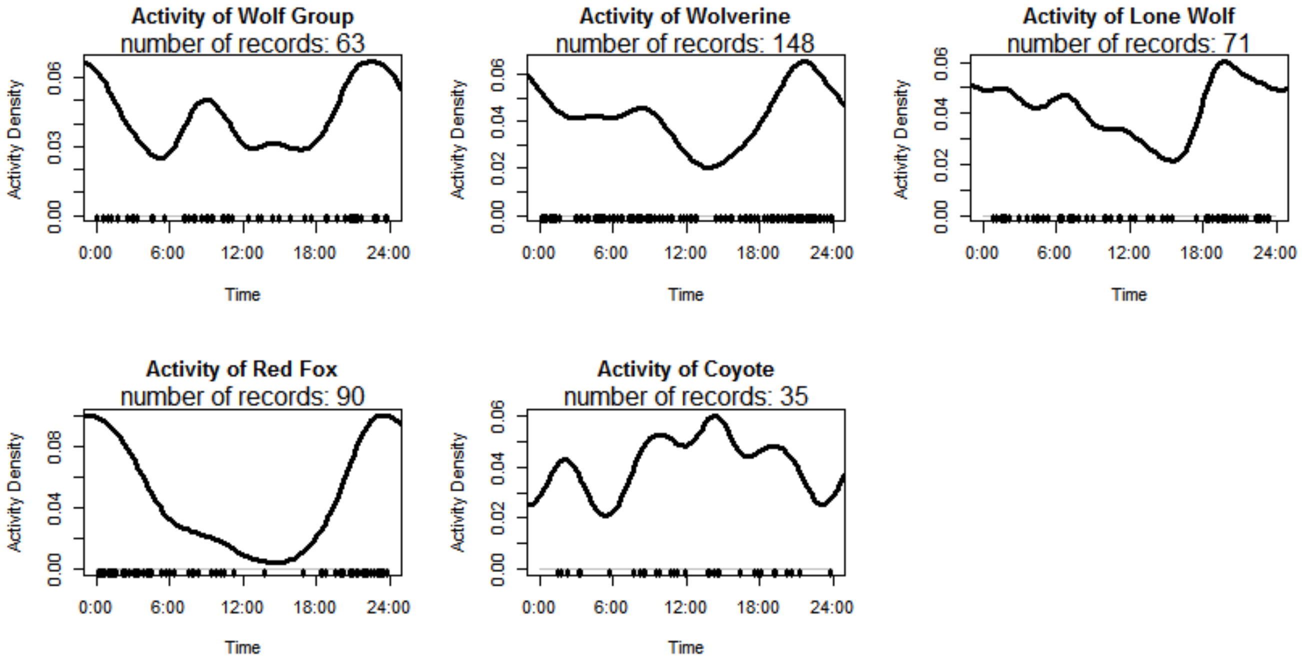


Figure 2-7. Diel patterns of activity of four scavenging species (wolves separated by group size) at wintertime carcass sites in Denali National Park and Preserve, Alaska. Tick marks along the x-axis (rug values) indicate carcass site visits as captured by trail cameras.

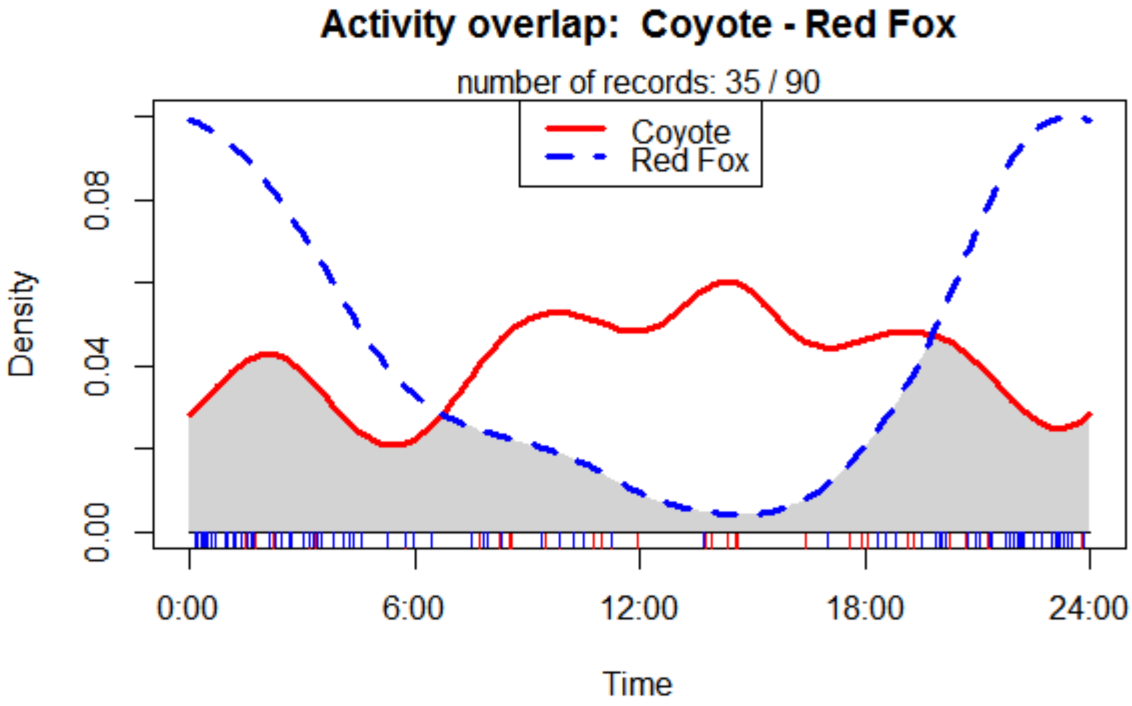


Figure 2-8. Diel patterns of activity of coyote (solid red line) and red fox (dotted blue line) at wintertime carcass sites in Denali National Park and Preserve, Alaska. Shaded area indicates overlap, and tick marks along the x-axis (rug values) represent scavenging visits as captured by trail cameras.

### *Return Interval*

Return interval varied by species, with coyotes having the longest (12.7 days) and red foxes the shortest (2.5 days; Table 2-4). Return intervals were unpredictable for all species, with coefficients of variation >100% for all species (Table 2-4).

Table 2-4. The average return interval (time between visits) at wintertime carcass sites, CI, CV, and *n* of four mammalian scavengers.

| Species | Return Interval (days) | 95% CI | Coefficient of Variation | N |
|---|---|---|---|---|
| Wolves | 5.6 | 3.8 – 7.7 | 183 | 111 |
| Wolverine | 3.5 | 2.4 – 4.6 | 197 | 127 |
| Coyote | 12.7 | 7.8 – 19.2 | 105 | 23 |
| Red Fox | 2.5 | 1.8 – 3.4 | 153 | 79 |

## Discussion

Our findings reveal a pattern of high use of carcass sites and less time dedicated to vigilance by wolves and wolverines, somewhat lower use by foxes, and very low use by coyotes. Origin of the carcass, long-term wolf risk, and site age had the overall greatest effects on carcass use and vigilance, which sheds light on what factors are most important to the risk-reward balance of these scavengers. Overall, scavengers in this system appear to mediate risk primarily by altering their presence and use of carrion rather than through vigilance behavior or temporal partitioning. The high use by wolves and wolverines and low use by smaller species supports our hypothesis that carcass sites are subject to guild-wide competition and therefore risky to scavengers. This evidence of competition suggests reframing carrion's status as a trophic resource, and allows for a better determination of how much benefit different species are able to enjoy from carrion, and how the presence of large carnivores affects competition for carrion.

When comparing use and vigilance across scavengers, wolverines stood out as dominant among the mesocarnivores. Their high numbers of visits combined with their relatively high duration of visits and shorter return intervals allowed them to take extensive advantage of carrion resources. The heavy use of carcasses by wolverines is in accordance with published data indicating that wolverines are accomplished scavengers (Dijk, Andersen, et al. 2008; Mattisson et al. 2011). Counter to our predictions, their limited vigilance implies that they do not view wolves or any other carnivore species as a serious threat, despite the frequent presence of wolves at the carcass sites and documented instances of wolves killing wolverines (Palomares and Caro 1999; White et al. 2002). Their use pattern of carcass sites supports the hypothesis that the wolverine population may track the wolf population more closely than other mesocarnivores do based on their heavy use of this resource (Dijk, Gustavsen, et al. 2008). Caching behavior was evident on camera, and it is likely that individual wolverines often remained in the general area of the carcass for hours or days at a time. The tendency of wolverines to dominate the activity at carcass sites, combined with their fearless nature, suggests that wolverines could be as much or more of a limiting factor for coyote and red fox use of carrion than wolf presence, despite wolverines' low population densities.

The other two mesocarnivore species showed much lower use of carcass sites than wolverines. Coyotes showed the lowest use of all species and had the highest return interval, indicating that one visit was not likely to be followed up by another for nearly two weeks on average. This low level of carrion use differs from that recorded in lower latitudes in North America (Paquet 1991; Merkle et al. 2009). It also contrasts with a concurrent (2013-2014) study in Denali National Park and Preserve (DNPP) which found that coyotes had substantial amounts of ungulate hair in their scats, presumably from scavenging (Sivy, Pozzanghera, Colson, et al. 2017). This discrepancy is puzzling, as our cameras only recorded a total of ten minutes of actual feeding by coyotes. We suggest several hypotheses: first, caching behavior by coyotes could have extended presence of carrion in the scat. Alternately, coyotes could have been targeting carcass conditions poorly represented in our study, such as the period immediately after abandonment, or very fresh natural deaths. Finally, other ecological factors could have led to a general decrease in coyote scavenging from 2013-2017, such as variable prey base or winter severity. Our results highlight the need for additional research directly linking observed scavenging behavior with subsequent scat analysis.

Foxes seemed to fall somewhere in the middle of use spectrum: they were the least likely to appear at a site, so their net consumption of carrion was limited, but once at sites they had comparable use and vigilance levels as wolves and wolverines. They also had the shortest return intervals, indicating frequent use of carcass sites after discovery. Analysis including the fox outlier (high number of visits) showed no difference in overall trends other than increased variance driven by the unusually high representation of the characteristics of that site. The low number of carcass sites at which foxes appeared stands in contrast to findings in Europe, which reveal red foxes to be one of the most prolific scavengers in that region, visiting upwards of 80-90% of carcasses (Scholten, 2012; Selva, 2004; Wikenros, Ståhlberg, & Sand, 2014), although these studies do report foxes displaying levels of vigilance comparable to our data. The low use of carrion by coyotes and foxes could be explained by high risk levels at carcass sites for these species, and suggests that coyotes and foxes may perceive carcass sites to be riskier than has previously been documented in other systems. More research is needed to resolve the ecological or behavioral factors driving differences between our findings and other studies.

The regular visits to and sometimes extensive use of carcass sites by wolves even after initial abandonment, though routinely acknowledged in passing (Vucetich et al. 2004; Selva et al. 2005; Metz et al. 2011), has not been well quantified, and the variation in published work suggests further research and more standardization of methods is warranted. Most studies found or implied a comparable rate of wolf (re)visitation to carcasses as our study found, although differences in methods made comparisons of overall carcass use difficult (Palm 2001; Jędrzejewski et al. 2002; Selva 2004; Nordli and Rogstad 2016). However, some studies indicated a much lower use of carcass sites by wolves, suggesting that further research is needed to identify the factors determining wolf scavenging patterns (Sand et al. 2008; Cortés-Avizanda et al. 2009; Wikenros et al. 2013). In our study, wolves spent more time on camera than the other scavenger species (~60% of all photos), driven largely by the extended duration of visits by groups of wolves; a finding that clearly identifies them as active players in the scavenging arena. Long visits by wolf groups generally represented visits by packs that seemed to have settled in, with individuals coming and going from the carcass for a number of hours. Previous studies suggested that by smoothing out the annual distribution of carrion, wolves ultimately increase the carrion available to scavengers on a yearly basis (Wilmers, Crabtree, et al. 2003; Wilmers and Getz 2004). However, these studies did not take into the account the subsequent effect of wolves as competing scavengers. Our data suggest that wolves reduce the availability of carrion resources to mesocarnivores in the sub-arctic by successfully competing with them for carrion and causing carcass sites to be high-risk, and that this influence has the greatest effects on foxes and coyotes and the least influence on wolverines.

Origin of the carcass, long-term wolf use, and carcass age were the most consistently important attributes affecting scavenger use and behavior. Vegetation and distance to cover had mostly weak and inconsistent effects by comparison, suggesting they do not strongly influence scavenger behavior in this system – a finding which contrasts to similar studies in Europe (Wikenros et al. 2014). We had expected wolf kills to be used most heavily because they were already known to the wolves, and because wolf kills generate sounds and odors which can be readily detected by scavengers (Wilmers, Stahler, et al. 2003; Wilmers, Crabtree, et al. 2003). Instead we found that natural death carcass sites received greatest use by all species except coyotes. We hypothesize that high use of non-predated carcasses occurs because these carcasses have more to offer the scavengers who discover them, unlike wolf kills which are mostly consumed prior to abandonment. In addition, non-predated carcasses typically freeze before discovery by scavengers, meaning additional time is necessary for scavengers to consume them. The fact that even wolves spent the most time at natural death sites means they could potentially monopolize the caloric benefit from not only their own kills, but from other carcasses as well (Haber 1977). Natural death sites, with their high use, were also generally associated with higher vigilance by the mesocarnivores, offering some evidence of behavioral risk-mediation at high-activity sites.

The intensity of wolf activity on the landscape (i.e., long-term wolf use) had strong but variable effects on scavenging activity. The somewhat non-intuitive finding that wolf use of carcass sites was not universally higher within core areas of wolf activity might be explained by the fact that these sites were in frequently traveled areas and were therefore quickly consumed and of little extended interest. Wolf use intensity of the area also had mixed effects on wolverine use of carcasses. Wolverines were far less likely to repeatedly visit carcasses in the core of wolf home ranges, but the likelihood of at least one visit was actually higher and duration of visits longer in wolf core activity areas. This pattern may represent an increase in feeding intensity by wolverines due to the higher risk of the site. The strong decrease in use by coyotes and foxes in response to long-term wolf use is consistent with a pattern in which coyotes and foxes must mediate wolf risk when scavenging. Also, most observations of coyotes and foxes fell within the lower half of the range of observed long-term wolf use values, indicating that sites in core wolf areas may be functionally off-limits altogether to those species.

