DIRECT AND INDIRECT EFFECTS OF WOLVES ON INTERIOR ALASKA'S MESOPREDATOR COMMUNITY

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A

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Abstract

Large carnivores may indirectly benefit small predators by suppressing competitively dominant mesopredators. However, our current understanding of interactions within the carnivore guild does not account for carrion subsidies provided by large carnivores, which could facilitate mesopredators during times of prey scarcity. This could be particularly relevant in northern ecosystems characterized by long harsh winters and decadal prey cycling. In Alaska, state-sponsored wolf (*Canis lupus*) control programs reduce wolf populations by as much as 50-80% across 8 game management units that collectively total over 165,000 km^2, yet the impact of this practice on the Alaska's diverse mesopredator community remains unknown. We used a quasi-experiment resulting from a wolf control program in the upper Susitna River Basin that was adjacent to Denali National Park and Preserve lands, where wolves occur at naturally regulated densities. From January-March 2013 and 2014, we collected coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) scats and conducted snow track surveys for wolves, mesocarnivores, and their prey. I quantified the relative strengths of direct and indirect effects of wolves on 5 mesopredator species while accounting for snowpack characteristics and small mammal abundance, and assessed winter diet overlap and composition by coyotes and red foxes in response to wolves and small prey availability. My findings indicated that wolves could strongly influence mesocarnivore communities in the Denali and Susitna systems, however despite a strong effect of wolves on coyotes, there was no evidence to support a mesopredator release cascade mediated by coyotes. Rather, I observed a near guild-wide response to wolf presence, whereby mesopredators were positively associated with wolves within each study area. The relative strength of top down versus bottom up effects in this study system further indicated that during a period characterized by low small mammal abundance, wolves were the strongest predictor of canid and wolverine occurrence. Coyote and red fox diet further revealed that carrion was a heavily used resource during this time of low prey abundance, yet red foxes may minimize competition with coyotes for carrion by increasing their use of voles. Finally, I present a hypothesis that local scale facilitation by large carnivores could lead to landscape patterns of suppression by large carnivores, suggesting a key link between abundance patterns and the structure of carnivore communities at different spatial scales relevant to conservation and management.

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Chapter 1 General Introduction

1.1 Introduction

Carnivores are integral components to ecosystem functioning via their strong influence on community structure and food webs (Ray et al. 2005; Ripple et al. 2014). This includes direct (i.e., predation, consumption) and indirect (e.g., predation risk, non-consumption) pathways that influence the population structure, abundance, behavior, physiology and distribution of other species (Peckarsky et al. 2008). Through these pathways, the presence of intact, healthy carnivore populations has ultimately been linked to biodiversity and ecosystem health and functioning in marine and terrestrial systems alike (Berger et al. 2001; Ripple et al. 2001, 2014).

Throughout the globe, large carnivore populations have undergone dramatic range contractions and population declines after decades of habitat loss and centuries of persecution (Morrison et al. 2007). Yet recent recovery efforts in North America and Europe highlight the shifting perception that these animals are now considered of utmost conservation value (Ritchie et al. 2012; Chapron et al. 2014; Ripple et al. 2014). For example, returning large carnivores to their native range can alleviate impacts triggered by overabundant ungulate populations, as predicted by trophic cascade theory (Hairston et al. 1960; Berger et al. 2001; Côté et al. 2004; Beschta & Ripple 2009; Ripple & Beschta 2012a, 2012b). However, as the prospect of carnivores as ecosystem restoration tools has gained traction with conservation groups eager to tout the benefits of carnivores recolonization, many have overlooked that the extent of carnivore cascades can be highly context dependent, and in-depth examinations have been limited to a handful of ecosystems largely contained within protected areas (Mech 2012).

Moreover, as the significance of dynamics within the carnivore guild continues to be revealed, there is increased recognition of how changes to carnivore community structure precipitated by the presence or absence of large carnivores can result in cascading influences on other carnivores. Such carnivore cascades can impact prey species, community stability, and overall ecosystem health (Soulé et al. 1988; Crooks & Soulé 1999; Berger et al. 2008; Ritchie & Johnson 2009; Miller et al. 2012). Thus, managing for a desired carnivore species and ecological outcome is challenging from a socioeconomic standpoint, when manipulating the abundance of one carnivore species based one set of conservation objectives could indirectly influence another carnivore species and inadvertently cause a new suite of management challenges. As large carnivore recovery efforts take place, it will be critical to refine our understanding of how apex carnivores influence carnivore communities, in order to better predict outcomes with respect to management and conservation goals.

1.2 The role of suppression in carnivore communities

Carnivore communities are hierarchically structured by a network of complex interaction pathways linked by competition, shared food resources, and intraguild predation (Holt & Polis 1997; Palomares & Caro 1999; Roemer et al. 2009; Ritchie & Johnson 2009). "Apex" carnivores are large bodied, top-tier consumers that tend to be exclusively carnivorous and occur at relatively low densities. Mesopredators, however, are middle-ranking carnivores of small to intermediate body size. They are typically generalist predators that exhibit some degree of omnivory and may occur at relatively high densities (Roemer et al. 2009; Prugh et al. 2009). Because competition is predicted to be most intense among carnivores with high niche overlap and similar body sizes (Donadio & Buskirk 2006), these smaller carnivores can be greatly impacted by their competitively dominant counterparts. In the most extreme cases, intraguild predation occurs when a dominant competitor kills and consumes an inferior competitor as a food resource, which commonly occurs among mammalian carnivores and can lead to further exclusion of the subordinate carnivore (Polis & Holt 1992; Palomares & Caro 1999).

Mesopredator populations are thus limited by higher-ranking carnivores through direct lethal encounters, yet are also susceptible to fear-induced behavioral changes that could ultimately influence reproduction, survival, and population growth (Ritchie & Johnson 2009). The population and community-level outcomes of these intraguild interactions can reduce the distribution or abundance of mesopredators. Thus, in the absence of top down regulation from an apex carnivore, populations of mesopredators can expand their distribution or abundance, known as "mesopredator release" (Soulé et al. 1988; Crooks & Soulé 1999).

Numerous studies throughout the globe have documented the preponderance of this ecological cascade (Ritchie & Johnson 2009). For example, the expansion of coyotes (*Canis latrans*) throughout the United States from their native range in the Midwest is largely attributed to mesopredator release following the near extirpation of wolves (*Canis lupus*) in the early 20th century. Subsequent re-introduction of wolves to the Greater Yellowstone Ecosystem in the 1990s is hypothesized to have caused dramatic changes to coyote behavior and abundance (Smith et al. 2003; Ripple et al. 2013). In Australia, the presence of dingoes (*Canis dingo*) may limit populations of invasive red foxes (*Vulpes vulpes*), with cascading influences on small mammals (Colman et al. 2014). Across Europe, increases in red foxes are associated with declines in Eurasian lynx (*Lynx lynx*) and wolves (Elmhagen & Rushton 2007; Elmhagen et al. 2010; Pasanen-Mortensen et al. 2013). And in Africa, hyenas (*Crocuta crocuta*) and African lions (*Panthera leo*) may limit densities of African wild dogs (*Lycaon pictus*) (Creel & Creel 1996).

Mesopredator release can lead to ecosystem imbalances by increasing predation pressure on prey species (Berger & Conner 2008; Miller et al. 2012; Prugh & Arthur 2015). Yet for diverse carnivore guilds comprised of several mesopredators that overlap in resource use, share similar prey, or are possible prey themselves, the presence or absence of large carnivores could further initiate a cascade of indirect effects through the suppression or release of a dominant mesocarnivore (Linnell & Strand 2000). For example, coyotes are widely documented to outcompete and even exclude red foxes through interference, exploitation, and intraguild predation where they overlap in range (Harrison et al. 1989; Sargeant & Allen 1989; Theberge & Wedeles 1989; Gese et al. 1996b). However, where wolves are also present, decadal trends suggest a tri-trophic cascade in abundance patterns among wolves, coyotes and foxes (Levi & Wilmers 2012; Newsome & Ripple 2015). Coyotes and lynx (*Lynx canadensis*) compete for shared prey (snowshoe hares (*Lepus americanus*)) and exploit similar habitats (Buskirk et al. 2000), causing speculation that wolf presence could also benefit lynx conservation efforts by suppressing coyotes (Ripple et al. 2011). Because lynx may adversely affect red foxes (Sunde et al. 1999; Helldin et al. 2006), an interaction cascade could be possible among wolves, coyotes, lynx and red foxes. Finally, cascading effects could amplify for mustelids such as marten and fishers (*Martes* spp.), and weasels (*Mustela* spp.). These species may be adversely impacted by lynx, coyotes, and red fox, evidenced by high diet overlap, negatively correlated abundance patterns, and incidents of intraguild predation (Storch et al. 1990; Lindstrom et al. 1995; Bull & Heater 2001; St-Pierre et al. 2006; Hodgman et al. 2013; Lapoint et al. 2014). These small mesopredators at the "bottom" tier of the mesopredator guild may be especially susceptible to indirect effects resulting from carnivore cascades.

A substantial body of research from North America and Europe examining interactions between large carnivores and mesocarnivores suggests that patterns of suppression and release could lead to a multitude of indirect effects (Ritchie & Johnson 2009). Yet these piecewise examinations are limited in providing a broader picture of how large carnivores may influence entire communities. Equally important is that relatively few studies have examined patterns of suppression and release with respect to spatial scale. Of the few studies that have examined these influences at scales relevant for conservation and management, patterns of suppression, and the mechanisms that produce them, have not been as clear (Gehrt & Prange 2007; Berger et al. 2008; Allen et al. 2014, 2015; Colman et al. 2014). Competitive forces may not be the sole driver of carnivore community dynamics.

1.3 The role of facilitation in carnivore communities

Though competition is a dominant force in species interactions and community structure, ecologists are beginning to explore the significance of positive interactions in community stability and persistence (Selva & Fortuna 2007; Gross 2008; Filotas et al. 2010). In particular, facilitation is a blend of mutualism and commensalism, and occurs when the actions or behavior of a facilitator species benefits one or more other species, while the "facilitator" remains unaffected (Bruno et al. 2003). The asymmetrical interactions originating from even a single facilitator species can strongly influence the diversity and resistance of plant, aquatic, and animal communities through modification of the physical or biotic environment that ultimately minimizes environmental or biotic stressors for one or more recipient species (Stachowicz 2001; Barrio et al. 2013).

Facilitation presents a compelling framework to evaluate the relative strength of positive interaction pathways among carnivores, and could provide an alternative explanation for unclear patterns of suppression and mesopredator release apparent in some systems. Large carnivores, through predation on large herbivores, provide substantial food subsidies to a diverse community of insect, avian, and mammalian scavengers (Moleón et al. 2014). Despite the growing acknowledgement in the scientific literature of the prevalence and importance of scavenging, especially among mammalian carnivores, this process remains underestimated in food webs and community ecology by as much as 16-fold (Devault et al. 2003; Selva & Fortuna 2007; Wilson & Wolkovich 2011; Elbroch & Wittmer 2012; Pereira et al. 2014; Moleón et al. 2014). Nonetheless, scavenging is a foraging strategy shared by many mesopredators, and carrion inputs provided by intact large carnivore populations present rich supplemental food resources. Following wolf reintroduction in Yellowstone, carrion from wolf-killed ungulates provided an average of 13,220 kg of edible biomass to scavengers in winter through early spring (Wilmers et al. 2003b). Unlike seasonal pulses of non-predation ungulate mortality (e.g., winter kill, drought, hunting), ungulates killed by large carnivores are more evenly distributed in space and time, which is predicted to stabilize communities (Ostfeld & Keesing 2000; Wilmers et al. 2003b). These additional resource inputs allow mesocarnivores to persist during periods when they are otherwise limited by availability of small prey (Wiens 1993; Killengreen et al. 2011; Newsome et al. 2014; Pereira et al. 2014), and the net benefits of scavenging from large carnivore-provided carrion can ripple through to multiple trophic guild levels (Cortés-Avizanda et al. 2009).

Gradients of environmental stress could strongly influence the net effects of competitive versus facilitative pathways in animal communities (Stachowicz 2001; Barrio et al. 2013). In high stress environments, facilitation is expected to predominate, whereas in low stress environments, competition is expected to dominate (Bertness & Callaway 1994; Stachowicz 2001). In northern climates, inherently long, cold winters place high energetic demands on winter residents (Anderson & Jetz 2005). These ecosystems are further stressed by dramatic fluctuations in prey availability as a result of snowshoe hare and vole population cycles (Korpimaki & Krebs 1996), which creates "feast or famine" conditions for predators. Therefore, the facilitative pathways from large carnivores to mesopredators could be a particularly relevant area of research in northern ecosystems characterized by environmental and biotic stressors.

Winter food subsidies made available by large carnivores could allow mesopredators to persist in environments where they may otherwise be excluded by gradients of environmental stress (Bruno et al. 2003). Carrion is regularly used by scavengers in northern climates (Gibson et al. 1984; Selva et al. 2003, 2005; Dalerum et al. 2009; Mattisson et al. 2011), and winter food resources that coincide with pre-breeding periods may be a key determinant of reproductive success for many mesocarnivore species (Gese et al. 1996a; van Dijk et al. 2008; Needham & Odden 2014). Facilitation of mesopredators during periods of high energetic demand (e.g., winter) when mesocarnivores are otherwise limited by availability of their primary prey (e.g., hares) could outweigh the negative effects resulting from competition or predation by large carnivores. Compared to other ecosystems where scavenging occurs but environment conditions are less extreme, winter carrion subsidies when small mammals are scarce could translate to a net positive effect of large carnivores on mesopredators, which could strongly influence the net effect of large carnivores on the community as a whole.

1.4 Summary

Quantifying the strength of facilitative versus suppressive pathways within the carnivore guild will be a critical advancement for understanding community structure, especially in environments that naturally fluctuate between extremes in seasonality, prey availability, or both. As anthropogenic impacts continue to compound in ways strongly expected to influence environmental extremes (e.g., temperature, precipitation), understanding the role of large carnivores in carnivore community dynamics should yield promising insights, as large carnivores could serve as important buffers against the predicted extremes of climate change and anthropogenic impacts (Wilmers & Getz 2005; Wilmers & Post 2006; Pereira et al. 2014). Given the high profile topic of large carnivores as restoration tools, a holistic examination of these links over scales relevant to conservation and management is especially timely, and will be an important step in elucidating the role of large carnivores in community stability.

1.5 Study system

The gray wolf is the prominent large carnivore in Alaska. While gray wolves were nearly extirpated in the lower 48, populations in Alaska have persisted, and even thrived, prompting citizens to argue for predator control in the interest of ensuring ungulate hunting opportunity for humans. At present, predator control programs reduce wolf densities by 50-80% across 8 management units, collectively totaling over 165,000 km^2 (ADF&G 2015). Coyotes first appeared in Alaska in the early 1900s, with locally abundant populations now present throughout the state (Parker 1995). Wolves strongly suppress coyote populations through direct killing and by inducing avoidance behaviors that result in altered habitat use (Palomares & Caro 1999; Arjo & Pletscher 2004; Berger & Gese 2007; Ritchie & Johnson 2009). Increased coyote presence in

Alaska has prompted specific concern for native species managed as furbearers, specifically red foxes, Canada lynx, and American marten (*Martes americanus*). However, wolf-provided carrion may benefit coyotes, other mesopredators, and wolverines (*Gulo gulo*), especially in northern ecosystems characterized by long, harsh winters and cyclic fluctuations in small mammal abundance. The abundance of Alaska's mesocarnivores is closely linked to the availability of small prey, in particular snowshoe hares and voles (Elton 1924; Korpimaki & Krebs 1996; O'Donoghue et al. 1997). The density of snowshoe hares can change 10-25 fold during their natural population cycling that peaks every 8-11 years (Krebs et al. 2001). However, hares have remained low in interior Alaska since their last peak in 2008-2010 (C. McIntyre, unpub. data). This presents an ideal opportunity to evaluate the relative strength of direct and indirect influences of wolves on interior Alaska's mesopredator community during a period of scarcity. Finally, climate change is expected to strongly influence snow characteristics that are in part thought to moderate resource overlap among mesocarnivores (Buskirk et al. 2000), which could further contribute to the strength and consequence of suppression versus facilitation.

1.6 Research objectives

I used a quasi-experiment presented by state predator control to examine the direct and indirect influence of wolves on mesopredators in interior Alaska. Unfortunately, logistics prevented the examination of more than a single control and treatment site, and the treatment was not randomly assigned or quantified. Therefore, I used a number of observational and quasi-experimental study concepts to support my inferences (Platt 1964, Cooke and Campbell 1979, Rosenbaum 2002), and my objectives were two-fold:

1) Determine the relative influence of wolves, prey, and snowpack on patterns of mesopredator occurrence. Repeated snow track surveys were conducted during winters 2013 and 2014 to examine patterns of space use by wolves and five mesopredator species in two study areas, one where the wolf population was naturally regulated and another where the wolf population was artificially reduced by predator control. I assessed the relative strengths of hypothesized facilitation and suppression pathways among wolves and mesopredators, using a novel integration of occupancy and structural equation models (SEM). The results of this work are presented in Chapter 2 of this thesis.

2) Determine coyote and red fox diet composition, and whether carrion use influences diet overlap between two sympatric mesopredators. Coyote and red fox scats were collected in winter 2013-2014 to examine diet composition, overlap, diversity and richness in two study areas, one where the wolf population was naturally regulated and another where the wolf population was artificially reduced by predator control. I hypothesized that diet overlap between coyotes and red foxes would increase with wolf presence, as a result of both species increasing selection for carrion in their diet; alternatively I hypothesized diet overlap and carrion selection would decrease in order to minimize competition. The results of this work are presented in Chapter 3 of this thesis.

Chapter 2 Guild-wide responses of mesopredators to wolves, prey and snowpack[1]

2.1 Abstract

Mesopredator release predicts range expansion of mesopredators in the absence or reduction of large carnivores, which can result in cascading ecosystem effects. However, few studies have examined guild-wide responses to large carnivores, which are likely to vary in strength due to complex interaction pathways. We examined patterns of space use by wolves (*Canis lupus*) and five mesopredator species to quantify the relative strengths of hypothesized direct and indirect pathways, while accounting for variation in prey and snow conditions. Snow track surveys were conducted in two study areas in interior Alaska that differed in wolf density because of a state-sponsored wolf control program. We integrated occupancy and structural equation models (SEM) to evaluate two hypotheses: 1) suppression-induced cascade, whereby wolves were predicted to have a net negative effect on coyotes (*C. latrans*) that would result in indirect, positive effects on smaller mesopredators, and 2) facilitation-induced cascade, whereby wolves were predicted to have a net positive effect on coyotes, due to carrion provisioning, that would result in indirect, negative effects on smaller mesopredators. We observed a near guild-wide, positive response of mesopredators to localized wolf presence, however we found no evidence that coyotes elicited either a facilitation or suppression induced cascade. The relative strength of top-down versus bottom-up effects in this study system indicated that during a period characterized by low small mammal abundance, wolves were the strongest predictor of canid and wolverine (*Gulo gulo*) occurrence. In contrast to local-scale patterns, a comparison across study areas supported a guild-wide negative response of mesopredators in the study area where wolves

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[1] Sivy. K.J., C.P.Pozzanghera, J. B. Grace, and L.R. Prugh. 2015. Guild-wide responses of mesopredators to wolves, prey and snowpack. Prepared for submission to *The American Naturalist*

were more abundant. We discuss how local-scale association with large carnivores could lead to landscape patterns of mesopredator suppression, suggesting a key link between abundance patterns and the structure of carnivore communities.

2.2 Introduction

Large carnivores strongly influence community structure and food webs through pathways that affect the behavior and distribution of numerous species, including small to intermediate-sized carnivores (i.e., mesopredators; Ripple et al. 2014; Ray et al. 2005; Peckarsky et al. 2008). In the absence of large carnivores, the mesopredator-release hypothesis predicts that loss of top-down control will lead to increased abundance and range expansion of mesopredators, which can drastically alter community interactions (Soulé et al. 1988; Crooks & Soulé 1999; Prugh et al. 2009). Given the recent efforts to restore large carnivores in parts of North America and Europe following near global declines over the last century (Chapron et al. 2014; Ripple et al. 2014), it is especially important to elucidate the role of top predators in structuring community dynamics.

Although numerous studies indicate the preponderance of mesopredator release (Ritchie & Johnson 2009), there is a paucity of studies examining the net effect of large carnivores on entire mesopredator guilds. The mesopredator-release hypothesis implies that negative interactions between large and small carnivores, such as competition and predation, are the predominant forces that structure carnivore communities. This has led to the prediction that large carnivores may indirectly benefit smaller mesopredators by suppressing populations of competitively dominant mesopredators (Ripple et al. 2011, 2013). For example, wolves (*Canis lupus*) may indirectly benefit red foxes (*Vulpes vulpes*) through coyote (*C. latrans*) suppression

(Levi & Wilmers 2012; Newsome & Ripple 2015). However, this framework disregards carrion subsidies from large carnivores that could substantially influence net effects on mesopredators, many of which are avid scavengers (Wilmers et al. 2003a; Filotas et al. 2010; Pereira et al. 2014).

In addition to the influence of carrion subsidies, prey availability can moderate the strength of top-down intraguild interactions among carnivores (Elmhagen & Rushton 2007), and high spatiotemporal variability that characterizes small prey abundance could result in patchy distributions of mesopredators at local scales. On the other hand, co-occurring species may segregate due to competition (Diamond 1975; Gotelli 2000), or due to use of non-overlapping resources or habitat attributes across the landscape, otherwise known as "habitat filtering" (Weiher & Keddy 1999). Accounting for the influence of key habitat characteristics should aid interpretation of patterns of species abundance as resource-driven or interaction-driven.

We took advantage of a quasi-experiment resulting from a state-sponsored wolf control program in Alaska to quantify the guild-wide response of mesopredators to the relative influence of wolves, prey, and snowpack. Wolves are the dominant large carnivore of Alaska's diverse carnivore community, yet wolf control programs reduce wolf densities by 50-80% across 8 game management units that collectively total over 165,000 km^2 (ADF&G 2015a). Coyotes first appeared in Alaska in the early 1900s, and locally abundant populations are now present throughout the state (Parker 1995). Wolves may suppress coyotes (Paquet 1991; Thurber et al. 1992; Palomares & Caro 1999; Smith et al. 2003), and coyotes are capable of suppressing numerous small mesopredators, including foxes, felids, and mustelids (Palomares & Caro 1999; Linnell & Strand 2000; Ritchie & Johnson 2009). Increased coyote presence in Alaska could therefore be a concern for native mesopredators such as red foxes, Canada lynx (*Lynx* *canadensis*), and American marten (*Martes americanus*). However, wolf-provided carrion may benefit coyotes, other mesopredators, and wolverines (*Gulo gulo*) that rely on scavenging, thus making the net effect of wolves on mesopredators unclear, especially in northern ecosystems characterized by long, harsh winters and cyclic fluctuations in small mammal abundance.

We examined carnivore occurrence patterns in two study areas, one within a game management unit where wolves were artificially reduced by wolf control, and one in adjacent National Park and Preserve land where wolves occured at naturally regulated densities. To assess the relative strengths and direction of hypothesized interaction pathways among wolves, mesopredators, prey and snow conditions, we conducted repeated snow-track surveys during winters 2013 and 2014 and used an integration of occupancy models and structural equation modeling (SEM) to analyze snow track data. Occupancy analysis uses repeat presence-absence surveys to provide unbiased estimation of the proportion of sites occupied while accounting for imperfect detection (MacKenzie et al. 2005) Although occupancy models are increasingly used to examine species interactions (Richmond et al. 2010; Burton et al. 2012; Bailey et al. 2014), multi-species occupancy models remain limited to inferences regarding species pairs rather than a suite of interacting species. SEM, however, provides a multivariate framework for simultaneously evaluating the relative strengths of hypothesized relationships, with the ability to isolate and compare direct and indirect effects within a system of interest (Grace 2006).