Optimal foraging theory predicts that resource use should decline as the marginal gains from foraging decrease (Charnov 1976). Indeed, we found that carrion use tended to decrease as sites aged. Also as predicted, the effect of higher temperatures, when significant, was to decrease scavenging activity in almost all cases. However, neither age nor temperature showed the consistent strong trends that we had expected, given how much these factors influence availability at the site and the incentive to eat it (Selva et al. 2005). However, food availability did not steadily decrease with age at several sites due to environmental conditions that temporarily affected access to the carcass, such as overflow and snow drifting. Thus, linear time may not be as consistent a proxy for caloric availability as we assumed. Direct measurement of carcass biomass is advised to better address the relationship between use and available biomass.

We found no evidence of temporal partitioning by any species. Our data indicate that the presence of other scavenging species at a site in the previous 48 hours does not impact how long a second scavenger will wait to approach the carcass. However, even within the restriction to gaps of 48 hours or less, the average gap was still 14 hours, suggesting that the overall low encounter rate could have resulted in limited cases where a scavenger arrived at a carcass soon enough after the previous visitor for it to matter. Alternately, an initial approach followed by the decision not to visit a carcass could happen outside the limited field of view of the camera. The fact that most species had very similar activity patterns throughout the day indicates that temporal partitioning was not a primary mechanism of competition avoidance at carcass sites. It is interesting to note, however, that in this and several other elements of the analysis (such as use of carcass types), the greatest differences appeared between coyotes and foxes, which ecologically speaking may be the closest competitors among the four species (Sargeant et al. 1987; Harrison et al. 1989; Gosselink et al. 2003; Levi and Wilmers 2012).

Low densities of all mesocarnivore species combined with a relatively small sample size of carcasses could have skewed results if not all carcasses were discovered by all species, though this seems unlikely given the extended monitoring periods. Wintertime wolf density in the study are during this time ranged from 2.76 to 4.73 per 1000km$^2$, somewhat lower than historic averages (National Park Service Annual Reports, available online). Long-term data for mesocarnivore density in this area are limited, but coyotes were estimated at roughly 14 per 1000km$^2$, foxes at 15 per 1000km$^2$, and wolverines at 9.5 per 1000km$^2$ (Alaska Department of Fish and Game 2015; Pozzanghera 2015; Prugh unpublished data).

Low mesocarnivore population density was driven in part by the relative scarcity of small mammal prey, a factor we were not able to directly incorporate. Snowshoe hares were at the lowest part of their cycle during the study period, while vole populations fluctuated (Sivy, Pozzanghera, Colson, et al. 2017; Schmidt et al. 2017). The effect that a dramatic increase in small prey base (and thus mesocarnivore populations) could have on scavenging activity is difficult to predict – it could result in decreased scavenging by virtue of food switching, or it could boost the mesocarnivore populations and ultimately increase the pressure to scavenge as competition for prey increases (Needham et al. 2014; Mattisson et al. 2016). Higher population densities could also result in higher rates of intra- and interspecific encounters, and consequently we might expect temporal partitioning to play a larger role under these circumstances. Further work during other phases of the hare cycle, when mesocarnivore populations are higher, could shed light on the role of scavenger densities in mediating activity levels and behaviors at carcass sites.

The extended nature of our camera deployments (up to one year) allowed us to document continuing activity at the sites which stretched on for months at levels higher than comparable random sites (L. Prugh, unpublished data). During our analysis period, 43% of visits were three minutes or less, with 33% of all visits being one minute or less. A similar trend of short visits continued into the spring and summer. Thus activity persisted well after the edible components were gone, sometimes through multiple seasons. This raises the question of the utility of an animal continuing to "check on" a site even when no significant feeding is attempted or possible. One hypothesis is that the sites function as social "signposts." We observed repeated scent marking by multiple species beginning at the time of the kill which continued for extended periods, possibly functioning as an informational attractant even after edible material was gone. Another hypothesis was hinted at by a particular site in which a freshly-abandoned wolf kill, with plenty of edible material remaining, was almost entirely encased in rapidly-generated overflow ice. The ice covered the carcass for over a month, during which time both wolves and wolverines visited the site without successfully feeding. As the warmer temperatures of March began to weaken the ice, the wolves and wolverines returned and were able to excavate the carcass and feed. Situations like this in which the passage of time does not denote a decrease in available food could function as sufficiently strong intermittent re-enforcement to result in continued checking of old sites. In either case, the continued activity indicates that carcass sites have the potential to structure animal behavior, interspecific encounter rates, and communication beyond their span as food items.

## Conclusion

Our findings indicate that a framework in which apex predators are situated as providers of carrion and mesocarnivores as benefactors is not appropriate for subarctic systems in North America. Instead, we demonstrated that carrion is a resource subject to guild-wide competition, and one which is dominated by wolves and wolverines. It seems likely that carrion represents an essential resource for these species during the winter months. Consequently, scavenging is a risky activity for animals in this system, especially for smaller species like coyotes and foxes, resulting in decreased use of carrion by these species, and increased vigilance at high-activity sites. Wolverines' high use of carrion resources and low vigilance despite their being of comparable size to coyotes indicates that risk-sensitivity and competition for carrion is driven by more than body mass. We did not find evidence of temporal partitioning or temporal risk mediation by scavengers. The high level of wolf use recorded here positions wolves as a “top scavenger” as well as a top predator in this system. The potential for a species to hold such a position may bear further investigation in this and other systems, and traditional views of the trophic role of carrion may need to be revised. Scavenging deserves further attention, particularly in harsh environments, as an important food resource and thus key arena of inter-guild competition.

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# Supplementary Material

## *Body Mass*

Table S2-1. Average body mass of species in kg, as drawn from indicated sources, with males and females averaged if listed separately in publication.

| Species | Average Body Mass (kg) | Published body mass (kg) | Citation | Location of specimens |
|---|---|---|---|---|
| Red fox | 5 | 3.75 | (Larivière and Pasitschniak-arts 1996) | Ontario |
| | | 5.45 | (Harestad and Bunnel 1979) | Mixed |
| Coyote | 13 | 12.00 | (Thurber and Peterson 1991) | Alaska |
| | | 13.4 | (DNPP capture records) | Alaska |
| Wolverine | 12 | 15.05 | (Ballard et al. 1982) | Alaska |
| | | 8.66 | (Raush and Pearson 1972) | Alaska |
| Wolf | 41 | | (DNPP capture records) | Alaska |

## *Carcass Site Information*

Table S2-2. Summary information on carcass sites

| Site Name | Study Year | Prey species | Origin of the Carcass | Age of the carcass at camera deployment (days) | Total scavenging events by focal species |
|---|---|---|---|---|---|
| Big Creek | 2016 | moose | Wolf kill | 3 | 30 |
| Carlo Pass | 2014 | moose | Wolf kill | 7 | 10 |
| Dry Creek | 2014 | moose | Wolf kill | 2 | 17 |
| Dry Creek Bluffs | 2016 | moose | Wolf kill | 103 | 41* |
| Greg's Property | 2016 | moose | Wolf kill | 10 | 14 |
| Healy Creek | 2014 | moose | Unknown | 4 | 4 |
| Highway | 2016 | caribou | Wolf kill | 4 | 10 |
| Hines Creek | 2014 | moose | Unknown | 31 | 16 |
| Jenny Creek | 2015 | moose | Not a wolf kill | 3 | 8 |
| Jenny Creek | 2017 | moose | Wolf kill | 13 | 13 |
| Karma Ridge | 2015 | moose | Unknown | 61 | 6 |
| Lower East Fork | 2014 | moose | Unknown | 12 | 31 |
| Mile 10 | 2014 | moose | Unknown | 42 | 1 |
| Mile 10 | 2016 | moose | Wolf kill | 6 | 5 |
| Mile 5 | 2015 | moose | Not a wolf kill | 2 | 2 |
| Mile 9 | 2015 | moose | Wolf kill | 20 | 2 |
| Mountain Vista | 2016 | moose | Not a wolf kill | 3 | 18 |
| Panguine Creek | 2014 | moose | Wolf kill | 1 | 25 |

| | | | | | |
|---|---|---|---|---|---|
| Riley Creek | 2016 | moose | Not a wolf kill | 17 | 15 |
| Sanctuary | 2015 | moose | Unknown | 26 | 4 |
| Sanctuary Cabin | 2016 | caribou | Wolf kill | 31 | 22 |
| Slate Creek | 2015 | moose | Wolf kill | 4 | 15 |
| Tek Hills | 2016 | moose | Wolf kill | 2 | 19 |
| Tek Park Road | 2014 | moose | Wolf kill | 27 | 15 |
| Tek River | 2014 | caribou | Wolf kill | 6 | 1 |
| Tek West Hills | 2014 | moose | Unknown | 9 | 5 |
| Thumb | 2015 | moose | Unknown | 59 | 13 |
| Upper Dry Creek 1 | 2016 | moose | Wolf kill | 20 | 15 |
| Upper East Fork | 2014 | Dall sheep | Not a wolf kill | 1 | 2 |
| Upper Hines Creek | 2016 | moose | Not a wolf kill | 23 | 16 |
| Upper Savage | 2016 | moose | Wolf kill | 11 | 12 |

* Including the 35 fox visits

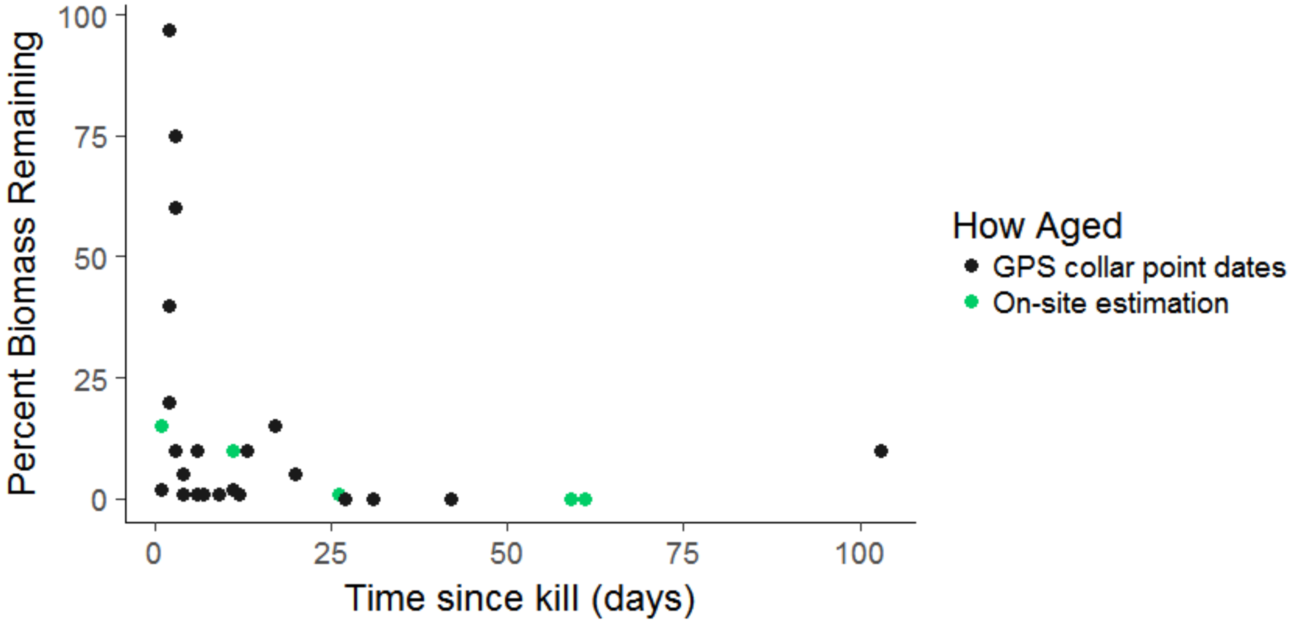


Figure S2-1. Percent biomass remaining at the discovery of carcass sites as time since kill increases, in Denali National Park, Alaska. Colors differentiate sites aged by using the date of GPS locations from collared wolves, with first location within 300m assumed to be date of kill, and those aged using field signs only.

*Model Results*

To save the reader the difficulty of having to compare species' responses to variables by comparing coefficients of interactions (which are themselves a comparison to the reference state), we ran our models with each species as the reference group, and present the coefficients as they pertain directly to that species.

Table S2-3. Effect of environmental variables on likelihood of visitation to a carcass site by four mammalian scavengers in Denali National Park and Preserve. Continuous variables have been scaled to mean=0, SD =1. Scaled units are as follows: Carcass age at deployment 22 days, Vegetation 30%, Distance to cover 8m, Wolf Risk 8e-10 units, Camera duration 30 days.

| | Wolf Groups | | | Lone Wolves | | | Wolverines | | | Coyotes | | | Red Fox | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Odds Ratio | CI | p | Odds Ratio | CI | p | Odds Ratio | CI | p | Odds Ratio | CI | p | Odds Ratio | CI | p |
| (Intercept) | *2.33* | 0.75 – 8.80 | 0.17 | 2.19 | 0.71 – 8.11 | 0.19 | 2.82 | 0.80 – 13.96 | 0.14 | 0.31 | 0.08 – 0.95 | 0.05 | 1.01 | 0.28 – 4.98 | 0.99 |
| Carcass age at deployment | *1.41* | 0.59 – 4.51 | 0.47 | 0.56 | 0.20 – 1.43 | 0.21 | 1.50 | 0.54 – 7.69 | 0.54 | 0.61 | 0.20 – 1.46 | 0.29 | 3.40 | 0.89 – 54.11 | 0.24 |
| Vegetation | *1.73* | 0.73 – 4.65 | 0.23 | 0.62 | 0.22 – 1.48 | 0.31 | 0.84 | 0.33 – 1.92 | 0.68 | 0.66 | 0.26 – 1.48 | 0.33 | 1.82 | 0.64 – 6.51 | 0.29 |
| Distance to cover | *2.65* | 0.89 – 11.71 | 0.12 | 1.60 | 0.56 – 5.46 | 0.39 | 0.58 | 0.21 – 1.49 | 0.27 | 0.68 | 0.22 – 1.77 | 0.46 | 0.96 | 0.25 – 3.09 | 0.94 |
| Source of the Carcass | | | | | | | | | | | | | | | |
| *Not a wolf kill* | *2.11* | 0.18 – 28.65 | 0.56 | 5.02 | 0.38 – 150.99 | 0.26 | 0.76 | 0.06 – 9.40 | 0.83 | 2.25 | 0.17 – 29.79 | 0.52 | 0.43 | 0.01 – 7.21 | 0.58 |
| *Unknown* | *0.42* | 0.03 – 3.87 | 0.46 | 0.25 | 0.01 – 2.47 | 0.26 | 0.93 | 0.07 – 12.89 | 0.96 | 6.46 | 0.68 – 89.67 | 0.12 | 0.04 | 0.00 – 1.11 | 0.17 |
| Wolf Risk | *0.68* | 0.26 – 1.75 | 0.42 | 0.87 | 0.34 – 2.39 | 0.77 | 2.03 | 0.81 – 6.95 | 0.18 | 0.53 | 0.16 – 1.36 | 0.24 | 0.53 | 0.16 – 1.36 | 0.21 |
| Camera duration | *1.75* | 1.07 – 3.01 | 0.03 | 1.75 | 1.07 – 3.01 | 0.03 | 1.75 | 1.07 – 3.01 | 0.03 | 1.75 | 1.07 – 3.01 | 0.03 | 1.75 | 1.07 – 3.01 | 0.03 |