We used snow-track data to estimate detection and occupancy probabilities for wolves and mesocarnivores. Occupancy probabilities were then input into an SEM. The use of SEM enabled simultaneous evaluation of the strength (magnitude of path coefficients) and direction (+/-) of direct and indirect effects of wolves on five mesopredator species, while accounting for the effects of prey abundance and snow conditions, because these factors can mediate interactions among sympatric mesopredators (Raine 1983; Halpin & Bissonette 1988; Storch et al. 1990; Fuller 1991; Murray & Boutin 1991; Murray et al. 1994; Mech et al. 1998; Buskirk et al. 2000; Arjo & Pletscher 2004). For example, snowshoe hares (*Lepus americanus*) are the primary small prey for mesopredators in northern ecosystems, and hare density can change 10-25 fold during population cycles that peak every 8-11 years (Krebs et al. 2001). Populations of microtine rodents (e.g.,voles), another important group of small mammal prey, likewise undergo irruptive boom-bust cycles (Elton 1924; Korpimaki & Krebs 1996). Our study occurred during the low phase of the snowshoe hare population cycle, providing the opportunity to examine interactions among predators during a period of resource scarcity. We evaluated the following hypotheses:

1) <u>Suppression-induced cascade</u>-- Wolves suppress coyote occurrence, resulting in an indirect, net benefit to species most likely to be adversely impacted by coyotes (red foxes, lynx, and marten; Ripple et al. 2011; Levi & Wilmers 2012). Wolves should not suppress smaller mesopredators based on lower diet overlap and smaller body size ratios (Donadio & Buskirk 2006). Species most likely to be impacted by wolves due to competitive dominance and intraguild aggression will have a negative association with wolves (Palomares & Caro 1999).

2) <u>Facilitation-induced cascade</u>-- Wolves promote coyote occurrence due to carrion provisioning, resulting in an indirect, net negative effect on species most likely to be adversely impacted by coyotes. Species most likely to benefit from scavenging (coyotes,

red foxes, wolverine) will have a positive association with wolves (Gese et al. 1996; Wilmers et al. 2003b; Dalerum et al. 2009).

2.3 Methods

2.3.1 Study area

This study took place in two study areas in interior Alaska (Fig. 2.1), the Denali study area and Susitna study area (hereafter, "Denali" and "Susitna"). The region is a subarctic ecosystem characterized by long, cold winters averaging -24°C and short, mild summers averaging 17°C. Study areas were generally similar in climate, topography, composition of major habitat types, and anthropogenic use. There are few roads in either study area, limiting winter access. Primary winter transportation is by snowmobile, dog team, or small aircraft. The elevation ranged from 330-1,900 meters (Denali, $\bar{x}$ = 653 m ± 134 m SD; Susitna, $\bar{x}$ = 916 m ± 148 m SD). Predominant plant communities in both study areas were boreal forest and mixed deciduous forest (*Betula* sp. and *Populus tremuloides*; ($\bar{x}$ percent habitat cover, Denali = 0.27 ± 0.24 SD ; Susitna = 0.18 ± 0.19 SD), high and low elevation tussock and low shrub tundra (Denali, $\bar{x}$ = 0.622 ± 0.28 SD; Susitna, $\bar{x}$ = 0.694 ± 0.20 SD), shrubs (*Salix* spp. and *Alnus* spp.; Denali, $\bar{x}$ = 0.07 ± 0.12 SD; Susitna, $\bar{x}$ = 0.05 ± 0.06 SD), and alpine graminoid meadows. Moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall's sheep (*Ovis dalli*) were the sole ungulates. Small mammalian prey includes snowshoe hares, red squirrels (*Sciurus vulgaris*), and 5 species of voles (*Myodes rutilus* and *Microtus* spp.). Avian prey included willow ptarmigan (*Lagopus lagopus*) and spruce grouse (*Falcipennis canadensis*). The terrestrial mesopredator guild consisted of coyotes, red fox, Canada lynx, wolverine, American marten, and weasels (*Mustela nivalis, M. erminea*). Two aquatic mesopredators, the Northern river otter (*Lutra* *canadensis*) and mink (*M.vison*), were also present in both areas, but their distributions were restricted to riparian corridors and they were rarely encountered during track surveys. Although brown bears (*Ursus arctos*) and black bears (*U. americanus*) were present in both sites, they hibernate in the winter and were therefore not considered.

Denali was a 2,000-km^2 area overlapping the north-east corner of Denali National Park and Preserve (DNPP), which included 500 km^2 of state-managed land known as the Stampede corridor. Wolves are protected from hunting and trapping within the original Denali National Park boundary, yet subject to harvest in the Stampede corridor according to Alaska Department of Fish and Game (ADF&G) regulations and subsistence harvest in bordering Denali National Park and Preserve lands. However, harvest was not found to impact population dynamics within our study area (Borg et al. 2014), and we therefore considered this population to be naturally regulated. Wolf density in Denali averaged 7.6 wolves per 1,000 km^2 during the study period and was stable among years (S. Arthur, *personal communication*).

Susitna was located 200 km southeast of Denali and consisted of 1,800 km^2 of remote land in the upper Susitna River basin largely managed by the state, with some private and Native land allotments. As part of the larger Nelchina Basin Game Management Unit (GMU13), the wolf population in Susitna has been subject to 36-80% annual removal via aerial shooting since 2000 to achieve a target population size of 135-165 wolves over a 60,000-km^2 area. Although we could not quantify wolf density for our analysis, average track counts based on aerial surveys in 2012, 2013 and 2015 roughly translated to 3-3.5 wolves per 1,000 km^2, which was slightly higher than management objectives (ADF&G 2015b).

2.3.2 Snow track surveys

We conducted snow track surveys for wolves, mesopredators, and small prey along transects in randomly selected grid cells in Denali and Susitna from January-March 2013 and 2014. We used ArcGIS v10.0 (Environmental Systems Research Institute, Redlands, CA) to superimpose a grid of 4-km^2 cells over maps of each study area. This cell size represents the average home range size of marten, the smallest mesocarnivore in our study (Buskirk 1983). We re-classified land cover types identified by satellite imagery (Boggs et al. 2001, Kreig 1987) and assigned each grid cell to one of four major habitat types (tundra/meadow, spruce/mixed forest, tall shrub, and low shrub) based on the highest percentage of each habitat type present. We randomly selected a total of 100 cells stratified by habitat to survey in 2013. To increase sample size and maximize efficiency in 2014, we re-surveyed cells surveyed in 2013 and also surveyed all cells intercepted along trails travelled en route (Fig. 2.1).

Snow track surveys were conducted by snowmobile, dog team, or on foot (ski or snowshoes). To estimate detection probabilities, all cells were surveyed multiple times as either temporally replicated line transects or spatially replicated square transects based on terrain and snowmachine access (snowmobile use was prohibited within wilderness areas of DNPP). Linear transects were surveyed along pre-existing and temporary trails established and maintained for the duration of the study. When possible, trails were routed to bisect the grid cell with a minimum distance of 2 km. In cases where this was not possible (e.g., due to terrain or vegetation), trail distance was a minimum of 1 km and passed as close to the center of the grid cell as possible. Each individual track survey within a given cell corresponded to a single temporal replicate. For cells surveyed as square transects, observers travelled along a 4 km square-shaped transect by ski, snowshoes, or snowmobile. Each 1 km side of the square represented one replicate, for a total of four replicates surveyed in a single tracking session. Square transects were mapped ahead of time using ArcGIS and coordinates were uploaded to handheld GPS units (Garmin eTrex®30, Garmin Ltd.) for field navigation.

Snow track surveys were conducted a minimum of 24 hours after a track obliterating snowfall to allow for track accumulation. For each carnivore track detected, we identified species and recorded GPS coordinates and maximum age of track based on timing of snowfalls and surveys. Snow depth along survey routes was measured to the nearest centimeter using a meter stick. Snow compaction was indexed with a 200 gram cylinder weight (diameter = 8.2 cm, height = 4.2 cm) released 50 cm above the snow surface (Kolbe et al. 2007). Microhabitat (vegetation composition and percent cover within a 10 m radius), snow depth, and snow compaction were recorded at 500 meter intervals along each transect and averaged for each survey cell. Prey tracks (snowshoe hare, red squirrel, and vole) were tallied over 500-meter intervals and converted to tracks per kilometer, adjusted for days since last snow, and averaged for each survey cell.

2.3.3 Data analysis

Single-season, single-species occupancy models were constructed for wolf, coyote, red fox, lynx, wolverine and marten. The number of occasions was the maximum number of repeats conducted in survey cells, with unequal replicates between cells treated as missing data (MacKenzie et al. 2005). Occupancy probability, Psi (ψ), was modeled with study area (*area*) and survey year (*yr*) as grouping variables. No other covariates were used to model Psi because these factors (e.g., wolf and mesopredator presence, prey abundance, snow pack) would be accounted for in the SEM analysis. Detection probability for all species was modeled with the logit link and included survey method (*meth*), distance surveyed (*dist*), days since last snowfall (*dss*), observer team (*obs*), and year (*yr*) as covariates. Goodness of fit for the global detection model was assessed with the Pearson's χ^2-square test using 10,000 parametric bootstraps of the over-dispersion parameter, $\hat{c}$ (MacKenzie & Bailey 2004). Because sampling resolution was less than the average home range size for all species except marten, we interpreted occupancy probabilities as probabilities of use (Nichols et al. 2008; Kendall et al. 2013). Species-specific derived occupancy probabilities for each cell-year were estimated in Program PRESENCE v6.7. (Hines 2009) and used as input for the SEM analysis.

Cell-specific detection and occupancy probabilities for wolves and mesocarnivores modeled from snow track data were used as input to an SEM. We included cell-specific estimates of average snow depth, average snow compaction, and prey abundance (hares, voles, and red squirrels) as variables to account for the influence of prey and snowpack on carnivore occurrence. Prey track data were log-transformed to meet assumptions of normality (Zar 1999). Remaining study area effects were assessed by including the binary variable "study area," whereby 1 = Denali (naturally regulated wolf densities), and 0 = Susitna (wolf densities reduced by predator control).

We specified an a priori model of direct and indirect pathways in our study system based on our hypotheses and knowledge of species' life history in boreal ecosystems from literature review. We used a global estimation approach, which compares the covariance matrix of paths among observed data variables in our model to the covariance matrix implied by paths among variables specified in the a priori model. Maximum likelihood techniques were used for parameter estimation. Model fit was evaluated with Pearson's χ^2 test, whereby $p < 0.05$ indicates inconsistencies between the observed and model-implied covariance matrices and $p > 0.05$ indicates acceptable model fit (West et al. 2012). When biologically justified, model paths were modified to achieve fit based on modification indices (M.I.) greater than 3.84, which is the critical value for a single degree-of-freedom chi-square test at $\alpha = 0.05$. The M.I. thus estimates the expected change to the model χ^2 critical value for each single path. Correlated error terms were specified between variables to account for unmeasured factors influencing a directed path between a predictor and response. Unstandardized (raw) path coefficients were considered significant at an alpha level of $p < 0.05$.

The hypothesized relationships among variables are represented as a series of multiple regressions evaluated by comparing the observed data covariance matrix with the model-specified covariance matrix. Direct effects in SEM are the partial regression coefficients between a predictor (e.g., wolves) and a response variable (e.g., red fox). Indirect effects in SEM are the product of two or more direct path coefficients between a predictor and a response, through one or more moderating response variables (e.g., the effect of wolves on red fox, moderated through coyotes). Total effects in SEM are the sum of indirect and direct path coefficients, and represent the "net" effect of a predictor variable on a response variable, after accounting for indirect effects from other variables. Because variables were recorded in different measurement units (e.g., cell-specific occupancy probabilities, log-transformed prey tracks per km, and snow measurements in cm increments), and for interpretability of the finalized SEM, we presented standardized path coefficients of modeled pathways. Standardized direct path coefficients are interpreted as the expected change of a variable, in standard deviation units, to a one unit change in standard deviation of a given predictor (Grace & Bollen 2005). Standardized indirect paths are interpreted as the expected change in a response variable to a unit change in a given predictor, while holding all other predictors constant. SEM analyses were conducted using AMOS software (IBM SPSS v22.0.0).

2.4 Results

2.4.1 Snow track surveys

From January-March 2013 and 2014, we conducted repeated surveys on ~520 km of trail intersecting a total of 300 survey cells (Denali, 315 km, n = 173 cells; Susitna, 208 km, n = 127 cells). Each cell was surveyed between 2 and 9 times per winter ($\bar{x}$ = 3.46) with an average 19.4 days between repeats. Prey abundance was generally low both years throughout both study sites. Susitna had fewer tracks per km for hares, voles, and red squirrels than Denali (Fig. 2.2). Snow depth was greater in Susitna ($\bar{x}$ = 55.05 ± 1.70 cm) compared to Denali ($\bar{x}$ = 28.27 ± 1.12 cm). Snow penetrability was similar between sites (Denali, $\bar{x}$ = 6.29 ± 0.18 cm; Susitna, $\bar{x}$ = 6.43 ± 0.28 cm).

2.4.2 Occupancy models

All focal species (wolves, coyotes, lynx, red foxes, wolverine and marten) were detected in both study areas. The global detection model *Psi (area+ yr), p(meth + dist + dss + obs + yr)* did not converge for wolves, likely due to sparse detections in Susitna. We therefore used AIC model selection (Burnham & Anderson 2002) to identify the highest-ranked detection model to reach convergence among a candidate set of models that included all combinations of detection covariates. The top-ranking detection model to converge was *Psi (area + yr), p(meth + dist)*. Bootstrap goodness-of-fit test indicated adequate model fit ($\hat{c} < 1.0$) for the final models for all predators ($\hat{c}$: coyotes = 1.0821, red fox = 0.494, lynx = 0.233, marten = 0.11, wolverine = 0.625, wolf = 0.156).

2.4.3 SEM model

We resolved initial lack of fit in our a priori model ($\chi^2 = 69.989$, df = 17, $p < 0.001$) by correlating errors between voles and wolves (M.I. = 8.117), wolverine and marten (M.I. = 6.556), and including directed paths from local and landscape wolf to marten (M.I. = 6.531, 5.239). The final model (Fig. 2.3) fit the observed data well ($\chi^2 = 13.182$, df = 11, $p = 0.282$). The final model explained 61% of the variance in wolf occupancy ($R^2 = 0.611$), 23% of coyotes ($R^2 = 0.229$), 44% of wolverine ($R^2 = 0.437$), and 21% of marten. However, only 14% of lynx and 11% of red fox variance was explained, suggesting additional sources of variation for these species remained unaccounted for in our model. Correlations among snow characteristics and prey abundance were low ($r \leq 0.43$, Table 2.1).

2.4.4 Mesopredator cascades

The average cell-specific occupancy probability for wolves was lower in Susitna, where wolves were subject to wolf control ($\psi = 0.233 \pm 0.0912$ SE), compared to Denali, where wolves occurred at naturally regulated densities ($\psi = 0.882 \pm 0.17$ SE). The SEM showed that study area significantly predicted occurrence of wolves (Table 2.2; Table 2.3, standardized path coefficient = 0.537). Within study areas, all mesopredators except marten were positively associated with wolves (Table 2.3, wolf). Although the presence of wolves tended to promote coyotes at local scales, the weak path coefficients between coyotes and red foxes (0.016), lynx (0.057) and marten (-0.036) indicated no support for a coyote suppression-induced or facilitation-induced mesopredator cascade, nor were there strong path coefficients suggesting prominent indirect effects of wolf presence through suppression of coyotes (Table 2.3, indirect effects). The only notable negative associations among the mesopredators occurred between lynx and red fox (-0.095), and lynx and marten (-0.185). Across study areas, occurrence probabilities across the mesopredator guild were lower in the Denali study area, where wolves were abundant, than in the Susitna study area, where wolf numbers were reduced (Table 2.2; Table 2.3, study area). The strongest responses were from coyotes (-0.669) and wolverines (-0.707).

The direct effect of wolves was considerably stronger in predicting occurrence of all mesopredators compared to the indirect influence of wolves (Table 2.3, indirect effects). The direct effects of study area and local wolf presence on coyotes accounted for only a marginal proportion of the indirect effects of wolves on other mesopredators (Fig. 2.3, Table 2.3).

2.4.5 Responses to prey and snow

Within each study area, coyotes and foxes had a significant, positive association with wolves, of similar or greater magnitude than the response to each species' prey (Table 2.3). Hares were a significant predictor of coyote occurrence (0.179), yet the positive association between coyotes and wolves was nearly equivalent (0.171). Red foxes exhibited a stronger response to wolf occurrence (0.215) than voles (0.113), their primary prey. Wolverines were also positively associated with local-scale wolf occurrence (0.143), however red squirrels remained their strongest predictor (0.271). Similarly, lynx responded positively to local wolf occurrence (0.13) but this path was not significant and lynx occurrence was more strongly predicted by red squirrels (0.242). Snowshoe hares had a surprisingly weak effect on lynx occurrence (0.039). Marten responded positively to voles (0.106), yet the negative effects of lynx (-0.185) and local occurrence of wolves (-0.178) on marten were stronger.

Among all the carnivores, wolves exhibited the strongest response to snowpack and favored shallow, fluffy snow (snow depth = -0.325, snow penetrability = 0.175). Although snow depth was a negative predictor for lynx (-0.201) and red fox (-0.144), the magnitude of these responses were weak relative to the effects of wolves (for red foxes) and prey (for lynx). Snow depth and penetrability were not significant predictors for coyotes or wolverine (Table 2.2). Of all the explanatory factors in the SEM, marten responded most strongly to snow penetrability (0.324). Although the direct effects of snow conditions were comparatively weak for most mesopredators, the indirect effects of snow depth, mediated through other factors, increased the total or "net" effect of snow by 20-40% for all mesopredators (Table 2.3, Total effects). For marten, the negative effect of snow depth increased the most (70%), and changed from a negative to a positive due to indirect effects via intraguild interactions. The cumulative influence of all indirect pathways (mesopredator interactions, prey, and snowpack) dampened the total negative effects of wolves on all mesopredators across study areas, with the exception of marten.

2.5 Discussion

Contrary to our predictions, we did not find support for indirect effects of wolves on smaller carnivores mediated by coyotes. Although study area and local-scale wolf presence exerted strong (and opposing) influences on coyotes, the resulting patterns of occurrence for other mesopredator species did not support existence of a suppression-induced or facilitation-induced mesopredator cascade. Coyotes exerted a negligible influence on the occurrence of other mesopredators in our study area, suggesting that competitive interactions among mesopredators were not a dominant driver of community structure. Rather, we documented a near guild-wide positive response to wolf presence within each study area. Across a landscape scale, study area was the strongest predictor of canid and mustelid occurrence when compared with local wolf presence, prey and snowpack, whereas lynx presence remained most strongly predicted by prey.

The weak effect of coyotes on other mesopredators may have been due to low resource availability, as productivity is an important factor mediating interactions and encounters among carnivores (Polis et al. 1989; Elmhagen & Rushton 2007). From the perspective of mesopredators, productivity is determined by small prey biomass. In northern ecosystems, natural population cycling of hares and voles creates feast or famine cycles that can strongly influence the numerical response, and therefore densities of both generalist and specialist predators (Hornfeldt 1978; Angelstam et al. 1985; Boutin et al. 1995; O'Donoghue et al. 1997a). During this study, hares remained low since their population peak between 2008-2010 (C. McIntyre, *unpublished data,* Krebs et al. 2013), and vole abundance was generally low as well (Sivy 2015). The association of lynx with red squirrels, rather than hares, in our SEM is consistent with previous documentation of predation on red squirrels as an alternative prey when hares are scarce (O'Donoghue et al. 1997a, 1997b).

Although competition theory predicts that crashes in small mammal abundance should increase resource competition between sympatric competitors (Pianka 1981), predator densities could have been low enough to sufficiently reduce encounter rates, weaken interference competition, and ultimately dampen the mesopredator-release effect, as was observed in this study by the lack of influence of coyotes on other mesopredators. Density thresholds are not accounted for in previous studies of mesopredator release and should be an important consideration for predicting the effects of large carnivores on mesopredators. In northern systems, predator densities tend to be an order of magnitude lower than more productive regions at lower latitudes. However, as hares rebound from periodic population crashes in the North, thus increasing productivity, mesopredator densities are expected to increase, with a 1-2 year time lag (O'Donoghue et al. 1997a). In light of our findings, we hypothesize that competition between coyotes and mesopredators is most likely to intensify immediately following a crash in prey availability, when predator densities are high and resource availability rapidly dwindles.

Interestingly, we observed lynx presence to be a negative predictor of marten presence. The propensity for Eurasian lynx (*Lynx lynx*) to prey on marten and red foxes (Jobin et al. 2000; Valdmann et al. 2005; Helldin et al. 2006) has led to the hypothesis that intraguild predation may contribute to suppression of foxes and mustelids in boreal ecosystems in Scandinavia (Holt & Polis 1997; Sunde et al. 1999; Pasanen-Mortensen et al. 2013). Although the smaller-bodied Canada lynx have a slightly different ecological role in North America, the potential for lynx and similar-sized felids (e.g., bobcats, *L. rufus*) to adversely influence mustelids relative to their canid counterparts remains understudied in North America. Marten commonly use red squirrel middens for resting and thermal regulation, which could facilitate opportunistic predation by lynx (Buskirk 1983; Brainerd & Rolstad 2002), especially when hares are low and lynx switch to preying primarily on red squirrels. Given recent marten declines in interior Alaska (S. Arthur, *personal communication*) and conservation efforts to restore marten populations in the Northwest, Midwest, and Northeast US (Zielinski et al. 2001; Moruzzi et al. 2003; Carlson et al. 2014), our observations suggest that further examination of felid-mediated trophic pathways is needed.

Finally, we found wolves to exhibit the strongest direct responses to snowpack, favoring shallow, fluffy snow. Wolves could have been responding to snow conditions that favor their ungulate prey; while deep snow facilitates pursuit and capture of moose and caribou, these ungulates are more likely to occur in areas of shallow, fluffy snow that does not impede movement or foraging (Fuller 1991; Mech et al. 1998; Sand et al. 2006). With the exception of marten, wolves' relatively strong response to snow accounted for the majority of the negative, indirect effects of snow on all mesopredators. The indirect effects were marginal in strength for all mesopredators, but contributed to an overall stronger, total negative response to snow (Table 2.3, Total effects). Considering that wolves reacted strongly to snowpack, and that wolf occurrence accounted for the majority of the indirect effects of snow, it would be reasonable to expect that the total effect of snow on mesopredators, mediated by wolves, could increase during heavy snow years.

Also noteworthy is the martens' weak, negative, direct response to snow depth that was outweighed considerably by the comparatively strong, positive indirect effects of snow depth, as a result of direct and indirect paths with wolves and lynx. Both wolves and lynx responded negatively to snow depth, and had strong negative effects on marten. The net effect of these paths resulted in the strongest indirect response to snow of the mesopredators, and suggest that the tendency for deep snow to have a total, positive effect (as opposed to a negative, direct effect) could be attributed to the negative response of marten to lynx and wolf occurrence. While it is unlikely that marten select for snow conditions based on wolf and lynx occurrence alone, these paths illustrate potentially compounding negative effects that snow and predators could have on marten occurrence patterns.

2.5.1 Positive associations with wolves

Rather than the predicted coyote-mediated cascade, we observed local scale, positive associations between mesopredators and wolves within each study area. Localized wolf presence appeared to promote mesopredator occurrence, and for coyotes and red foxes, the positive association was at strengths similar to or greater than that of each species' respective prey. Positive path coefficients in response to wolves were assumed to be a result of carrion provisioning, and negative path coefficients were assumed to be a result of displacement or avoidance behaviors resulting from interference competition. Although the positive local scale effects of wolves on mesopredators could have been due to coincidental habitat selection (i.e., habitat filtering; Weiher & Keddy 1999), preliminary analyses of the influence of microhabitat did not indicate a strong influence on occupancy probabilities (Pozzanghera 2015). Inclusion of major habitat types in preliminary SEM analyses did not account for additional variation and masked the influences of prey and snowpack, which accounted for only a small proportion of the net effect of wolves. Differences in home range size and resource use among wolves and mesopredators make coincidental habitat selection unlikely to have led to the strong and consistent space use patterns we documented (Buskirk 1983; Gibson et al. 1984; Banci & Harestad 1990; Paragi et al. 1996; O'Donoghue et al. 1997b; Mech et al. 1998; Buskirk et al. 2000; Levi & Wilmers 2012; Newsome & Ripple 2015).