Null deviance: 213.78 on 154 degrees of freedom     Residual deviance: 163.37 on 119 degrees of freedom     AIC: 235.37

Table S2-4. Effects of environmental predictor variables on number of visits made by scavenging species to carcass sites in Denali National Park and Preserve, presented as incident rate ratios (IRR). Continuous variables have been scaled to mean=0, SD =1. Scaled units are as follows: Carcass age 22 days, Vegetation 30%, Distance to cover 8m, Long-term wolf use (UD value) 8e-10 units.

| | Wolf Groups | | | Lone Wolves | | | Wolverines | | | Coyotes | | | Red Fox | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IRR | CI | p | IRR | CI | p | IRR | CI | p | IRR | CI | p | IRR | CI | p |
| (Intercept) | 0.05 | 0.03 – 0.08 | <0.01 | 0.06 | 0.04 – 0.10 | <0.01 | 0.12 | 0.07 – 0.18 | <0.01 | 0.04 | 0.02 – 0.08 | <0.01 | 0.03 | 0.01 – 0.07 | <0.01 |
| Carcass age | 0.70 | 0.43 – 1.06 | 0.12 | 1.06 | 0.71 – 1.56 | 0.79 | 0.46 | 0.29 – 0.69 | <0.01 | 0.77 | 0.29 – 2.04 | 0.58 | 2.41 | 1.18 – 5.23 | 0.02 |
| Vegetation | 0.76 | 0.52 – 1.10 | 0.12 | 0.99 | 0.66 – 1.48 | 0.96 | 0.72 | 0.48 – 1.05 | 0.05 | 1.40 | 0.61 – 3.54 | 0.43 | 4.22 | 1.83 – 10.76 | <0.01 |
| Distance to cover | 1.26 | 0.79 – 2.02 | 0.37 | 1.33 | 0.76 – 2.37 | 0.32 | 1.02 | 0.60 – 1.75 | 0.95 | 0.92 | 0.39 – 2.01 | 0.83 | 2.13 | 1.00 – 4.91 | 0.06 |
| Source of the Carcass | | | | | | | | | | | | | | | |
| *Not a wolf kill* | 4.46 | 1.49 – 13.69 | 0.01 | 2.59 | 0.95 – 6.88 | 0.04 | 3.96 | 1.57 – 10.59 | <0.01 | 0.53 | 0.07 – 2.89 | 0.48 | 58.36 | 9.07 – 459.93 | <0.01 |
| *Unknown* | 1.19 | 0.33 – 4.09 | 0.80 | 1.09 | 0.27 – 4.10 | 0.91 | 1.59 | 0.58 – 4.47 | 0.36 | 2.07 | 0.53 – 8.07 | 0.25 | 1.92 | 0.47 – 9.00 | 0.38 |
| Long-term wolf use | 1.31 | 0.76 – 2.25 | 0.28 | 1.65 | 1.12 – 2.46 | 0.01 | 0.50 | 0.32 – 0.73 | <0.01 | 0.61 | 0.25 – 1.39 | 0.25 | 0.43 | 0.18 – 0.94 | 0.04 |

|  |  |
|---|---|
| Deviance Residuals:<br>Min: -2.91128 1Q: -0.60170 Median: -0.08473 3Q: 0.46082<br>Max: 2.27028<br>Theta: 3.92<br>Std. Err.: 1.08 | 2 x log-likelihood: -387.415<br>Null deviance: 203.324 on 83 degrees of freedom<br>Residual deviance: 78.703 on 49 degrees of freedom<br>AIC: 459.42 |

Table S2-5. Effects of environmental predictor variables on number of visits made by red fox, when including the outlier, to carcass sites in Denali National Park and Preserve, presented as incident rate ratios (IRR). Continuous variables have been scaled to mean=0, SD =1. Scaled units are as follows: Carcass age 22 days, Vegetation 30%, Distance to cover 8m, Long-term wolf use (UD value) 8e-10 units.

| | Red Fox | | |
|---|---|---|---|
| | IRR | CI | p |
| (Intercept) | 0.04 | 0.02 – 0.08 | <0.01 |
| Carcass age | 3.84 | 1.92 – 8.23 | <0.01 |
| Vegetation | 4.31 | 1.86 – 11.09 | <0.01 |
| Distance to cover | 2.47 | 1.15 – 5.73 | 0.02 |
| Source of the Carcass | | | |
| *Not a wolf kill* | 51.04 | 7.76 – 411.71 | <0.01 |
| *Unknown* | 0.77 | 0.20 – 3.42 | 0.71 |
| Long-term wolf use | 0.43 | 0.18 – 0.97 | 0.04 |
| Dispersion parameter for Negative Binomial (3.9248) family taken to be 1<br>Null deviance: 214.075 on 83 degrees of freedom<br>Residual devianc: 79.677 on 49 degrees of freedom | AIC: 463.42<br>Theta: 3.92<br>Std. Err.: 1.08 2 x log-likelihood: -391.418 | | |

Table S2-6. Effects of environmental predictor variables on duration of visits made by scavenging species to carcass sites in Denali National Park and Preserve. Continuous variables have been scaled to mean=0, SD =1. Scaled units are as follows: Site age 45 days, Temperature 7 degrees C, Vegetation 33%, Distance to cover 7m, Long-term wolf risk 7e-10 units.

| | *Wolf Groups* | | | *Lone Wolves* | | | *Wolverines* | | | *Coyotes* | | | *Red Fox* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Predictors* | *IRR* | *CI* | *p* | *IRR* | *CI* | *p* | *IRR* | *CI* | *p* | *IRR* | *CI* | *p* | *IRR* | *CI* | *p* |
| (Intercept) | 3.21 | 2.75 – 3.68 | <0.01 | 2.66 | 2.24 – 3.08 | <0.01 | 2.66 | 2.30 – 3.01 | <0.01 | 1.51 | 0.80 – 2.22 | <0.01 | 3.41 | 2.73 – 4.10 | <0.01 |
| Site Age | -1.39 | -1.93 – -0.85 | <0.01 | -0.32 | -0.73 – 0.08 | 0.12 | -0.90 | -1.24 – -0.55 | <0.01 | -0.30 | -1.09 – 0.49 | 0.46 | -0.46 | -1.46 – 0.55 | 0.37 |
| Temperature | -0.37 | -0.68 – -0.06 | 0.02 | -0.74 | -1.14 – -0.34 | <0.01 | -0.02 | -0.34 – 0.29 | 0.89 | 0.08 | -0.34 – 0.49 | 0.72 | -0.53 | -1.03 – -0.03 | 0.04 |
| Vegetation | -0.49 | -0.88 – -0.10 | 0.01 | -0.06 | -0.49 – 0.37 | 0.77 | 0.26 | -0.04 – 0.56 | 0.08 | -0.75 | -1.69 – 0.19 | 0.12 | -0.70 | -1.51 – 0.10 | 0.09 |
| Distance to cover | -0.29 | -0.73 – 0.15 | 0.19 | 0.26 | -0.28 – 0.79 | 0.34 | 0.31 | -0.13 – 0.75 | 0.17 | 0.31 | -0.50 – 1.12 | 0.45 | -0.50 | -1.10 – 0.11 | 0.11 |
| Origin of the Carcass | | | | | | | | | | | | | | | |
| *Natural Death* | 1.05 | -0.25 – 2.34 | 0.11 | 0.81 | -0.54 – 2.17 | 0.24 | 1.09 | 0.29 – 1.90 | 0.01 | -1.27 | -3.73 – 1.19 | 0.31 | -0.05 | -1.95 – 1.85 | 0.96 |
| *Unknown* | 0.53 | -0.47 – 1.52 | 0.30 | -1.01 | -2.00 – -0.03 | 0.04 | 0.59 | -0.41 – 1.58 | 0.25 | 0.76 | -0.35 – 1.86 | 0.18 | -1.75 | -2.69 – -0.81 | <0.01 |
| Long-term wolf risk | -0.89 | -1.40 – -0.38 | <0.01 | -0.19 | -0.56 – 0.18 | 0.31 | 0.24 | -0.12 – 0.60 | 0.19 | -1.04 | -1.78 – -0.30 | 0.01 | 0.07 | -0.66 – 0.81 | 0.84 |

AIC: 3313.5 BIC:3477.8 logLik: -1615.7 deviance: 3231.5 df.resid: 366 Overdispersion parameter for negative binomial family (): 0.618

Table S2-7. Effect of environmental variables on proportion of time spent vigilant at carcass site by four mammalian scavengers in Denali National Park and Preserve. Estimates and CIs are on the link scale. Continuous variables have been scaled; scaled units are as follows: Site age 45 days, Temperature 13 degrees F, Vegetation 33%, Distance to cover 7m, Long-term wolf use 7e-10 units, Duration of visit 56 minutes.

| | Wolf Groups | | | Lone Wolves | | | Wolverines | | | Coyotes | | | Red Fox | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | -1.77 | -2.13 – -1.40 | <0.01 | -1.69 | -2.01 – -1.38 | <0.01 | -2.22 | -2.51 – -1.93 | <0.01 | -1.72 | -2.38 – -1.06 | <0.01 | -1.65 | -2.20 – -1.10 | <0.01 |
| Site Age | -0.08 | -0.58 – 0.42 | 0.75 | -0.16 | -0.46 – 0.14 | 0.30 | 0.02 | -0.24 – 0.27 | 0.89 | -0.30 | -0.87 – 0.28 | 0.31 | 1.56 | 0.98 – 2.15 | <0.01 |
| Temperature | -0.17 | -0.41 – 0.06 | 0.15 | -0.02 | -0.29 – 0.25 | 0.91 | -0.16 | -0.35 – 0.03 | 0.11 | -0.02 | -0.34 – 0.30 | 0.91 | -0.31 | -0.57 – -0.05 | 0.02 |
| Vegetation | -0.08 | -0.36 – 0.21 | 0.60 | -0.21 | -0.52 – 0.10 | 0.18 | -0.02 | -0.23 – 0.20 | 0.87 | -0.08 | -0.64 – 0.49 | 0.79 | 0.58 | 0.11 – 1.05 | 0.02 |
| Distance to cover | 0.11 | -0.18 – 0.40 | 0.46 | 0.02 | -0.32 – 0.37 | 0.89 | 0.08 | -0.25 – 0.40 | 0.64 | 0.33 | -0.17 – 0.83 | 0.20 | 0.38 | 0.02 – 0.75 | 0.04 |
| Origin of Carcass | | | | | | | | | | | | | | | |
| *Not a wolf kill* | 0.17 | -0.65 – 0.98 | 0.69 | 0.29 | -0.56 – 1.13 | 0.51 | 0.81 | 0.32 – 1.30 | <0.01 | 1.01 | -0.38 – 2.41 | 0.156 | 1.68 | 0.23 – 3.13 | 0.02 |
| *Unknown* | -0.49 | -1.34 – 0.36 | 0.26 | -0.31 | -1.25 – 0.62 | 0.51 | 0.02 | -0.70 – 0.73 | 0.97 | 0.43 | -0.45 – 1.31 | 0.34 | -1.14 | -1.86 – -0.42 | <0.01 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Long-term wolf use | 0.06 | -0.29 – 0.40 | 0.75 | 0.12 | -0.13 – 0.36 | 0.35 | -0.02 | -0.24 – 0.19 | 0.84 | -0.40 | -1.01 – 0.20 | 0.19 | 0.10 | -0.48 – 0.67 | 0.74 |
| Duration of visit | 0.04 | -0.13 – 0.21 | 0.62 | 0.26 | -0.05 – 0.57 | 0.10 | 0.30 | 0.12 – 0.49 | <0.01 | -0.18 | -0.95 – 0.59 | 0.65 | 0.16 | -0.11 – 0.43 | 0.24 |

AIC: -855.1 logLik: 473.5 deviance: -947.1 df.resid: 361 Overdispersion parameter for beta family: 3.7

Table S2-8. Comparison of gap time between subsequent visits by pairs of species at carcass sites in Denali National Park and Preserve.

| | Gap Time (min) | | |
|---|---|---|---|
| | *Estimate* | *CI* | *p* |
| (Intercept) | 886.00 | 210.01 – 13411.64 | <0.01 |
| Species Pair | | | |
| *Coyote,Wolf Group* | 0.67 | 0.04 – 6.40 | 0.74 |
| *Coyote,Wolverine* | 1.54 | 0.07 – 33.42 | 0.75 |
| *Lone Wolf,Coyote* | 0.08 | 0.00 – 1.74 | 0.07 |
| *Lone Wolf,Red Fox* | 0.96 | 0.05 – 9.13 | 0.97 |
| *Lone Wolf,Wolf Group* | 0.73 | 0.05 – 3.57 | 0.76 |
| *Lone Wolf,Wolverine* | 1.70 | 0.10 – 10.74 | 0.63 |
| *Red Fox,Coyote* | 0.29 | 0.02 – 2.74 | 0.30 |
| *Red Fox,Lone Wolf* | 1.07 | 0.07 – 5.90 | 0.95 |
| *Red Fox,Wolf Group* | 1.13 | 0.07 – 7.12 | 0.91 |
| *Red Fox,Wolverine* | 0.91 | 0.06 – 5.33 | 0.93 |
| *Wolf Group,Coyote* | 1.85 | 0.09 – 40.30 | 0.65 |
| *Wolf Group,Lone Wolf* | 0.57 | 0.04 – 2.65 | 0.57 |
| *Wolf Group,Red Fox* | 1.58 | 0.10 – 7.83 | 0.65 |
| *Wolf Group,Wolverine* | 0.83 | 0.05 – 6.03 | 0.87 |
| *Wolverine,Coyote* | 1.63 | 0.09 – 15.53 | 0.68 |
| *Wolverine,Lone Wolf* | 1.37 | 0.08 – 7.28 | 0.76 |
| *Wolverine,Red Fox* | 0.84 | 0.05 – 5.30 | 0.87 |
| *Wolverine,Wolf Group* | 0.80 | 0.05 – 4.24 | 0.83 |

Deviance Residuals:
Min:-2.9326 1Q:-1.0274 Median:-0.1836 3Q:0.4043 Max:1.8195
Dispersion parameter for Gamma family taken to be 0.9283683
Null deviance: 99.743 on 88 degrees of freedom
Residual deviance: 82.369 on 70 degrees of freedom
AIC: 1404.7

Table S2-9. Comparison of gap time across log-ration body mass of subsequent species at carcass sites in Denali National Park and Preserve.

| | Gap Time (min) | | |
|---|---|---|---|
| | *Estimate* | *CI* | *p* |
| (Intercept) | 869.52 | 723.89 – 1056.99 | <0.01 |
| logratio | 1.05 | 0.96 – 1.16 | 0.35 |
| Null deviance: 99.743 on 88 degrees of freedom<br>Residual deviance: 98.884 on 87 degrees of freedom<br>AIC: 1389.5 | | | |

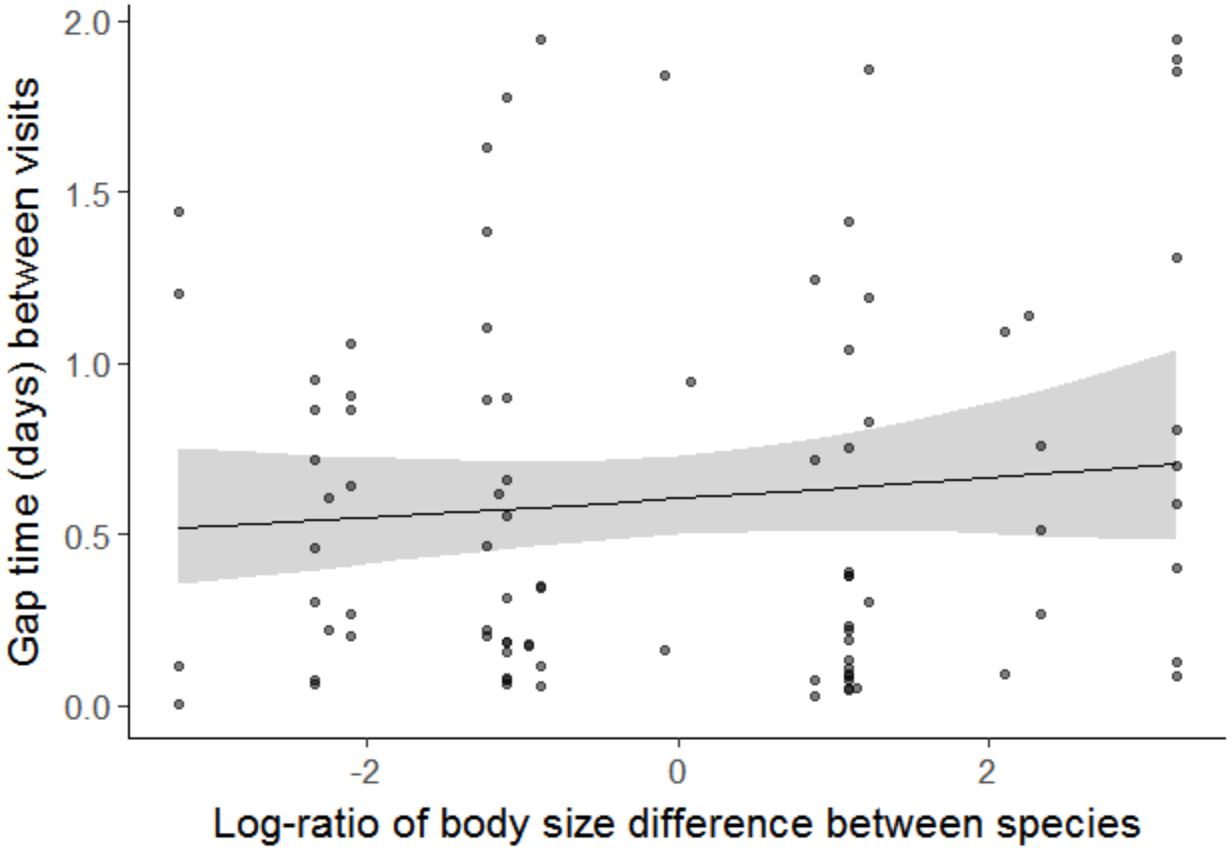


Figure S2-2. The gap time (days) between scavenging visits as an effect of log-ratio body mass of scavenging species pairs. Lower log-ratio body sizes indicate a small species followed by a large species; high log-ratio body size indicates the reverse. Species mass taken from published literature and Denali National Park and Preserve capture records. Analysis restricted to gaps of less than 48 hours.

# Chapter Three

# Living on the Edge:

## Coyote space use, survival, and response to wolves in the sub-arctic

## Abstract

Understanding how mesopredators manage the risks associated with apex predators is key to explaining patterns of mesopredator space use and impacts of apex predators on mesopredator populations. Here we examine the space use and survival of coyotes (*Canis latrans*) in interior Alaska, and investigate their spatial response to wolves (*Canis lupus*) using data from sympatric individuals fitted with GPS collars. We demonstrate that coyotes maintain extremely large territories and experience low survival, indicating resource-limitation in this harsh environment. We also show that coyotes do not universally avoid wolves, but instead demonstrate season-specific responses to long-term use of the landscape by wolves. Specifically, although coyotes universally selected to avoid wolf proximity, coyotes switched from avoiding areas of long term wolf use in the summer to preferring these areas in the winter. This combination of attraction and avoidance predicated season and possibly habitat suggests that mesopredators use complex behavioral strategies to mediate the effects of apex predators.

## Introduction

The risk of injury or death by predation is a key driver of habitat selection (Thomson et al. 2006; Valeix et al. 2009; Laundre et al. 2010; Oriol-Cotterill et al. 2015; Breed et al. 2017). Because risk varies in time and space, at-risk individuals can use behavioral strategies to take advantage of spatial and temporal windows of reduced risk. (Lima and Bednekoff 1999; Valeix et al. 2009; Bischof et al. 2014; Stewart et al. 2016). Response strategies to risk can be broadly classified as reactive or predictive (Valeix et al. 2009; Broekhuis et al. 2013; López-bao et al. 2016). A reactive response to risk is based on the immediate proximity of a predator, while a predictive response is based on consistent patterns of predator use – for example, avoiding areas or times with frequent predator activity. A reactive risk response can therefore be described as one which is sensitive to short-term risk, and a predictive response as one which is sensitive to long-term risk.

Response to risk of predation has primarily been studied for prey species, yet it applies to many predator species as well (Lourenço et al. 2014, Oriol-Cotterill et al. 2015). Interspecific killing among Carnivora is well documented (Palomares and Caro 1999), so mesocarnivores must balance the risk of interspecific killing against other habitat features such as prey availability when making habitat use decisions. Demographically, larger carnivores have been shown to suppress mesocarnivores populations, and it has been hypothesized that that changes in habitat use driven by predation risk facilitate this suppression (Schmitz et al. 1997; Prugh et al. 2009; Ritchie and Johnson 2009; Elmhagen et al. 2010; Lourenço et al. 2014). Despite continued study of intraguild population dynamics, the patterns and mechanisms of mesocarnivore suppression and release remain elusive (Elmhagen and Rushton 2007; Ford and Goheen 2015; Bergstr et al. 2017; B.L. Allen et al. 2017). Part of this difficulty lies in the fact that unlike in classic predator-prey dynamics, large carnivores present a mix of risk and reward for smaller carnivores.

Despite the threat of interspecific killing, mesocarnivores may also benefit from proximity to large carnivores by gaining access to carrion resources or by using large carnivore presence as a shield against competition and risk from other mesocarnivores (Switalski 2003; Khalil et al. 2014; Allen et al. 2015; M.L. Allen et al. 2017). This trade-off serves as an incentive for mesocarnivores to respond flexibly to large carnivore risk depending on the circumstances. Thus it is not surprising that behavioral responses of mesocarnivores to large carnivores, as measured by habitat use, have not always demonstrated patterns of avoidance as is generally assumed (Ritchie and Johnson 2009; Swanson et al. 2014; Balme et al. 2017; Sivy, Pozzanghera, Grace, et al. 2017). Additional research is needed to establish when and how mesocarnivores avoid or are attracted to large carnivore activity, whether they tend to be reactive or predictive in their response to large carnivore presence, and if their response is flexible based on factors such as habitat and season.

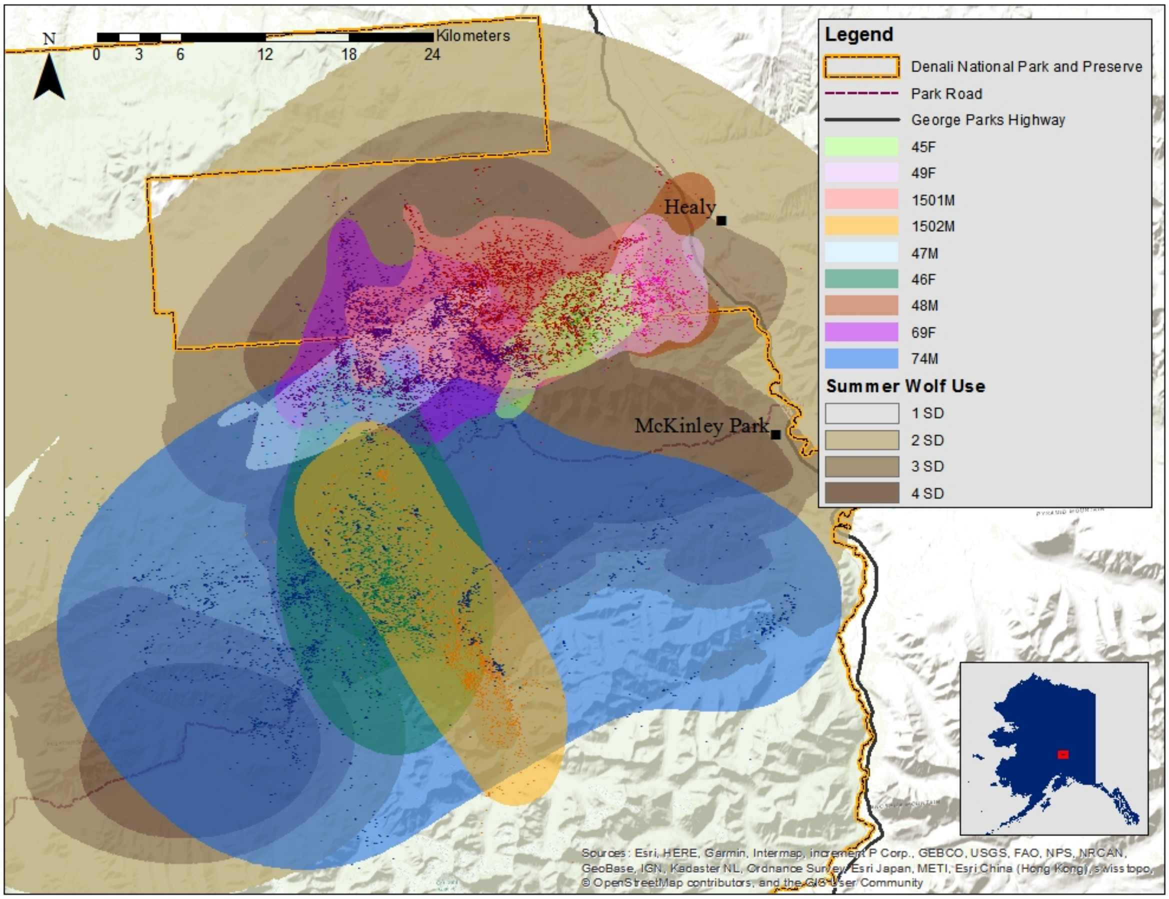
The recent re-colonization by wolves of many parts of their historic range in North America has allowed considerable research documenting the ecological changes following recolonization, including suppressive effects on coyote populations (Berger and Gese 2007; Berger et al. 2008; Merkle et al. 2009; Latham et al. 2013; Ripple et al. 2013). It has been hypothesized that widespread extirpation of wolves facilitated the coyote's massive range expansion over the past two hundred years, yet coyotes also expanded their range into Canada and Alaska, regions with robust wolf populations (Thurber and Peterson 1991; Berger and Gese 2007; Berger et al. 2008; Gese et al. 2008; Ripple et al. 2013). Far less is known about coyotes and the wolf-coyote relationship in areas of northern coyote range expansion, with limited information on the natural history of coyotes in the north and their response to wolves (Thurber 1992; Latham et al. 2013; Sivy, Pozzanghera, Grace, et al. 2017). No previous study has used GPS collar technology on sympatric wolves and coyotes to evaluate their interactions, thus fine-scale spatial information needed for detailed examination of coyote-wolf interactions has been lacking. The sub-arctic is changing quickly in response to climate change, and it represents a habitat quite distinct from other parts of the coyote's range. There is a clear need for better understanding of how coyotes operate in, and potentially impact, the subarctic environment.

In this paper, we examine coyote space use, survival, and response to wolf risk in a sub-arctic environment using data from sympatric GPS-collared wolves and coyotes in Denali National Park and Preserve (DNPP), Alaska. Specifically, we examine whether coyotes respond predictively or reactively to wolves by comparing their response to wolf proximity versus long term wolf use; we establish if that response is one of attraction or avoidance; and we determine whether response direction or type varies by season and habitat. To simultaneously capture coyote spatial response to wolves as well as additional characteristics of coyote habitat selection, we use a resource selection function (RSF) framework, incorporating wolf risk as a feature of the habitat. We also report territory size, annual survival, and sources of mortality. We predicted that coyotes would reactively avoid wolves, allowing them to otherwise optimize habitat selection and potentially take advantage of carrion in a harsh environment with limited prey base. We predicted that avoidance would be strongest in habitats with poor visibility, and in the summer when small prey are more readily available. We predicted that if coyotes did show attraction to wolves, it would be during the winter, when the potential rewards offered by carrion may be the most important. This kind of context-dependent response would imply that coyotes take advantage of differences in risk in different habitats or seasons to use areas that have a higher wolf risk, either because they are more desirable habitat or because of some benefit offered by wolf presence, such as carrion availability. As a null hypothesis we predicted that coyotes would select habitat based only on habitat characteristics, with no response to wolf risk, and that this would hold true for all season and habitat types. This would indicate limited support for a potential spatial mechanism of mesocarnivore suppression/release.