We suggest carrion exploitation to be the most likely explanation for the observed local-scale, positive space-use patterns in relation to wolves, for several reasons. First, carrion is an important resource for northern red foxes and wolverines (van Dijk et al. 2008; Dalerum et al. 2009; Andrén et al. 2011; Needham & Odden 2014), and has been documented as an alternative food source for coyotes and lynx during previous hare declines (Brand et al. 1976; Poole 2003; Prugh 2005). Second, analysis of prey remains in coyote and red fox scats collected concurrently in our study areas showed high use of carrion, which accounted for 40-62% of coyote diet and 10-35% of red fox diet across study areas (Sivy 2015). Third, all mesopredators (except marten) were documented scavenging at kill sites by motion-triggered cameras placed at carcasses during our study (K. Sivy, *unpublished data*).

Ungulate kill sites are acknowledged as powerful attractants for a diverse community of mesopredators, luring scavengers into areas of past and present large carnivore activity (Wilmers et al. 2003b; Selva & Fortuna 2007; Yarnell et al. 2013). Although large carnivores present a considerable risk to smaller carnivores, scavengers seeking carrion may be attracted to large carnivores at fine spatial scales in order to exploit scavenging opportunities (Atwood & Gese 2010). To our knowledge, this study is the first to document occurrence patterns by an entire mesopredator guild in relation to wolves, and our findings of near guild-wide, positive associations suggest that the degree of reliance on scavenging could be an important factor in studies of mesopredator abundance patterns in relation to carrion-provisioning carnivores. In particular, during periods of low prey availability, the tendency for mesopredators to follow wolves may be further incentivized, as wolves could represent a risky, yet predictable food source.

To minimize risk of encounter with wolves, coyotes rely on spatial and temporal avoidance (Thurber et al. 1992; Atwood & Gese 2008; Atwood et al. 2009). For example, following wolf colonization in northern Montana, coyotes scavenging from wolves during winter months had higher home range overlap with wolves, yet adjusted daily activity patterns around wolf activity (Arjo & Pletscher 1999). Fine scale spatial partitioning has been observed for wolverines scavenging from wolves in Norway (Van Dijk et al. 2008). These strategies are likely employed by other species that regularly scavenge or must avoid large carnivores (Linnell & Strand 2000; Van Dijk et al. 2008; Swanson et al. 2014). Interestingly, cell-specific occupancy probabilities for coyotes and wolverines, each dominant scavengers, were more patchily distributed with a greater cell-to cell variation in the Denali study area, where wolves were abundant, compared to the Susitna study area, where wolf density was reduced by predator control (Fig. 2.4, Table 2.5). The difference was not as pronounced for mesopredators less negatively impacted by study area at a broader spatial scale (red fox, lynx, and marten). If these study area differences were driven by differences in wolf density, this pattern indicates that large carnivore density may have particularly strong effects on the distribution and movements of scavengers that are highly susceptible to suppression.

2.5.2 Comparisons between study areas

Across our study areas, we observed a strong, guild-wide negative response whereby occupancy probabilities of mesopredators were lower in the Denali study area, where wolves occurred at naturally regulated densities, compared to Susitna, where wolf densities were artificially reduced. The relative strength of top down versus bottom up effects in this study system further indicated that study area was the strongest predictor of wolf, coyote and wolverine occurrence relative to snow pack characteristics and prey, whereas lynx presence remained most strongly predicted by prey. Due to the lack of replication at the landscape scale, it is possible that differences among our two study areas other than wolf abundance, prey abundance, and snow characteristics could have contributed to the patterns we observed. However, our sampling units in each of the two study areas were similar in general topography and major habitat composition (see study area description). Anthropogenic use was similar in both areas, and trail density and proximity to human settlements was a weak predictor of mesopredator occupancy in concurrent analyses (Pozzanghera 2015). We therefore maintain that variation in wolf density, due to more than a decade of wolf removal through aerial shooting in our Susitna study area, was likely a predominant factor affecting landscape scale mesopredator occupancy.

If local scale facilitation by wolves does lead to landscape scale suppression, we suggest a hypothesis of "fatal attraction," in that the magnitude of mesopredator suppression by large carnivores is dependent on the intensity of facilitation (i.e., scavenging) and resource overlap. Interspecific competition is predicted to intensify between species pairs that are similar in body size and have high niche overlap (Donadio & Buskirk 2006). The lower cell occupancy probabilities in the wolf-abundant study area was most pronounced for coyotes and wolverines, which, of the mesopredators in our study system, have body sizes most similar to wolves, and have highest potential diet overlap with wolves considering use of carrion resources and predation on live ungulates (Donadio & Buskirk 2006; Mattisson et al. 2011; Andrén et al. 2011; Prugh & Arthur 2015).

If scavenging-related mortality is high, the intensity of scavenging could lead to negative implications for population dynamics at broader spatial scales. Carcasses could act as a magnet for aggressive encounters, with severe consequences for the unsavvy. For example, in the Greater Yellowstone ecosystem, 75% of aggressive encounters between wolves and coyotes occurred at kill sites (Merkle et al. 2009). Wolves are documented as a considerable source of mortality; wolf predation accounted for 67% of radio-collared coyote mortalities on the Kenai Peninsula (Thurber et al. 1992) and 50% of coyote mortalities in Denali and a nearby area in the Alaska Range (L. Prugh, *unpublished data*; Prugh & Arthur 2015). Likewise, it is not uncommon for wolverines to be killed by wolves and mountain lions (also carrion providers), with predation accounting for 18% of 54 wolverine mortalities reported in 12 studies (Krebs et al. 2004). Although wolves have lower niche overlap with smaller mesopredators (e.g., marten and red foxes) that also exhibited lower cell occupancy probabilities in the Denali study area, co-occurrence of these species in the vicinity of carcasses and wolves could elicit a generalized predatory response from wolves. Although not testable within our study design, we speculate that the contrasting patterns of local scale association and suppression across study areas suggests that the negative effects of large carnivores on populations of smaller predators could be more widespread than previously recognized, especially when carrion is a heavily relied upon resource.

2.5.3 Conclusion

Large carnivores can influence mesopredators through direct and indirect pathways, yet the complexities driving intraguild interactions that lead to mesopredator release make predicting the outcomes of these ecological cascades extremely challenging. Here, we quantified the relative strengths of wolves, prey and snowpack on patterns of mesopredator occurrence, presenting the first community-level investigation of the direct and indirect influences of wolves on an intact mesopredator guild. The cascading effects of mesopredator release could be dependent on mesopredator densities, as we detected minimal influence of coyotes on other mesopredators when productivity was low. During this period, wolves were strong predictors of where mesopredators were found, which suggests that mesopredators could be tracking wolves for scavenging. Finally, the patterns observed in our study areas suggest an intriguing mechanism to account for the contrasting effects of large carnivores with respect to spatial scale. Studies examining mesopredator release have documented mesopredator release cascades at continental scales in North America, Europe and Australia (Johnson et al. 2007; Letnic et al. 2011; Levi & Wilmers 2012; Pasanen-Mortensen et al. 2013; Khalil et al. 2014; Lapoint et al.

2014). However, studies conducted at smaller spatial scales have had mixed findings (Mitchell & Banks 2005; Gehrt & Prange 2007; Berger et al. 2008; Allen et al. 2014, 2015; Colman et al. 2014). The contrasting patterns detected within versus between study areas elicits the question as to whether local scale facilitation by wolves, indicated by positive associations of mesopredators with wolves within study sites, could influence landscape patterns of suppression, presenting a potential mechanism between abundance patterns and the structure of carnivore communities at different spatial scales. Examination of scavenging benefits contrasted with scavenging-related mortality risk could greatly aid our understanding of the influence of large carnivores on mesopredators at spatial scales relevant to conservation and management.

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2.7 Figures

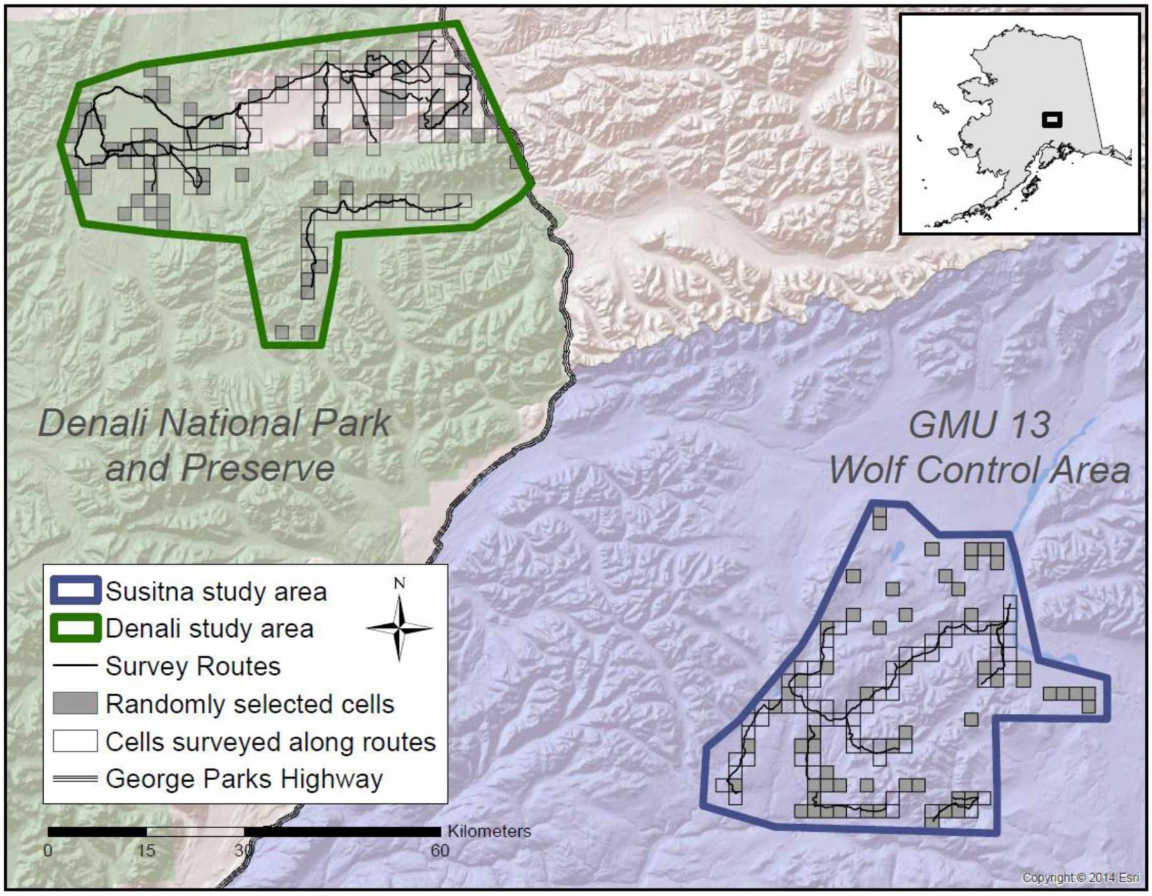

Figure 2.1 Study area map. Sampling grids surveyed for snow tracks of wolves, mesopredators and prey, in Denali and Susitna study areas winter 2013 and 2014.

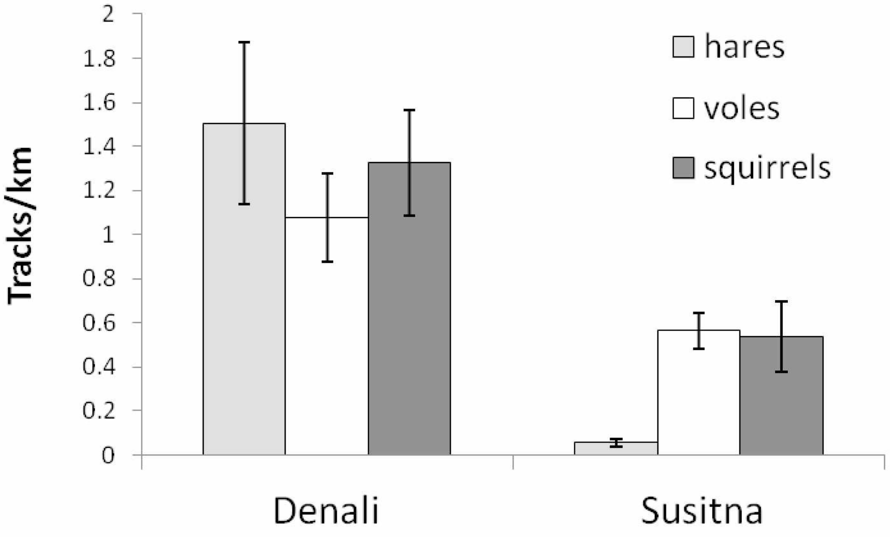

Figure 2.2 Prey tracks per kilometer, winter 2013-2014. Shown are mean (+/-) track frequencies of hares, voles, and squirrels winter in Denali and Susitna study areas.