## Methods

### *Study area*

This study took place in the north-eastern portion of Denali National Park and Preserve and adjacent state and private lands (Figure 3-1). The area is characterized by a sub-arctic climate with cold winters and cool summers. Average annual precipitation is 38cm, with average winter and summer temperatures of -15°C and 12°C respectively (Sousanes 2016). Elevation ranged from 373 to 2080 meters. Low elevations are characterized by mixed spruce (*Picea* sp) and deciduous forest (cottonwood [*Populus trichocarpa*], birch [*Betula* sp], and aspen [*Populus tremuloides*]), with willow (*Salix* sp) and alder (*Alnu*s sp) along riparian corridors and braided glacial rivers. Taiga and shrub (willow and dwarf birch [*Betula nana*]) make up the bulk of the middle elevations, rising to alpine vegetation on the higher slopes. Available small prey species include snowshoe hare (*Lepus americanus*), microtine rodents, arctic ground squirrel (*Spermophilus parryii*), hoary marmots (*Marmota caligata),* ptarmigan (*Lagopus spp*) and grouse (*Bonasa umbellus, Falcipennis canadensis*). Ungulates include moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall sheep (*Ovis dalli*). Other carnivore species present include grizzly and black bears (*Ursus arctos* and *Ursus americanus*), wolverines (*Gulo gulo*), red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), and marten (*Martes americana*). Trapping of coyotes and wolves is legal on state lands. Trappers are not required to report annual coyote take; but voluntary reporting to Alaska Department of Fish and Game suggests very low annual take (averaging 0-2 individuals) from the sub-unit containing this study area (Parr 2016; Parr 2017). Annual trapping of wolves has been found not to reduce the regional population, and it does not prevent wolf residency on state lands (Borg et al. 2015). There is limited human presence throughout most of the study area, and it is concentrated around roads and the few established trails.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, © OpenStreetMap contributors, and the GIS User Community

Figure 3-1. Map of coyote home ranges, point locations, and average summer wolf use in Denali National Park and Preserve, Alaska. Coyote locations and 95% autocorrelated kernel density home ranges are depicted with colored points and polygons, respectively. Wolf use was calculated as a localized density distribution (see Methods), and each shade transition in wolf use represents an increase of one standard deviation of wolf use intensity, with the lowest standard deviation rendered without color for clarity. Inset shows the location of the study area within Alaska.

### *Fieldwork*

Coyotes were collared during March 2013-2015. Coyotes were darted from a helicopter, immobilized with Telazol, and fitted with GPS store-on-board collars (Telonics, Inc, Mesa, AZ; TTW-4400) with a 2-year deployment period and automatic drop-off. In 2013, collars were programmed to record locations every 24 hours; in subsequent years the fix rate was altered to every three hours. Coyote collars were retrieved after the death of the animal or after programmed drop-off, whichever came first. Mortality sites were investigated and necropsies performed to determine cause of death when possible. As part of the long-term wolf monitoring procedure, DNPP staff deployed and maintained 1-3 GPS collars on wolves in each wolf pack that occurred in the study area, generally on breeding animals. Wolves were darted from helicopters, immobilized with Telazol, and fitted with Telonics GPS collars (Telonics, Inc, Mesa, AZ, multiple models; see Meier et al. 2009 for protocol details). Wolf collar fix intervals varied between four and 24 hours. Capture and handling procedures for wolves and coyotes were approved under National Park Service (NPS) IACUC protocol "AKR_YUCH and DENA_Burch_Wolves_2013."

### *Coyote home range and survival*

Coyote home ranges were calculated using autocorrelated kernel density estimation (Fleming et al. 2015; Fleming and Calabrese 2017), available in the R package ctmm (Calabrese et al. 2016). This technique refines classic kernel density estimation by explicitly modeling the degree of autocorrelation of locations for each individual before calculating the home range, thus replacing the correlated random walk model framework, which assumes independent locations, with the more appropriate continuous-time stochastic process framework (Fleming and Calabrese 2017). Location data for each coyote were screened for inaccurate locations and extra-territorial forays, and variograms were visually examined to ensure model assumptions of territoriality were met. The autocorrelation of the locations was then fit to five possible movement models, including a null model of complete independence, and the top model was selected with AIC (Calabrese et al. 2016). The top model was then used in combination with the location data to estimate an appropriate smoothing bandwidth, and the 95% home range KDE was generated using the function 'akde' (Calabrese et al. 2016). This process was repeated for each coyote, and the resulting 95% home range isopleths delineated the "available" area for each coyote used in the resource selection function. Because autocorrelated kernel density estimation does not treat locations as independent, this method may produce larger home ranges than traditional kernel density methods at high fix intervals (Fleming et al. 2015). We therefore present a comparison of home range size as calculated by autocorrelated kernel density, classic kernel density, and 95% minimum convex polygon as implemented in the package *adehabitatHR* (Calenge 2007). Classic kernel density distributions were created for each individual using the reference bandwidth and grid, and assuming a bivariate normal distribution.

We calculated annual coyote survival rates, mortality due to harvest, and mortality due to wolves using a staggered-entry Kaplan-Meir model (Pollock et al. 2016) with monthly time intervals.

### *Habitat variables*

We selected five habitat variables to be tested in the RSF: elevation, slope, aspect, distance to linear feature, and vegetation type. Elevation, slope, and aspect were generated from a five-meter digital terrain model (United States Geological Survey 2010). Aspect was binned into N, E, S, or W. Linear features comprised waterways and trails. We obtained a map of waterways from the National Hydrography Dataset (United States Geological Survey 2013), and we removed waterway segments above 1100m in elevation. This was necessary to eliminate waterways that could not function as viable travelways; in this study system, such high-elevation waterways are brush-choked ravines. Summer and winter trails were available in Denali GIS databases. We defined "summer" as being the months of April through September, and "winter" as being October through March, which generally corresponded to snow-free and snow-covered periods, respectively. The vegetative cover layer was drawn from the 2011 National Landcover Database (Homer et al. 2015). Based on description and distribution, we binned the landcover classes into three categories: "open," which in included alpine vegetation, dwarf shrub, and bare ground, "closed," which included evergreen and mixed deciduous forests, and "shrub," which included shrub-scrub and taiga areas.

### *Wolf Risk Variables*

We used two wolf risk variables in the RSF. The first, distance to the nearest wolf, represented short-term risk. The second, long-term wolf use intensity, represented long-term risk. To calculate distance to wolf, we identified all wolf locations within +/- 12 hours of each coyote location, calculated the distance to each in meters, and selected the minimum. Twelve hours was selected as the window because it allowed for the inclusion of all wolf collar daily location times, ensuring that calculations were not biased towards wolves with shorter fix intervals. To create a quantitative measure of long-term wolf use intensity, we created localized density distributions (LDDs) for winter and summer (Figure 3-2). LDDs are a measure of use similar to traditional utilization distributions (UDs), but weighted by the number of individuals in a social group (Kittle et al. 2015; Kittle et al. 2017). This approach allowed us to account for the fact that larger wolf packs likely represent a greater threat to coyotes than pairs or smaller packs. To do this, we first used *ctmm* as described above to generate UD rasters for each collared wolf by season and year. We included individuals in a given season only if they had been monitored for at least three months of the six-month season and did not disperse during that time. Because ctmm produces contour rasters, with the lowest values in the center of the home range, we inverted raster values to make them more intuitive. If there was more than one collared individual in a pack, we combined the individual UDs, averaging overlapping cell values. This yielded pack-level UDs for that season. We eliminated raster values <0.05 to create a 95% isopleth raster for that pack/season. We integrated pack UD values to one to standardize values across packs with different size territories. We then multiplied the cell values of each UD by the number of individuals in the pack, as determined by the official DNPP counts at the beginning of that season, which are based on multiple aerial sightings, as well as track counts and photographs. This created a "localized density distribution," or LDD. We then combined the LDDs of each pack within each season, summing overlapping values, and integrated the resulting LDD to one. Finally we combined the seasonal LDDs across years, averaging overlapping cells, to produce rasters which represented average summer and winter use by wolves, weighted by pack size. These rasters were then integrated to one to allow model coefficients to be directly compared.

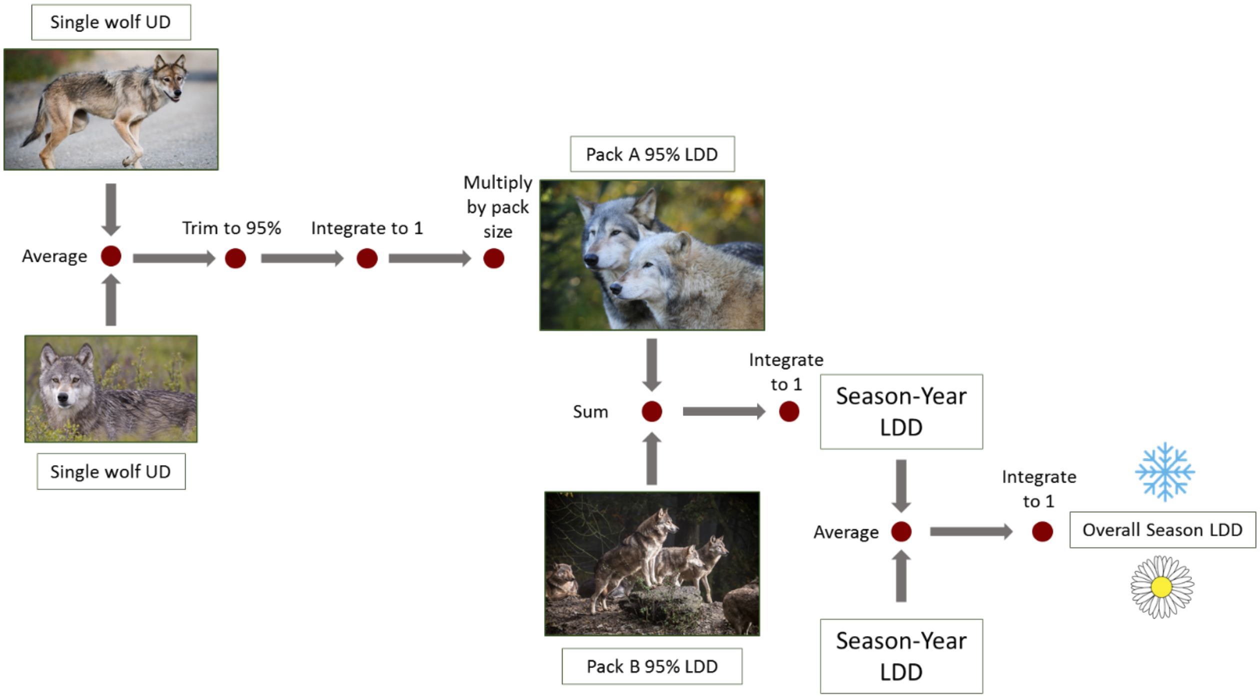


Figure 3-2. Workflow diagram for creating summer or winter location density distributions for wolves by combining individuals into packs, packs into seasons, and seasons across years.

*Available locations*

When generating "available" locations in a used-available design, it is critical to ensure that available locations adequately sample the habitat variables (Northrup et al. 2013). To this end, we generated a grid of points with 100m spacing across the merged 95% coyote home ranges and extracted the habitat values at each point. We then subsampled this "census" at resolutions of 200m, 400m, 1km, 2km, 4km, and 8km, examining mean and CV of each habitat variable for evidence of de-stabilization. We found that mean and CV remained stable for all variables up to the 400m resolution, but to be conservative we used a 200m grid (one point per 0.02 hectares) as the target sampling density. To achieve this for both summer and winter models, we generated points at a density of one per 0.01 hectares in each coyote territory, and then assigned each point a random date and time drawn from the window of the collar deployment of that coyote, thus subdividing the points into summer and winter, with each having an approximate density of one per 0.02 hectares. At each available point we extracted habitat values, including long term wolf risk, and calculated distance to nearest wolf within a 24-hour window.

*Resource Selection Modeling*

We examined all covariates for collinearity using a correlation matrix of the values of the 100m census grid, specifically looking for cases where Spearman correlation values > 0.6. We found that elevation was highly correlated with slope ($r = 0.64$) and distance to linear features ($r = 0.67$ and $r = 0.68$ summer and winter), and as the latter are more biologically informative, we discarded elevation.

Because coyote responses to distances from wolves and landscape features could be nonlinear, we investigated logarithmic and polynomial response forms. For continuous data, this is typically accomplished using a scatterplot of the data and visually examining it for possible nonlinear response forms. An equivalent process for binomial data is to predict the response variable given a parameter of interest using a loess smoothing function (which assumes local but not global linearity), and then plot the logit of these values against the range of the variable of interest. This will produce a plot approximating the response form of the variable. We found that coyote responses to slope and distance to linear feature were best represented by a quadratic function, and that response to distance from wolf was linear and required no transformation.

To model coyote habitat selection and response to wolf risk, we used generalized linear mixed models with binomial response and logit link, including individual coyote as a random effect, for both summer and winter. We scaled all continuous predictors to mean of zero and standard deviation of one to improve model convergence. Per our hypotheses, we included interactions between vegetation and both forms of wolf risk to see if risk response was habitat specific. We thus began with a global model of the form: "use = slope + slope$^2$ + distance to linear feature + distance to linear feature$^2$ + aspect + vegetation * distance to wolf + vegetation * LDD + (1 | CoyoteID)" for summer and winter respectively. We used the *dredge* function from package *MuMin* (Barton 2018) to run all possible subsets of the global model and rank them by AIC (Burnham and Anderson 2002). The top model was validated using 5-fold random cross-validation, and 4-fold cross-validation with individual blocking, with two coyotes per fold (Boyce et al. 2002; Roberts et al. 2017). Because observed values of distance to wolf ranged as high as 150km, we ran a sub-analysis where we restricted locations to those less than 18km from the nearest wolf. Eighteen kilometers was chosen because it is the average diameter of our home ranges, as measured from north to south and east to west, and thus captures the spatial extent at which coyotes can effectively respond to wolf presence, assuming they avoid territorial trespass while doing so.

## Results

### *Coyote Space Use and Survival*

Nine adult coyotes were collared, five males and four females. Males weighed an average of 13.9kg (SE 0.1) and females 12.8kg (SE 0.6) One female (46F) was re-collared after one year and switched from a 24 to a three hour fix interval. One male was legally trapped only 56 days after collaring and was therefore excluded from the RSF. Figure 3-3 shows the deployment timing of the collars (46F deployments combined). Summary collaring and location data can be seen in Table 3-1.

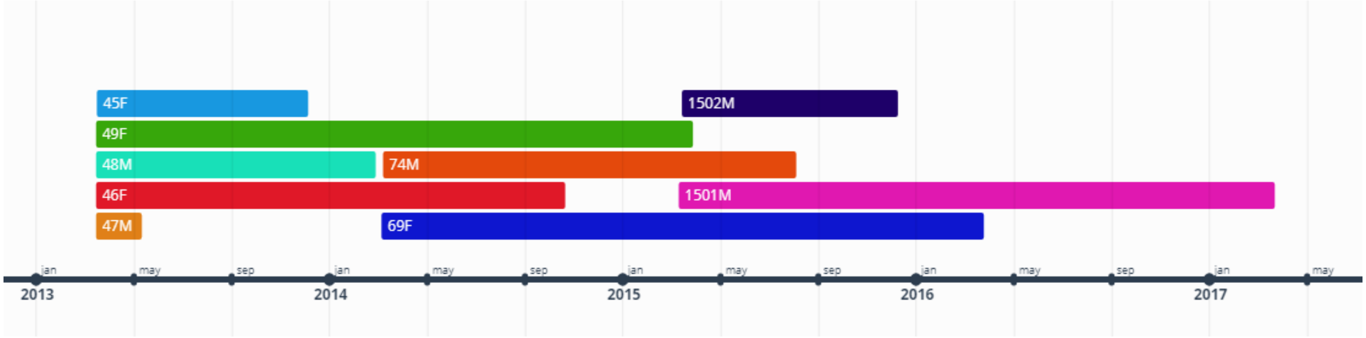


Figure 3-3. Deployment schedule of coyote collars in Denali National Park and Preserve. Deployments occurred in March and collars had a 2-year lifespan.

Average duration of deployment was 465 days (SE 78.5). In total, the collars generated 18808 territorial locations, and allowed a survival analysis on 14 animal-years of data. Sources of mortality included trapping, wolves, bears, and starvation. Three necropsied coyotes had porcupine quills in their bodies at time of death.

Table 3-1. Summary of collar deployments, locations, and mortality for coyotes in DNPP.

| Coyote | Fix rate (hours) | Number of locations | Start date | End Date | Total time (days) | End Cause |
|---|---|---|---|---|---|---|
| 1501M | 3 | 5392 | 3/10/2015 | 3/22/2017 | 743 | collar dropped |
| 1502M | 3 | 2082 | 3/14/2015 | 12/9/2015 | 270 | starvation |
| 45F | 24 | 261 | 3/16/2013 | 12/2/2013 | 260 | killed by wolves |
| 46F (first collar) | 24 | 326 | 3/15/2013 | 2/16/2014 | 337 | re-capture |
| 46F (second collar) | 3 | 1656 | 3/5/2014 | 10/21/2014 | 231 | killed by wolves |
| 47M | 24 | 60 | 3/15/2013 | 5/11/2013 | 56 | trapped |
| 48M | 24 | 346 | 3/15/2013 | 2/26/2014 | 289 | trapped |
| 49F | 24 | 542 | 3/15/2013 | 3/28/2015 | 729 | collar dropped |
| 69F | 3 | 5238 | 3/5/2014 | 3/25/2016 | 752 | collar dropped |
| 74M | 3 | 3371 | 3/7/2014 | 8/4/2015 | 521 | killed by bear |

The average coyote territory size was 291km$^2$ (SE = 130 km$^2$, Table 3-2). All coyote territories were encompassed by monitored wolf territories. Comparison between autocorrelated kernel density, traditional kernel density, and 95% MCP calculations of home range showed similar values (Table 3-2). All three methods showed smaller home ranges for coyotes with 24-hour fix intervals than for those with 3-hour intervals, even for comparable deployment lengths. The methods diverged the most on a coyote (74M) which exhibited consistent wide-ranging behavior, leading to a particularly large territory. There was a strong relationship between number of locations and territory size, with coyotes on 24-hour fixes having consistently smaller territories than those on 3-hour fixes (Figure 3-4).

Table 3-2. Comparison of 95% home range sizes of coyotes calculated using three methodologies: AKDE (autocorrelated kernel density calculation), KDE (standard kernel density estimation), and MCP (95% minimum convex polygon). See methods and supplementary material for details on these methodologies.

| Coyote | Fix Rate (hour) | 95% AKDE, $km^2$ | 95% KDE, $km^2$ | 95% MCP, $km^2$ |
|---|---|---|---|---|
| 1501M | 3 | 203 | 205 | 245 |
| 1502M | 3 | 262 | 236 | 323 |
| 45F | 24 | 57 | 70 | 50 |
| 46F | 3 | 324 | 201 | 285 |
| 47M | 24 | 76 | 122 | 49 |
| 48M | 24 | 76 | 84 | 67 |
| 49F | 24 | 63 | 71 | 56 |
| 69F | 3 | 199 | 202 | 213 |
| 74M | 3 | 1363 | 929 | 1096 |
| Average without 74M (SE) | | 158 (34) | 149 (23) | 161 (39) |
| Average (SE) | | 291(130) | 236 (84) | 265 (104) |

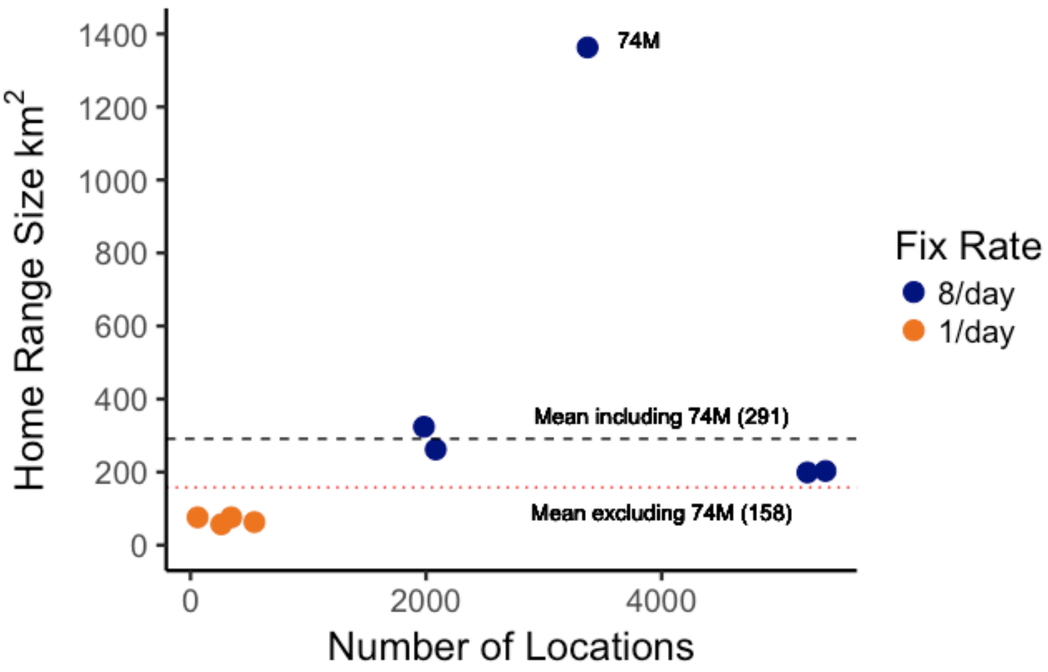


Figure 3-4. Relationship between fix rate, number of locations, and territory size for coyotes in Denali National Park, Alaska. Average territory size with (dashed line) and without (dotted line) exceptionally large territory included are shown.

Average annual survival of coyotes was 0.5 (SD 0.09; Table 3-3). Average annual mortality from harvest was the same as that from wolves, 0.14 (SD 0.04), but annual mortality from all large carnivores was 0.21 (SD 0.5).

Table 3-3. Average annual survival of collared coyotes in Denali National Park and Preserve, Alaska.

| Year | At risk | Died | Survival | SD |
|---|---|---|---|---|
| 2013 | 5 | 2 | 0.60 | 0.17 |
| 2014 | 5 | 3 | 0.40 | 0.14 |
| 2015 | 3 | 2 | 0.33 | 0.16 |
| 2016 | 1 | 0 | 1 | 0 |
| Total | 14 | 7 | 0.5 | 0.095 |

### *Model Selection and Validation*

For winter, AIC ranking supported the full model, with differences in AIC showing strong support for this model over other candidate models (delta AIC of 2.9 and 30.0 for second- and third-ranked models respectively; Table S3-1). For summer, the top model was the full model with the exception of 'distance to linear feature.' The second model, with a difference of only 1.1 AIC units, was the full model. No other models were well supported by comparison (Table S3-1). Because linear terms are conventionally included when quadratic terms are present in the model structure, we elected to use the full model for summer as well. Summer and winter models performed acceptably under 5-fold random cross-validation (Figure S3-1). As expected, model validation worsened slightly when validated with blocking by individual (Roberts et al. 2017), however it remained adequate for most bins, especially considering the small sample size (Figure S3.1).

### *Effects of topography, habitat, and wolf activity*

Coyotes selected intermediate slope values and south- or west-facing aspects (Figure 3-5). In summer, coyotes selected for intermediate distance to linear features, but in winter coyotes selected to be either close to or far from linear features, avoiding intermediate values (Figure 3-5). Wolf risk being at its mean value, coyotes selected for shrub areas in summer and closed forest areas in winter (Figure 3-5).

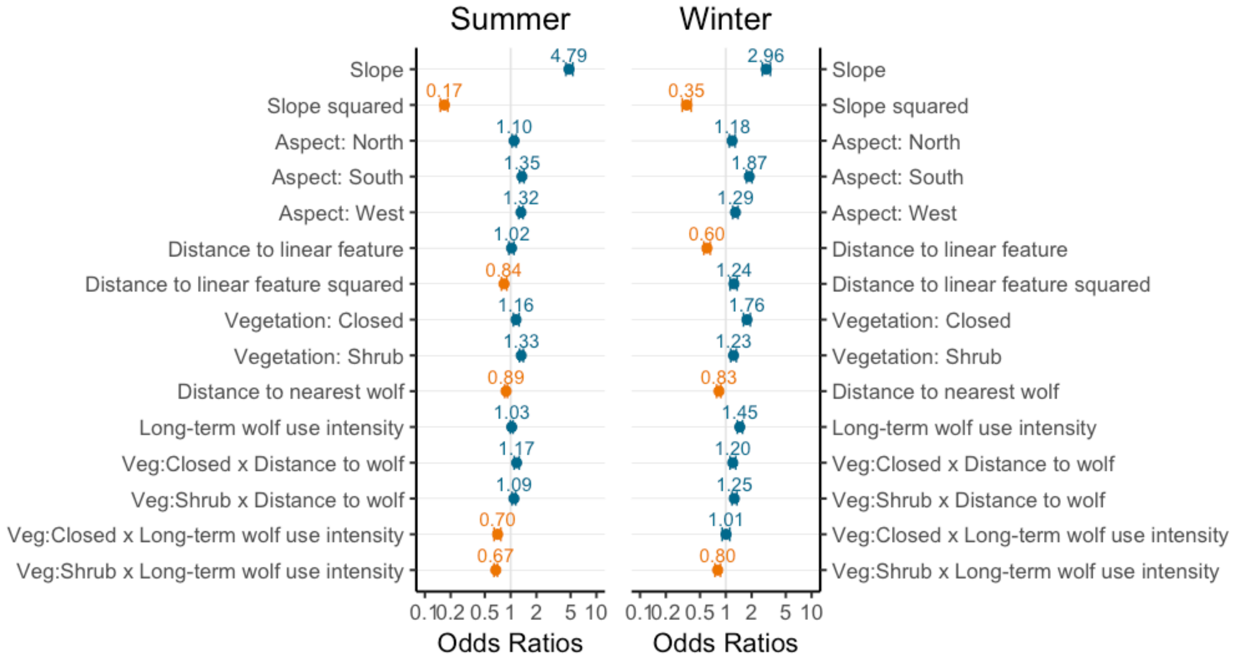


Figure 3-5. Estimated coefficients, on the odds ratio scale, of resource selection functions for coyotes in Denali National Park in summer (April-September) and winter (October-March). Error bars show bootstrapped 95% confidence intervals. Blue indicates odds ratios greater than one, indicating an increase in selection associated with that parameter; orange indicates the reverse. Distances are in kilometers. Slope and distance values have been scaled to mean of zero, standard deviation of one. Scaled units are as follows. Summer: Slope 11.6 degrees; Distance to linear feature 0.84km; Distance to nearest wolf 8.62km. Winter: Slope 11.6 degrees; Distance to linear feature 0.83km; Distance to nearest wolf 8.65km.

The non-restricted analysis of distance to wolf showed a different pattern of response than the restricted. Because the restricted analysis is more biologically appropriate, we draw on that analysis when reporting effect of distance to wolf. Based on the sub-analysis, coyotes responded consistently to short-term wolf risk (distance to nearest wolf) between land cover types and season (Figure 3-6). In both summer and winter, coyotes selected to be at greater distances from wolves, except for in the open in the winter, when distance to wolf had no effect (Figure 3-6).

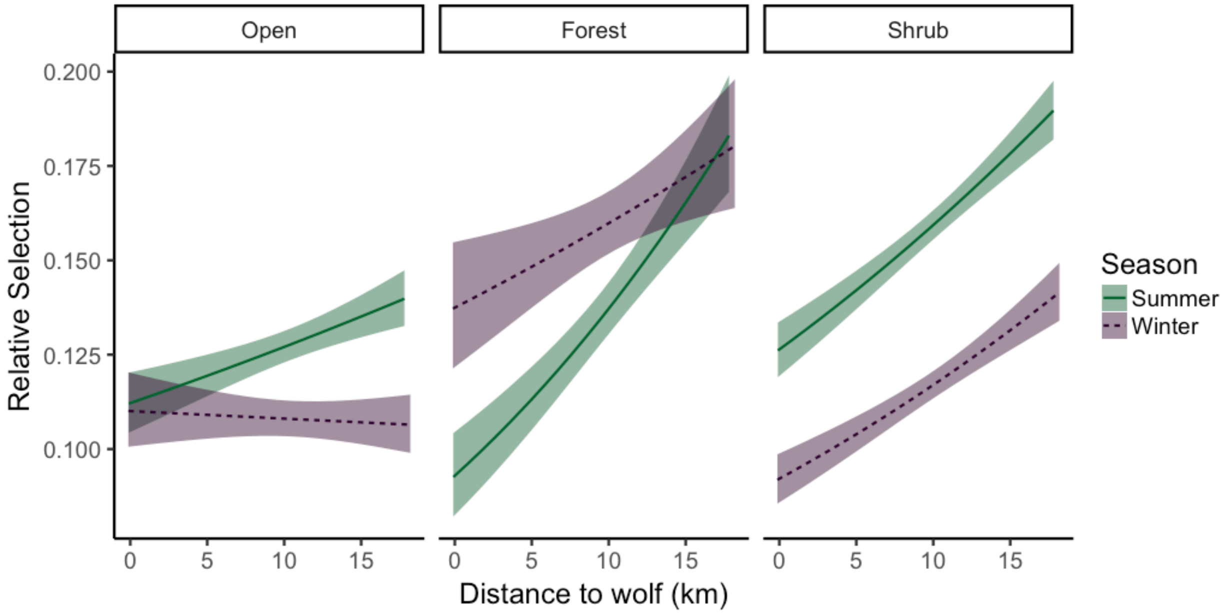


Figure 3-6. Effect of vegetation type (Open, Closed, Shrub), season (summer = green solid line, winter = purple dashed line), and distance to nearest wolf on relative habitat selection by coyotes in Denali National Park, Alaska. Error bars show 95% CI as determined from fixed effects only, and should therefore be considered conservative.