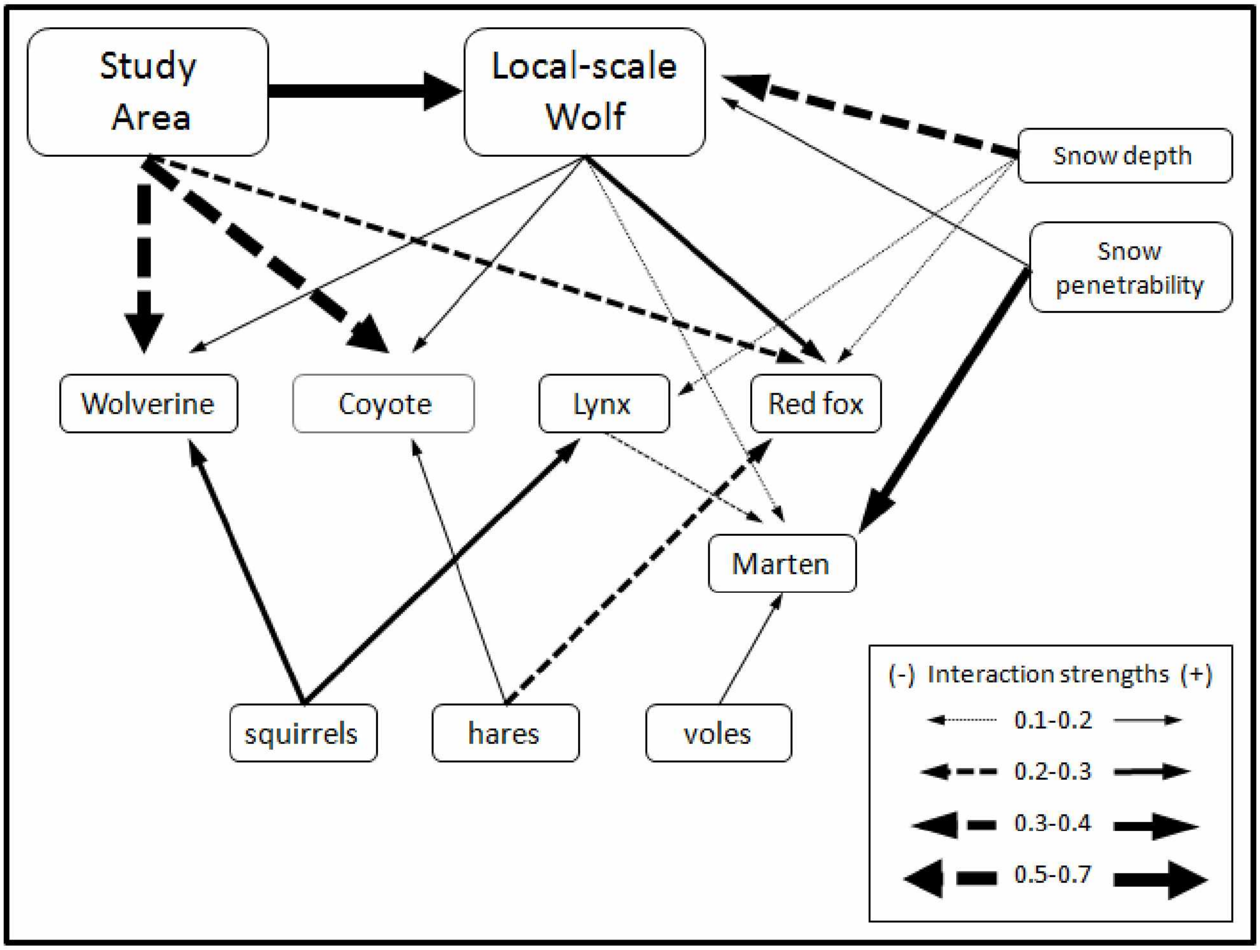

Figure 2.3 Finalized SEM of wolves, prey, and snowpack on mesopredator occurrence. Each arrow represents a direct path. Indirect pathways are two or more direct paths through a third variable (e.g., snow depth → lynx → marten). Arrow thickness represents the relative strengths of significant, standardized path coefficients (Table 2.4). Non-significant paths have been omitted for clarity.

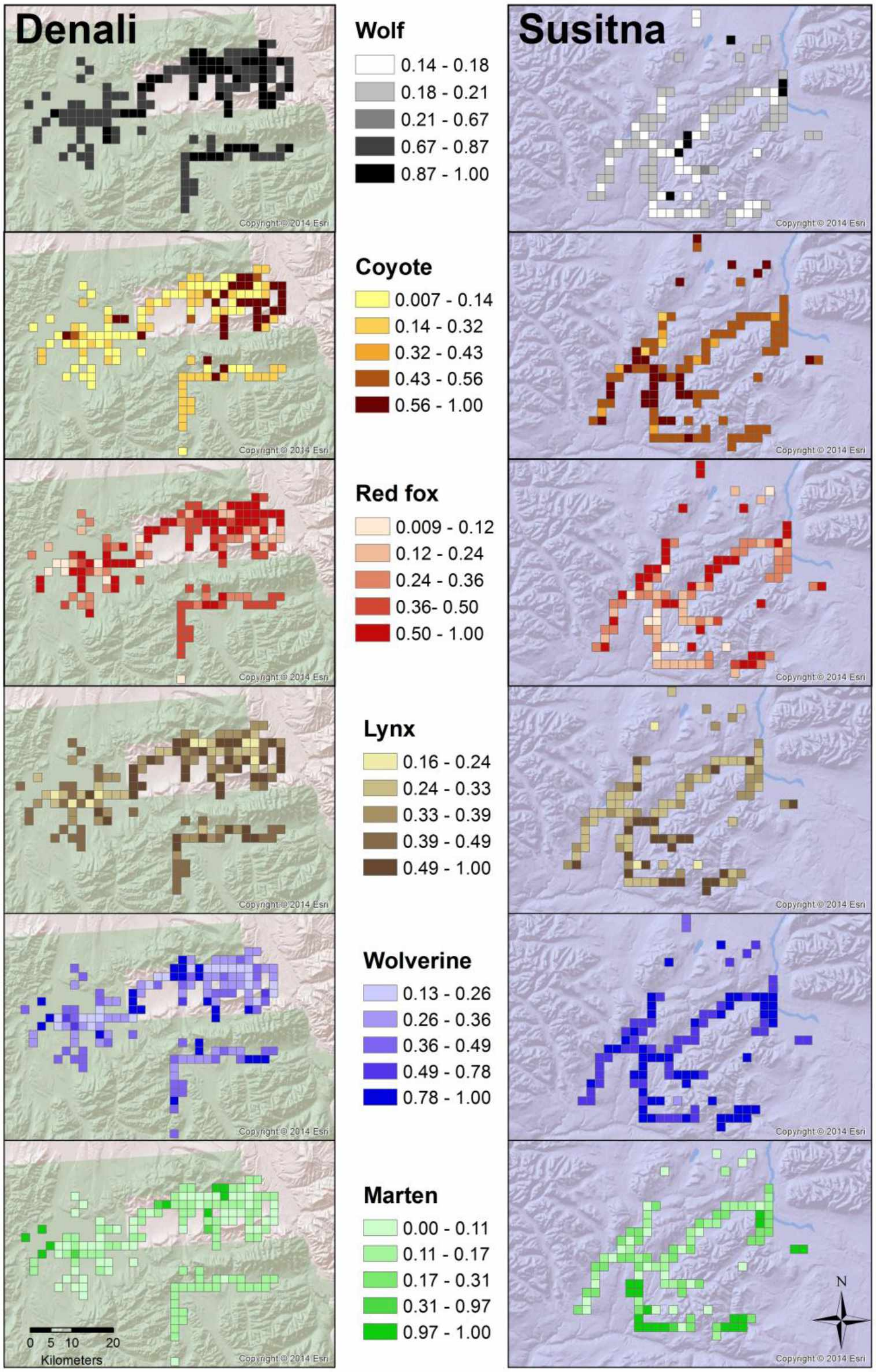

Figure 2.4 Cell-specific occupancy of wolves and mesocarnivores in Denali and Susitna. Legend values represent natural breaks in average occupancy probabilities for each species, 2013-2014.

2.8 Tables

Table 2.1 Correlations among prey and snow predictors.

	Hares	Voles	Squirrel	Snow depth	Snow penetrability
Hares	-	0.273	0.551	-0.095	0.318
Voles	0.273	-	0.383	-0.128	0.333
Squirrel	0.551	0.383	-	-0.068	0.433
Snow depth	-0.095	-0.128	-0.068	-	0.23
Snow penetrability	0.318	0.333	0.433	0.23	-

Table 2.2 Unstandardized coefficients of direct paths in final SEM model. Bold indicates significant effects at p=0.05, *** indicate p<0.001.

Predictor	**Response**	**Raw estimate**	**S.E.**	**p-value**
Study Area	Wolf	**0.376**	0.033	***
	Coyote	**-0.473**	0.059	***
	Lynx	**-0.109**	0.057	**0.056**
	Red Fox	**-0.143**	0.069	**0.038**
	Wolverine	**-0.422**	0.042	***
	Marten	-0.082	0.056	0.144
Wolf	Coyote	**0.173**	0.083	**0.038**
	Lynx	0.109	0.073	0.135
	Red Fox	**0.211**	0.088	**0.016**
	Wolverine	**0.122**	0.059	**0.04**
	Marten	**-0.162**	0.077	**0.036**
Coyote	Lynx	0.048	0.051	0.347
	Red Fox	0.016	0.061	0.797
	Marten	-0.032	0.051	0.533
Lynx	Red Fox	-0.112	0.068	0.099
	Marten	**-0.2**	0.058	***
Red fox	Marten	-0.06	0.049	0.219
Snow depth	Wolf	**-0.005**	0.001	***
	Coyote	-0.001	0.001	0.306
	Lynx	**-0.003**	0.001	**0.009**
	Red Fox	-0.002	0.001	0.071
	Wolverine	0.001	0.001	0.339
	Marten	0	0.001	0.777
Snow penetrability	Wolf	**0.022**	0.005	***
	Coyote	-0.012	0.008	0.129
	Lynx	0.009	0.007	0.203
	Red Fox	0.004	0.008	0.65
	Wolverine	-0.001	0.006	0.871
	Marten	**0.037**	0.007	***
Hare	Coyote	**0.029**	0.009	**0.003**
	Lynx	0.005	0.009	0.58
	Red Fox	-0.034	0.01	***
	Wolverine	-0.011	0.007	0.13
Squirrel	Lynx	**0.03**	0.008	***
	Wolverine	**0.034**	0.007	***
Vole	Coyote	0.007	0.01	0.479
	Red Fox	0.019	0.01	0.065
	Marten	0.016	0.009	0.061

Table 2.3 Standardized coefficients of direct, indirect, and total paths in final SEM model. Bold values indicate significant raw coefficients (Table 2.2). The effect of predictors (presented in columns) are shown as direct, indirect, and total effects for each response species, presented in rows. Study area shows effects across study sites, all other predictors show effects on mesopredators within study sites. Dashes (-) indicate pathways not evaluated in model.

	Study Area	**Wolf**	**Coyote**	**Lynx**	**Red fox**	**Hare**	**Squirrel**	**Vole**	**Snow depth**	**Snow penetrability**
Direct effects										
wolf	**0.537**	-	-	-	-	-	-	-	**-0.325**	**0.175**
coyote	**-0.669**	**0.171**	-	-	-	**0.179**	-	0.04	-0.075	-0.091
lynx	-0.185*	0.13	0.057	-	-	0.039	**0.242**	-	**-0.201**	0.082
red fox	**-0.207**	**0.215**	0.016	-0.095	-	**-0.221**	-	0.113	**-0.144**	0.03
wolverine	**-0.707**	**0.143**	-	-	-	-0.083	**0.271**	-	0.06	-0.008
marten	-0.13	**-0.178**	-0.036	**-0.185**	-0.065	-	-	0.106	-0.021	**0.324**
Indirect effects										
wolf	-	-	-	-	-	-	-	-	-	-
coyote	0.092	-	-	-	-	-	-	-	-0.056	0.03
lynx	0.037	0.01	-	-	-	0.01	-	0.002	-0.05	0.019
red fox	0.12	-0.011	-0.005	-	-	-0.002	-0.023	-	-0.048	0.027
wolverine	0.077	-	-	-	-	-	-	-	-0.046	0.025
marten	-0.042	-0.045	-0.011	0.006	-	-0.001	-0.043	-0.009	0.121	-0.051
Total effects										
wolf	0.537	-	-	-	-	-	-	-	-0.325	0.175
coyote	-0.577	0.171	-	-	-	0.179	-	0.04	-0.131	-0.061
lynx	-0.149	0.14	0.057	-	-	0.049	0.242	0.002	-0.25	0.102
red fox	-0.087	0.205	0.011	-0.095	-	-0.223	-0.023	0.114	-0.193	0.057
wolverine	-0.631	0.143	-	-	-	-0.083	0.271	-	0.013	0.016
marten	-0.172	-0.224	-0.047	-0.179	-0.065	-0.001	-0.043	0.096	0.1	0.272

Table 2.4 Strength of direct and indirect effects of wolves on mesopredators, moderated through coyotes. Direct effects are standardized path coefficients from pathways in SEM model (Table 2.2). Indirect effects are the product of direct pathways indicated in column header.

	Direct effects			Indirect effects	
	Study Area	Local Wolf	Coyote	Study Area → Coyote	Local Wolf → Coyote
Coyote	-0.669	0.171	-	-	-
Lynx	-0.185	0.13	0.057	-0.0105	0.0074
Red fox	-0.207	0.215	0.016	-0.0033	0.0034
Wolverine	-	-	-	-	-
Marten	-0.13	-0.178	-0.04	0.0047	0.0064

Table 2.5 Coefficient of variation for cell-specific occupancy of wolves and mesocarnivores. Higher values indicate higher cell-to-cell variability in occupancy probability, lower values indicate lower variability.

	Denali *n* = 173			Susitna *n* = 127		
Species	mean	SD	CV	mean	SD	CV
Wolf	0.882	0.086	0.098	0.233	0.2	0.86
Coyote	0.34	0.377	1.109	0.582	0.236	0.406
Lynx	0.51	0.29	0.568	0.456	0.294	0.645
Red fox	0.54	0.351	0.65	0.446	0.374	0.838
Wolverine	0.444	0.269	0.605	0.809	0.188	0.233
Marten	0.177	0.239	1.347	0.338	0.371	1.097

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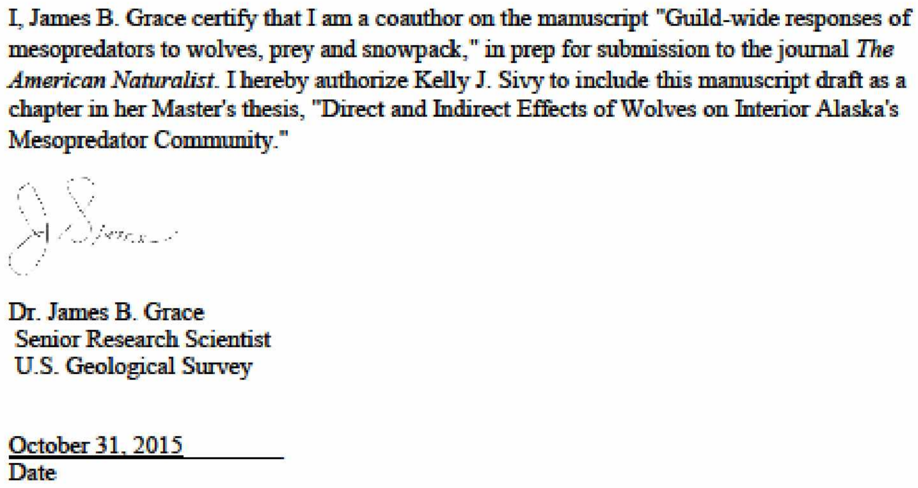
Appendix 2.1 Coauthor permission, J. Grace

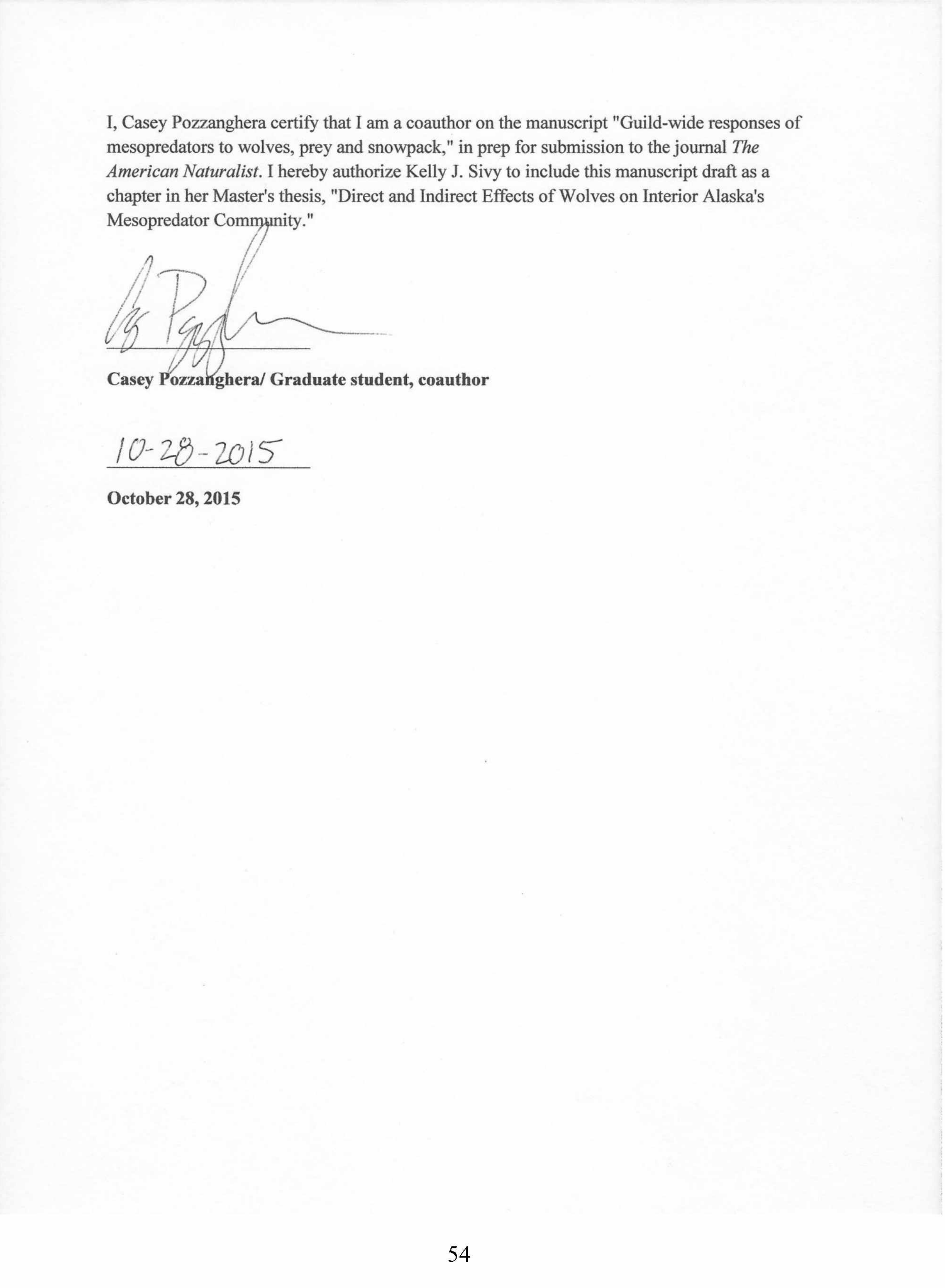


I, James B. Grace certify that I am a coauthor on the manuscript "Guild-wide responses of mesopredators to wolves, prey and snowpack," in prep for submission to the journal *The American Naturalist*. I hereby authorize Kelly J. Sivy to include this manuscript draft as a chapter in her Master's thesis, "Direct and Indirect Effects of Wolves on Interior Alaska's Mesopredator Community."

Dr. James B. Grace
Senior Research Scientist
U.S. Geological Survey

October 31, 2015
Date

Appendix 2.2 Coauthor permission, C. Pozzanghera, Chapter 2



I, Casey Pozzanghera certify that I am a coauthor on the manuscript "Guild-wide responses of mesopredators to wolves, prey and snowpack," in prep for submission to the journal *The American Naturalist*. I hereby authorize Kelly J. Sivy to include this manuscript draft as a chapter in her Master's thesis, "Direct and Indirect Effects of Wolves on Interior Alaska's Mesopredator Community."

Casey Pozzanghera/ Graduate student, coauthor

10-28-2015

October 28, 2015

Chapter 3 Coyote and red fox winter diet relative to wolf and small prey abundance[1]

3.1 Abstract

Large carnivores may indirectly benefit small predators through suppression of competitively dominant mesopredators. However, large carnivores also provide carrion subsidies that could influence diet partitioning and competition among sympatric mesopredators that rely on carrion when small prey is scarce. We collected coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) scats in winter 2013-2014 in two study areas representing nearly a 2.5-fold difference in wolf densities, to assess winter diet overlap and composition in relation to wolves (*C. lupus*) and small prey availability. We hypothesized that diet overlap between coyotes and red foxes would increase where wolves are more abundant, as a result of both species increasing selection for carrion in their diet. Alternatively, we hypothesized that diet overlap would decrease in order to minimize competition. We used molecular DNA analysis and observer certainty to confirm species identification of collected scats, and identified prey remains using microscopic evaluation of hair and bone fragments. We used counts of snowshoe hare fecal pellets, vole capture rates, and relative wolf densities from 2012-2014 as indices of prey and carrion abundance in each area. Snowshoe hares, voles, and carrion comprised over 70% of coyote and red fox diet across both study areas. Carrion was a major component of coyote (40-62%) and red fox (10-35%) diets in both study areas. Voles were an important resource for red foxes in both study areas (29-48%). Use of carrion, and diet overlap, was highest in the study area where wolves and small prey were less abundant, while diet diversity and richness was similar between study areas. Overall, these results suggest that smaller mesopredators could respond to increased

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[1] Sivy, K.J., C.P. Pozzanghera, K.Colson, M. Mumma, and L.R Prugh. 2015. Coyote and red fox winter diet in relation to wolves and small prey abundance. Prepared for submission to *Oikos.*

use of carrion by a dominant mesopredator by increasing use of small prey, in order to minimize competition.

3.2 Introduction

Throughout the globe, tri-level cascades within the carnivore guild suggest that large carnivores may indirectly benefit small predators through suppression of competitively dominant mesopredators (Creel & Creel 1996; Letnic et al. 2012; Pasanen-Mortensen et al. 2013; Newsome & Ripple 2015). Implicit in this hypothesis is that interactions within the carnivore guild are restricted to aggression and competition, which disregards the potential significance of facilitation though carrion subsidies made available by top predators (Wilmers et al. 2003a; Van Dijk et al. 2008; Pereira et al. 2014). Carrion subsidies provide an important food source to individual scavengers, with implications for community structure (Devault et al. 2003; Wilson & Wolkovich 2011). Carrion could reduce competition among mesopredators by increasing resource availability, or alternatively, this high-value resource could create hotspots of escalated resource competition between sympatric competitors, making the net effect of large carnivores on mesopredator communities challenging to predict. Quantifying the use of carrion resources by scavengers will contribute to understanding the long-term implications for mesopredator community dynamics where large carnivore re-colonization is proposed or naturally occurs.