Coyote response to long-term wolf risk varied by season but not by land cover except in one case (Figure 3-7). In winter, coyotes selected for areas of higher long-term wolf use, especially in closed canopy areas. In summer coyotes selected for lower long-term wolf use in shrub and closed habitats. Their selection in the open, though positive, was not significantly different from zero (*p* = 0.23) (Figure 3-6). For complete model output see Table S3-2.

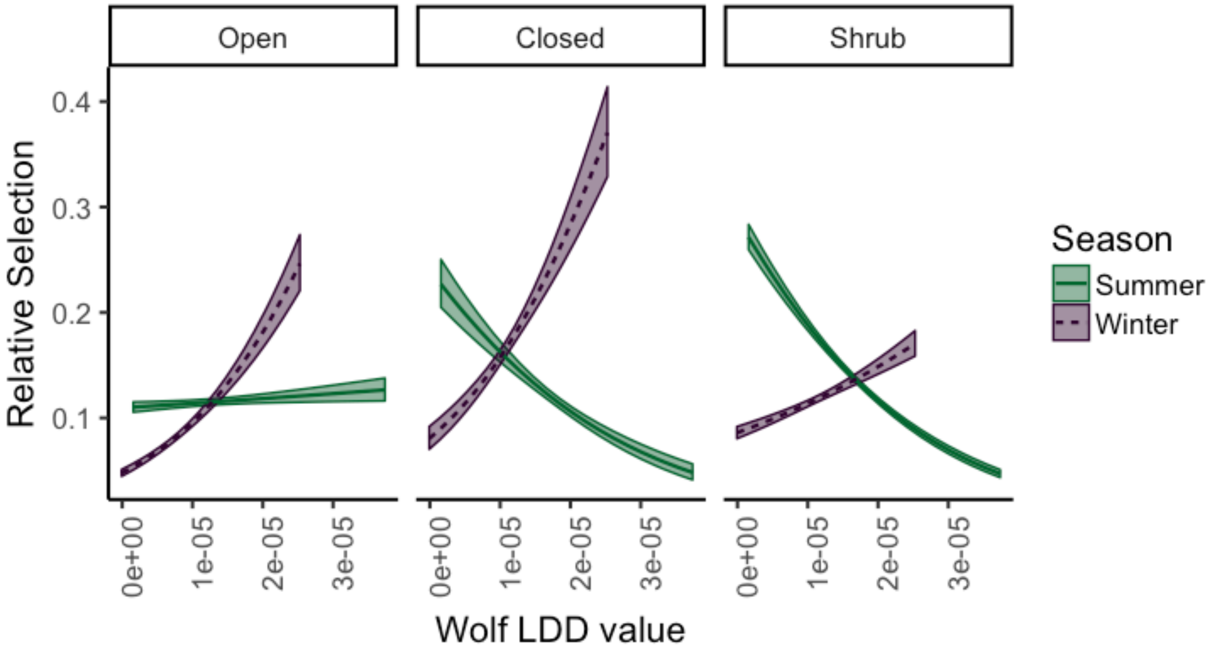


Figure 3-7. Effect of vegetation type, season, and long term wolf use (LDD value, see methods) on relative habitat selection by coyotes in Denali National Park, Alaska. Error bars show 95% CI as determined from fixed effects only, and should therefore be considered conservative.

## Discussion

We show that coyotes near the northern edge of their range in Alaska maintain very large territories and have seasonally-dependent responses to wolf risk. Coyotes consistently avoided proximity to wolves, but interestingly, coyote response to long-term wolf risk switched from one of avoidance in the summer to one of attraction in the winter. This pattern indicates a potential attraction to wolf-killed carrion resources, or a seasonal increase in risk tolerance due to restricted food availability and increased metabolic demands in winter. Ultimately the sub-arctic is a challenging place for coyotes due to marginal habitat quality, and our data suggest that season-specific responses to wolves help them balance the risk of interspecific killing with the acquisition of carrion, a key wintertime resource.

To our knowledge, our home range estimates (mean 291 km$^2$, range 57-1363 km$^2$) include the largest ever reported for coyotes. They are larger than home range sizes reported for other coyotes in Alaska: Thurber (1992) found an average MCP home range of 87 km$^2$, with one high outlier of 236 km$^2$, and Arthur (2003) found an average MCP home range of 118 km$^2$, although territories in areas without Dall sheep averaged 193 km$^2$. For comparison, coyote territories in Utah and Idaho were no larger than 40 km$^2$ on average, even during periods of low resource availability, and those in Texas were a mere 4 km$^2$ (Mills and Knowlton 1991; Gifford et al. 2017). This finding is in accordance with evidence suggesting that carnivore territories are generally larger at higher latitudes, and that this effect, as in other species, is driven by lower resource availability (Gompper and Gittleman 1991; South 1999; Withey and Marzluff 2009; Wilson and Shivik 2011). Reduced prey availability during cyclic lows in the snowshoe hare cycle could be an important limiting factor for northern coyote populations. As other authors have documented, animals with more locations were assigned larger territory values by all three methods (a phenomenon distinct from the under-calculation of kernel home ranges at extremely high fix rates) (Arthur and Schwartz 1999; Girard et al. 2002; Mills et al. 2006). Although the growing use of GPS collar technology means new studies generally have many locations per animal, we caution authors to keep this pattern in mind when comparing datasets with limited locations to those with many, even when the same technique was used to calculate home range size.

The average annual survival of coyotes reported here (0.50) is lower than other studies in Alaska (Thurber 1992; Prugh et al. 2005), and low compared to survival rates for adult coyotes documented in populations at lower latitudes (e.g. Bekoff 1977, Chamberlain and Leopold 2001, Gese 2001, 2005, Berger and Gese 2007). Anthropogenic mortality was low (0.14), suggesting that low coyote survival was not driven by exploitation. Instead, mortality from large carnivores was the leading cause of death. In other systems, mortality, including mortality from large carnivores, has been found to vary with age and residency class (Gese 2001; Berger and Gese 2007). We recommend further work to identify if particular demographic groups are more susceptible to interspecific killing or harvest in northern regions. Overall low resource levels may limit coyote survival directly, but may also drive secondary causes of mortality such as incurring risk by scavenging.

Despite being one of the most frequently studied apex-mesocarnivore dynamics, there are still many gaps in our understanding of the relationship between wolves and coyotes. For example, there is conflicting evidence on the key question of whether coyotes avoid wolves, ignore wolves, or are attracted to wolves (Berger and Gese 2007). In the cases demonstrating avoidance of wolves by coyotes, there is evidence for both reactive (e.g. Atwood & Gese, 2010) and predictive (e.g. Arjo & Pletscher, 1999) avoidance.

In this paper we demonstrate that coyotes in our system did not universally avoid wolf risk, but instead avoided wolves under some circumstances and were attracted to them under others. This contrasting pattern of attraction and avoidance is in accordance with previous work in this system which used snow tracking to reveal a positive spatial relationship between wolves and coyotes at fine spatial scales and a negative relationship at landscape scales (Sivy, Pozzanghera, Grace, et al. 2017). There are several reasons why coyotes could be selecting to be in areas of higher wolf use. The opportunity to scavenge could be a strong draw, especially in wintertime, and might explain coyotes' attraction to areas of high wolf use during this season (Switalski 2003; Merkle et al. 2009). Previous studies in Alaska have shown high levels of carrion in coyote diet (Prugh et al. 2008; Sivy, Pozzanghera, Colson, et al. 2017). Alternately, coyotes' use of common areas may be a by-product of environmental factors. For example, deep wintertime snows put strong constraints on energy use, and the pressure to select the easiest travel routes may force both wolves and coyotes into similar areas. This hypothesis is supported by coyotes' preference for south-facing slopes, which would have the lowest average snow load (Varhola et al. 2010). Our results also indicate that in open areas coyotes may not react as strongly to either long-term or short-term wolf risk, suggesting that vegetated areas may be perceived as riskier by coyotes, despite the higher relative selection values of those habitat types. Coyote territories and core areas were not restricted to the edges of wolf territories; a risk-avoidance method that has previously been hypothesized and reported for coyotes (Arjo and Pletscher 1999).

We also demonstrated that coyotes employ both reactive and predictive risk mediation strategies (or perhaps more accurately in this case, "predator response strategies," as wolves may have represented reward as well as risk), as evidenced by their spatial response to both short-term and long-term wolf risk. This suggests that memory, as well as sensory perception, is an important component of coyote spatial response to wolves. Consist with our finding that coyotes avoid proximity to wolves, other studies of mesocarnivore risk responses have demonstrated primarily reactive risk mediation, suggesting that selection for prey availability or other metrics of habitat quality supersede the risk of large carnivores except when they are actually present (Broekhuis et al. 2013; López-bao et al. 2016; Balme et al. 2017). However, the temporal duration of such work may have limited the ability to measure and detect responses to long-term risk. We encourage further work at temporal and spatial scales sufficient to detect both reactive and predictive responses.

There are several ways in which the measurement of the "risk landscape" for coyotes could be further refined. Both metrics of wolf risk in our analysis accounted only for the location and landscape use of collared wolves and the individuals with them. Transient wolves and sub-groups which split off from the pack may have added additional wolf risk to the landscape that we were unable to capture (Benson and Patterson 2015). This likely had greater impact on the distance-to-wolf calculations, and we suggest that additional research with greater temporal resolution and higher collaring rate be conducted to better assess coyote response to nearby wolves. In addition, the presence of bears on the landscape in summer likely represents a second important source of risk to coyotes, as well as affecting scavenging availability, as bears tend to monopolize carcasses and might reduce the opportunities for scavenging by coyotes (Tallian et al. 2017). Lastly, due to the limited geographic distribution of human use and development in the study area, we were unable to incorporate an element of human risk. However, as with wolf risk, we expect that coyotes would have a complex response to human use, as it combines direct mortality threats, potential food resources, and potential shielding effect from wolves and bears (Valeix et al. 2012; Newsome et al. 2015; Fedriani et al. 2016; Steyaert et al. 2016). Additional work at larger geographic scales, capturing a broad spectrum of human use in northern latitudes, is important for a complete understanding of coyote ecology in these areas.

As with any RSF approach, we made assumptions about "availability" that may not be supported (Kertson and Marzluff 2011). For example, even for such a wide-ranging animal as a coyote, all points within the home range are not feasibly "available" compared to a given location. In addition, if inter-specific risk does indeed strongly structure coyote selection, some areas within the home range will be functionally unavailable due to untenable risk levels, at least at certain times (e.g. area around a wolf den). The sampling resolution of our data precluded a supportable movement-based or UD-based evaluation of resource use, but using such techniques on data of a finer resolution would reduce uncertainty associated with characterizing availability.

This additional information on coyotes at high latitudes, including their response to wolves, helps predict changes in coyote population and space use associated with natural or anthropogenic reductions in the wolf population following increased development, harvest, or control. Northern environments are challenging for coyotes – the combination of limited prey resources, harsh abiotic conditions, and interspecific killing result in low density and low survival. For these reasons, we predict that coyotes would be unable to reach high densities in non-urban northern environments regardless of wolf presence. This information also aids in forecasting the consequences of habitat changes in the sub-arctic associated with climate change. Expansion of shrub and forest habitats is projected to change species distribution and abundance throughout the arctic (Clark et al. 2010; Tape, Gustine, et al. 2016; Tape, Christie, et al. 2016; Sokolov et al. 2018). This study and others found that coyotes prefer shrub and forested areas over open tundra (Pozzanghera 2015). We thus predict that coyotes will benefit from climate change because it will bring milder winter conditions, increase preferred habitat, and increase prey base, particularly snowshoe hare. Finally, insight into how coyotes were able to colonize and persist in areas with resident wolf populations helps clarify wolf-coyote population dynamics and apex-mesopredator population dynamics more broadly by offering evidence that apex-mesopredator interactions are driven by complex behavior patterns that vary in space and time. It also offers insight into the ecological dynamics of other expanding populations of mesocarnivores, such as golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), and raccoon (*Procyon lotor*) (Berteaux et al. 2015, Mori et al. 2015, Norén et al. 2015, Krofel et al. 2017, Larivière and Lariviere 2018, Salgado 2018, Sokolov et al. 2018), who may be using similarly complex risk mediation strategies to colonize and persist in novel environments.

## Conclusion

Although less frequently studied, coyotes at high latitudes have colonized areas with saturated wolf populations, indicating they can successfully manage the risk posed by wolves. These populations offer important opportunities to understand how mesopredators coexist with apex predators. We found that coyotes did not universally avoid the risk of wolves. Instead they leveraged variation in wolf risk associated with seasonality, and potentially habitat type, to take advantage of limited resources. There is evidence that this population of coyotes may be resource-limited, so effective use of prey-rich habitat and ability to take advantage of carrion may be key to coyote survival, and thus worth some increased risk of exposure to wolves. Further work investigating mesopredator response to the variable nature of apex predator risk should be conducted, as it has the potential to reveal nuances of behavior that underpin observed ecological patterns.

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## Supplementary Materials

### *Model Selection*

Table S3-1. Top five resource selection function models (out of 416), based on AIC ranking, for coyotes in summer (April-September) and winter (October-March) in Denali National Park and Preserve, Alaska. † Denotes full model.

| Model | K | logLik | AIC | delta | weight |
|---|---|---|---|---|---|
| Winter | | | | | |
| slope + slope$^2$ + aspect + vegetation type * distance to wolf + vegetation type * long term wolf use + distance to linear feature + distance to linear feature$^2$ + 1 \| CoyoteID † | 17 | -19610.6 | 39255.3 | 0.000 | 0.8064 |
| slope + slope$^2$ + aspect + vegetation type * distance to wolf + vegetation type * long term wolf use + distance to linear feature + 1 \| CoyoteID | 16 | -19613.1 | 39258.1 | 2.853 | 0.1936 |
| slope + slope$^2$ + aspect + vegetation type * long term wolf use + distance to linear feature + distance to linear feature$^2$ + 1 \| CoyoteID | 14 | -19628.7 | 39285.3 | 30.031 | 0.0000 |
| slope + slope$^2$ + aspect + distance to wolf + vegetation type * long term wolf use + distance to linear feature + distance to linear feature$^2$ + 1 \| CoyoteID | 15 | -19628.5 | 39287.0 | 31.758 | 0.0000 |
| slope + slope$^2$ + aspect + vegetation type * long term wolf use + distance to linear feature + 1 \| CoyoteID | 13 | -19631.0 | 39288.0 | 32.716 | 0.0000 |
| Summer | | | | | |
| slope + slope$^2$ + aspect + vegetation type * distance to wolf + vegetation type * long term wolf use + distance to linear feature$^2$ + 1 \| CoyoteID | 16 | -28167.9 | 56367.7 | 0.000 | 0.6376 |
| slope + slope$^2$ + aspect + vegetation type * distance to wolf + vegetation type * long term wolf use + distance to linear feature + distance to linear feature$^2$ + 1 \| CoyoteID † | 17 | -28167.4 | 56368.9 | 1.133 | 0.3618 |
| slope + slope$^2$ + aspect + distance to wolf + vegetation type * long term wolf use + distance to linear feature$^2$ + 1 \| CoyoteID | 14 | -28177.2 | 56382.4 | 14.620 | 0.0004 |
| slope + slope$^2$ + aspect + vegetation type * long term wolf use + distance to wolf+ distance to linear feature + distance to linear feature$^2$ + 1 \| CoyoteID | 15 | -28176.8 | 56383.6 | 15.825 | 0.0002 |
| slope + slope$^2$ + aspect + vegetation type * long term wolf use + distance to linear feature$^2$ + 1 \| CoyoteID | 13 | -28184.3 | 56394.6 | 26.809 | 0.0000 |

### *Model results*

Table S3-2. Effects of environmental variables and wolf risk variables on coyote habitat selection in Denali National Park Alaska. Distances are in kilometers. Slope and distance values have been scaled and centered, scaled units are as follows. Summer: Slope 11.6 degrees; Distance to linear feature 0.84km; Distance to nearest wolf 8.62km. Winter: Slope 11.6 degrees; Distance to linear feature 0.83km; Distance to nearest wolf 8.65km.

| | Summer | | | Winter | | |
|---|---|---|---|---|---|---|
| | Odds Ratio | CI | p | Odds Ratio | CI | p |
| Fixed Effects | | | | | | |
| (Intercept) | 0.11 | 0.07 – 0.19 | <0.001 | 0.08 | 0.05 – 0.14 | <0.001 |
| Slope | 4.79 | 4.34 – 5.28 | <0.001 | 2.96 | 2.65 – 3.30 | <0.001 |
| Slope^2 | 0.17 | 0.15 – 0.19 | <0.001 | 0.35 | 0.31 – 0.40 | <0.001 |
| Aspect | | | | | | |
| *Aspect: North* | 1.10 | 1.03 – 1.17 | 0.004 | 1.18 | 1.10 – 1.28 | <0.001 |
| *Aspect: South* | 1.35 | 1.27 – 1.44 | <0.001 | 1.87 | 1.74 – 2.02 | <0.001 |
| *Aspect: West* | 1.32 | 1.25 – 1.40 | <0.001 | 1.29 | 1.21 – 1.39 | <0.001 |
| Distance to linear feature (summer) | 1.02 | 0.95 – 1.10 | 0.522 | | | |
| Distance to linear feature (summer) squared | 0.84 | 0.77 – 0.91 | <0.001 | | | |
| Vegetation | | | | | | |
| *Vegetation: Closed* | 1.16 | 1.06 – 1.25 | <0.001 | 1.76 | 1.59 – 1.95 | <0.001 |
| *Vegetation: Shrub* | 1.33 | 1.25 – 1.41 | <0.001 | 1.23 | 1.13 – 1.34 | <0.001 |
| Distance to nearest wolf | 0.89 | 0.85 – 0.93 | <0.001 | 0.83 | 0.78 – 0.89 | <0.001 |
| Summer long-term wolf use intensity | 1.03 | 0.98 – 1.08 | 0.229 | | | |
| Veg:Closed x Distance to wolf | 1.17 | 1.09 – 1.26 | <0.001 | 1.20 | 1.10 – 1.31 | <0.001 |
| Veg:Shrub x Distance to wolf | 1.09 | 1.04 – 1.15 | 0.001 | 1.25 | 1.16 – 1.35 | <0.001 |
| Veg:Closed x Summer long-term wolf use intensity | 0.70 | 0.64 – 0.78 | <0.001 | | | |
| Veg:Shrub x Summer long-term wolf use intensity | 0.67 | 0.63 – 0.71 | <0.001 | | | |
| Distance to linear feature (winter) | | | | 0.60 | 0.55 – 0.66 | <0.001 |
| Distance to linear feature (winter) squared | | | | 1.24 | 1.10 – 1.40 | <0.001 |
| Winter long-term wolf use intensity | | | | 1.45 | 1.34 – 1.57 | <0.001 |
| Veg:Closed x Winter long-term wolf use intensity | | | | 1.01 | 0.90 – 1.13 | 0.909 |
| Veg:Shrub x Winter long-term wolf use intensity | | | | 0.80 | 0.73 – 0.88 | <0.001 |

Random Effects

| | | |
|---|---|---|
| Between-group variance, CoyoteID | 0.573 | 0.606 |
| N CoyoteID | 8 | 8 |
| ICC CoyoteID | 0.148 | 0.155 |
| Observations | 86073 | 60142 |
| Tjur's D | 0.130 | 0.180 |
| AIC | 55321.168 | 37260.361 |
| Deviance | 55231.425 | 37173.705 |

Table S3-3. Effects of environmental variables and wolf risk variables on coyote habitat selection in Denali National Park Alaska when locations are restricted to those 18m or less from the nearest wolf, Distances are in kilometers. Slope and distance values have been scaled and centered, scaled units are as follows. Summer: Slope 11.5 degrees; Distance to linear feature 0.79km; Distance to nearest wolf 4.6km. Winter: Slope 11.4 degrees; Distance to linear feature 0.77km; Distance to nearest wolf 4.6km.

| | Summer | | | Winter | | |
|---|---|---|---|---|---|---|
| | Odds Ratio | CI | p | Odds Ratio | CI | p |
| Fixed Parts | | | | | | |
| (Intercept) | 0.13 | 0.08 – 0.20 | <0.001 | 0.10 | 0.06 – 0.17 | <0.001 |
| Slope | 4.94 | 4.41 – 5.53 | <0.001 | 3.13 | 2.75 – 3.56 | <0.001 |
| Slope squared | 0.17 | 0.15 – 0.20 | <0.001 | 0.34 | 0.29 – 0.39 | <0.001 |
| aspect | | | | | | |
| Aspect: North | 1.11 | 1.04 – 1.20 | 0.004 | 1.22 | 1.11 – 1.33 | <0.001 |
| Aspect: South | 1.33 | 1.24 – 1.44 | <0.001 | 1.80 | 1.64 – 1.96 | <0.001 |
| Aspect: West | 1.33 | 1.24 – 1.42 | <0.001 | 1.24 | 1.14 – 1.35 | <0.001 |
| veg | | | | | | |
| Distance to linear feature (summer) | 1.11 | 1.01 – 1.22 | 0.036 | 1.58 | 1.41 – 1.77 | <0.001 |
| Distance to linear feature (summer) squared | 1.31 | 1.22 – 1.41 | <0.001 | 1.11 | 1.01 – 1.21 | 0.034 |
| Vegetation: Closed | 1.07 | 1.01 – 1.12 | 0.012 | 0.99 | 0.92 – 1.06 | 0.789 |
| Vegetation: Shrub | 1.04 | 0.99 – 1.10 | 0.148 | | | |
| Distance to nearest wolf | 0.99 | 0.91 – 1.08 | 0.904 | | | |
| Summer long-term wolf use intensity | 0.82 | 0.74 – 0.91 | <0.001 | | | |
| Veg:Closed x Distance to wolf | 1.15 | 1.05 – 1.25 | 0.002 | 1.09 | 1.00 – 1.20 | 0.057 |
| Veg:Shrub x Distance to wolf | 1.06 | 1.00 – 1.13 | 0.054 | 1.14 | 1.05 – 1.24 | 0.001 |
| Veg:Closed x Summer long-term wolf use intensity | 0.64 | 0.56 – 0.72 | <0.001 | | | |
| Veg:Shrub x Summer long-term wolf use intensity | 0.68 | 0.64 – 0.73 | <0.001 | | | |
| Distance to linear feature (winter) | | | | 1.33 | 1.22 – 1.45 | <0.001 |
| Distance to linear feature (winter) squared | | | | 0.58 | 0.52 – 0.65 | <0.001 |
| Winter long-term wolf use intensity | | | | 1.17 | 1.01 – 1.35 | 0.033 |
| Veg:Closed x Winter long-term wolf use intensity | | | | 0.97 | 0.85 – 1.10 | 0.647 |
| Veg:Shrub x Winter long-term wolf use intensity | | | | 0.80 | 0.72 – 0.88 | <0.001 |
| Random Parts | | | | | | |

| | | |
|---|---|---|
| $\tau_{00, \text{CoyoteID}}$ | 0.488 | 0.560 |
| $N_{\text{CoyoteID}}$ | 8 | 8 |
| $\text{ICC}_{\text{CoyoteID}}$ | 0.129 | 0.145 |
| Observations | 60686 | 42574 |
| Tjur's D | 0.122 | 0.167 |
| AIC | 40666.472 | 27195.986 |
| Deviance | 40580.117 | 27112.168 |

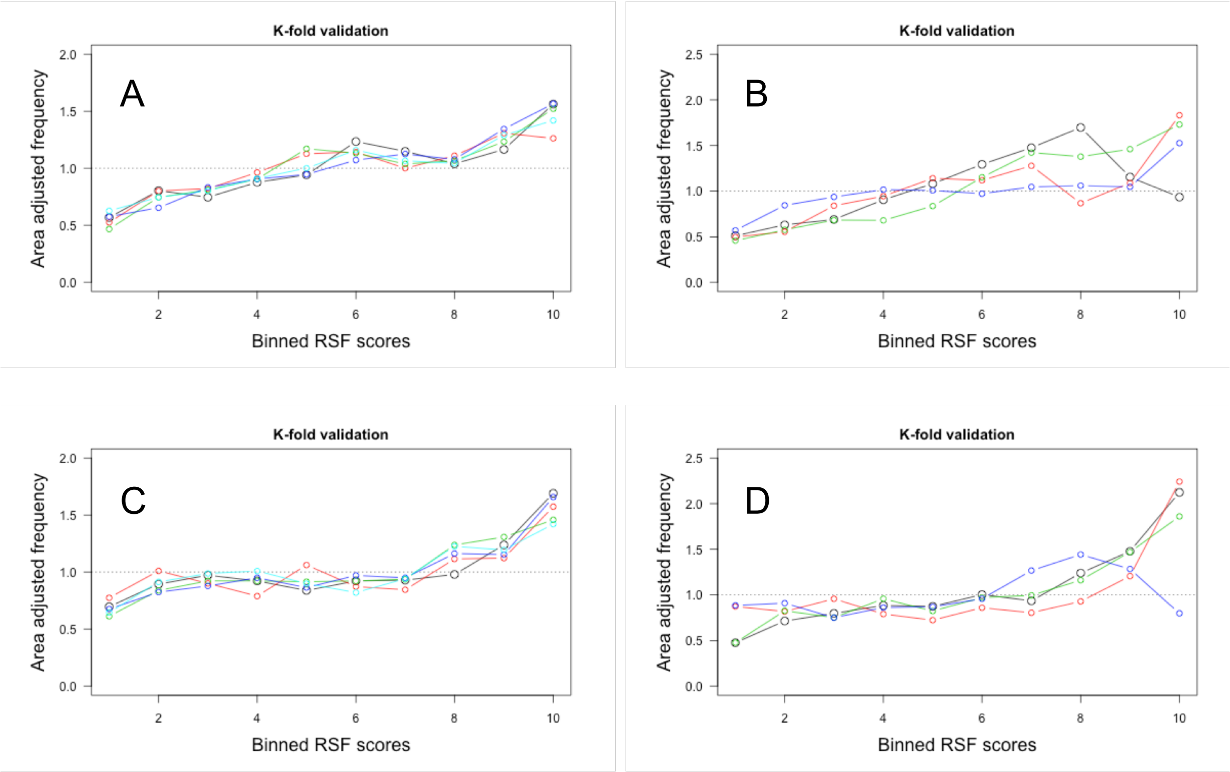

Figure S3-1. K-fold cross-validation results. A: summer, 5-fold random cross-validation. B: summer, individual blocking by coyote, two coyotes per fold. C: winter, 5-fold random cross-validation. D: winter, individual blocking by coyote, two coyotes per fold. Each color represents a fold.

# Chapter Four: General Conclusion

I demonstrated that mesocarnivore response to risk was both species-specific and context-dependent, and that the risk posed by large carnivores structures mesocarnivore behavior that ultimately informs scavenging patterns and habitat selection in this system. Contrary to the implication of the term "provisioning," wintertime carcass sites appeared to carry significant risk for coyotes and foxes, resulting in a low use of this resource by those species, and allowing wolverines and wolves to dominate carrion consumption on all carcass types. The importance of intraguild competition for carrion resources, including by apex predators who may also be "apex scavengers," deserves further study. I found that although coyotes have been able to successfully colonize an area with a robust wolf population, their large territory size and low survival suggest that limited resources and intraguild predation may prevent the population from achieving densities seen at lower latitudes. I also found that coyotes had a complex, context-dependent response to wolf risk wherein despite avoiding wolf proximity and selecting areas of low wolf activity in summer, they switched to selecting areas of high wolf activity in winter. I conclude that the demographic effects of top carnivores likely result from multiple mechanisms, especially in harsh environments where meeting fitness needs may involve unavoidable increases in risk. Additional studies should seek to examine these simultaneous and sometimes conflicting interactions by understanding the behaviors that underpin observed ecological patterns.