Here, we examined diet composition and overlap of two competing mesopredators, coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), in relation to small prey abundance and density of grey wolves (*C. lupus*). Wolves are beginning to recolonize the western United States after their reintroduction into the Greater Yellowstone Ecosystem, and are likewise beginning to recover in Europe (Chapron et al. 2014; Ripple et al. 2014). In North America, coyotes are a highly adaptable, generalist predator that in the absence of top-down regulation from wolves, can outcompete and displace native foxes in numerous ecosystems (Ritchie & Johnson 2009). Coyotes and red foxes prey on similarly sized food resources, leading to high niche overlap (Rosenzweig 1966). In temperate ecosystems, resource competition between coyotes and red foxes may be reduced by partitioning a diverse prey base (Major & Sherburne 1987; Azevedo et al. 2006). In northern ecosystems however, coyotes and red foxes rely heavily on snowshoe hares (*Lepus americanus*) and microtine rodents (O'Donoghue et al. 1998; Prugh 2005; Dell'Arte et al. 2007), which undergo dramatic fluctuations in population density with high spatial and temporal variability (Elton 1924; Korpimaki & Krebs 1996; Krebs et al. 2013). When hares are abundant, diet overlap between coyotes and red foxes can be high (Theberge & Wedeles 1989). However, when hare and vole populations are at cyclic lows, the degree of diet overlap between coyotes and red foxes, and their respective use of carrion as a supplemental resource, remains unknown.

We examined resource availability and winter diets of coyotes and red foxes during a low phase of the hare cycle, following a record peak in hare density between 2008-2010 (Krebs et al. 2013). Food availability and the presence of alternatives is expected to strongly influence resource competition (Oaten & Murdoch 1975; Pianka 1981; Wiens 1993). Resource provisioning by wolves could therefore influence the degree of niche overlap, and competition, among mesopredators when small prey are scarce. Competition theory predicts that when resources are limited, sympatric competitors minimize competition by preying on different items (Schoener 1974a), which should decrease diet overlap and diet diversity. In contrast, optimal foraging theory predicts that individuals should respond to resource limitation by increasing use of high value resources in the diet (MacArthur & Pianka 1966), which should increase diet overlap, and presumably competition.

In Alaska, red foxes are native, whereas coyotes first appeared in the early 1900s (Parker 1995), with locally abundant populations now reported throughout much of the state. Wolves are abundant in Alaska, yet state-sponsored wolf control programs currently reduce wolf densities by 50-80% in game management units that total over 165,000 km^2 (ADF&G 2015a). Coyotes and red foxes are widely documented to supplement their diets by scavenging, with carrion subsidies particularly beneficial in winter (Knowlton 1972; Gibson et al. 1984; Gese et al. 1996; Crabtree & Sheldon 1999; Killengreen et al. 2011; Needham & Odden 2014). We quantified availability of hares, voles, and carrion and collected 624 scats in two study areas, one with an active wolf control program that has reduced wolf densities by 36-80% annually for the past decade, and one where wolves occur at natural densities. We tested two alternative hypotheses:

1) *Subsidies increase diet overlap*: carrion use by coyotes and red foxes should increase with wolf abundance, because both species should exploit this highly profitable food resource as predicted by optimal foraging theory. As a result, diet overlap between coyotes and foxes should be higher where wolves are abundant than where wolf abundance is reduced. Coyote and red fox diet diversity and richness should decrease where wolves are abundant because of greater reliance on carrion.

2) *Subsidies reduce diet overlap*: Alternatively, carrion use by red foxes should decrease with wolf abundance to minimize competition with coyotes, as predicted by competition theory. As a result, diet overlap between coyotes and foxes should be lower where wolves

are abundant than where wolf numbers are reduced. Red fox diet diversity and richness should increase due to inclusion of alternate (i.e., not carrion) prey items in the diet.

3.3 Methods

3.3.1 Study area

This study took place in two sites in interior Alaska (Fig. 3.1). The region is a subarctic ecosystem characterized by long, cold winters averaging -24°C and short, mild summers averaging 17°C. Predominant plant communities include boreal forest, tussock and low shrub tundra, alpine graminoid meadows, shrubs (*Salix* spp. and *Alnus* spp.), and mixed deciduous forest comprised of birch (*Betula* sp.) and aspen (*Populus tremuloides*). Moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall's sheep (*Ovis dalli*) are the sole ungulates and main prey for wolves. Other mesopredators include Canada lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), American marten (*Martes americana*), Northern river otter (*Lontra canadensis*), and small mustelids (*Mustela nivalis*, *M. erminea*, *M. vison*). Small mammal prey includes snowshoe hares (*Lepus americanus*), red squirrels (*Sciurus vulgaris*), and 5 species of voles (*Myodes rutilus* and *Microtus* spp.). Also present are hoary marmots (*Marmota caligata*), porcupines (*Erethizon dorsatum*), beavers (*Castor canadensis*), and muskrats (*Ondatra zibethicus*). Common avian prey includes willow ptarmigan (*Lagopus lagopus*) and spruce grouse (*Falcipennis canadensis*).

The Denali study site (hereafter, "Denali") was approximately 2,000 km^2 overlapping the northeast corner of Denali National Park and Preserve, including 500 km^2 of state-managed land known as the Stampede corridor. Wolves are subject to limited subsistence harvest within National Park boundaries, and more frequent hunting and trapping within the Stampede corridor according to regulations managed by Alaska Department of Fish and Game (ADF&G).

Nonetheless, harvest was not found to greatly impact population dynamics within our study site (Borg et al. 2014), therefore this population was presumed to be naturally regulated, with density averaging 7.6 wolves/1,000 km^2 during this study (S. Arthur, *personal communication*). The Susitna study site (hereafter, "Susitna") was 200 km southeast of Denali and included 1,800 km^2 of land largely managed by the state, with some private inholdings and Native allotments. As part of the larger Nelchina Basin Game Management Unit 13, the wolf population in Susitna has been subject to intensive management practices authorizing lethal wolf removal by aerial shooting since 2000. Since then, wolf populations have been reduced by 36-80% annually to achieve a target population size of 135-165 wolves over a 60,520 km^2 area, roughly equivalent to an estimated 2.2-2.7 wolves/1,000km^2 (ADF&G 2015b).

3.3.2 Scat collection

Carnivore scats were collected daily from January-March in 2013 and 2014 along winter snowmachine trails, while backtracking individual coyotes and red foxes, and opportunistically at carcass sites. The location and estimated maximum age of each scat sample was recorded. Observers identified the species (field ID) that produced each scat based on characteristics of size and shape from published field guides and tracks or other sign present (Murie 1997; Elbroch 2003). Observers rated their certainty of species identification (from 35-95%) assigned to each scat. Although subjective, observer certainty has been shown to correlate well with the accuracy of species identification in this system (Prugh & Ritland 2005). After collection, scats were stored at -80°C for a minimum of two weeks to kill eggs of the *Echinococcus* parasite (Hildreth et al. 2004).

3.3.3 Molecular species identification

We used mitochondrial DNA analysis to confirm the species identification of each scat. Fecal samples were scraped with sterilized wooden craft sticks, and the tip of the stick bearing the sample was broken off inside a 1.5 mL vial. DNA was extracted using Qiagen DNA investigator kits (Valencia, CA). We added 250 µL buffer ATL, 250 µL buffer AL, and 25 µL proteinase K to each vial. Samples were incubated on a shaker-incubator at 56° C for 4 hours, and subsequent wash steps followed the manufacturer's protocol. Extractions took place in a dedicated pre-PCR room with negative controls included for every group of extractions to monitor for contamination. Each sample was identified to species using a modification of a previously developed mitochondrial DNA test (De Barba et al. 2014). Primer pair DL1F and DL5R (Palomares et al. 2002) and a forward primer, Gulo1F (Dalen et al. 2004), were combined with the primers H3R (Dalen et al. 2004), SIDL and H16145 (Murphy et al. 2000) to amplify DNA fragments of species-specific lengths. This method created diagnostic fragments for brown bears, black bears, red foxes, coyotes, wolves and dogs, without amplifying DNA of prey species. Red fox and coyote scats were verified via DNA fragments of ~346 base pairs (bps) and ~363 bps, respectively. Species ID protocols were verified using tissue samples obtained from specimens archived at the University of Alaska Museum of the North.

The conditions for our original 15 µL reaction were 0.2 µM DL1F, 0.2 µM DL5R, 0.2 µM Gulo1F, 0.4 µM SIDL, 0.4 µM H3R, 0.2 µM H161453, 3 µL H20, 1.26 µL TE buffer, 7.5 µL 1x Qiagen Master Mix, 1.5 µL Q solution, and 1.5 µL of DNA extract. We later scaled-down this reaction to 7 µL to reduce costs. Primer concentrations were maintained while adjusting the remaining solution volumes to 0.69 µL dH20, 0 µL TE buffer, 3.5 µL 1x Qiagen Master Mix, 0.7 µL 0.5x Qiagen Q solution, and 2 µL of DNA extract. The PCR profile for both the 15 and 7 µL reactions consisted of an initial denaturation step of 95°C for 15 minutes followed by 30 cycles of 95°C for 15 seconds, 46°C for 90 seconds, 72°C for 60 seconds with a final elongation step of 72°C for 15 minutes. Each sample was amplified a minimum of 2 times to ensure consensus and separated on an ABI 3730xl (Applied Biosystems, Foster City, CA). Fragment sizes were determined using GENEMAPPER 3.7 software.

Molecular identification results were compared to field ID to assess accuracy at each of four categories of observer percent certainty (0-55, 60-75, 75-85, and 90-100%). Samples that failed to amplify for molecular identification were assigned the species indicated by field ID when certainty levels exceeded 60% (see results). Scat samples with no molecular species ID and a field ID <60% certainty were excluded from further analyses.

3.3.4 Analysis of prey remains

After genetic processing, scats were transferred to nylon bags, washed in a regular clothes washing machine to remove fecal material, air-dried and weighed. Prey remains were identified based on microscopic evaluation of the medulla and cortex patterns of hairs, and comparison of bone fragments, teeth, and claws to published species keys (Moore et al. 1974; Debelica & Thies 2009) and a reference collection of hairs, skins and skulls from University of Alaska Museum of the North. Species of each prey item and visual estimation of the percent volume was recorded for each scat. Items constituting <1% total scat volume were recorded as trace amounts and excluded from further analysis to avoid over-representation of incidental items. Occurrences of moose and caribou hairs were assumed to be a result of scavenging because in this region, coyotes and red foxes are not documented to prey on adult moose and caribou (Gasaway et al. 1992), coyotes rarely prey on calves (Ballard et al. 1981; Adams et al. 1995; Valkenburg et al. 2004), and scat collection occurred prior to calving season.

3.3.5 Resource availability

Snowshoe hares- Pellet accumulation was tallied annually for three summers (2012-2014) on grids established in spruce and tall shrub habitat at 6 paired sites ($n = 12$) in Denali and 7 paired sites ($n = 14$) in Susitna (Fig. 3.1). Each pellet grid consisted of 50 circular plots with 0.5-m radii (0.79 m^2) spaced 15 m apart along linear transects (Prugh & Krebs 2004). All pellets were counted and removed from each plot. Pellets were categorized as "new" (< 1 year old) or "old" (> 1 year old) following guidelines described in Prugh and Krebs (2004).

Voles- We conducted a series of 1-night live-trapping sessions on trapping grids in meadow and spruce forest habitats at 17 sites in Denali (spruce $n = 8$, meadow $n = 9$) and 15 sites in Susitna (spruce $n = 7$, meadow $n = 8$; Fig. 3.1). One-hundred Sherman live traps (3" x 3.5" x 9", Sherman, Inc.) were spaced 10 m apart on each 90 m x 90 m grid. Traps were covered with roofing paper for rain protection and a wad of upholstery cotton was provided inside each trap for bedding and insulation. Traps were baited with sunflower seed at 2000 hours and checked the following morning at 0800 hours. Upon capture, each animal was identified to genus, sexed, weighed, and released. We converted the number of voles caught after 1 night to an index of vole density using the relationship between the first night's capture success (N_1) and density (voles per hectare) estimated from 5-night mark-recapture sessions (D). This relationship was estimated using Denali National Park's long-term (1992-2002) vole trapping dataset (L. Prugh, unpublished analysis: $D = 0.5157*N_1 - 0.0684$; $R^2 = 0.852$, $n = 43$ grid-years). All animal handling procedures were in accordance with University of Alaska Fairbanks IACUC permit #323540-1.

Normality of hare and vole data was assessed with Shapiro-Wilkes test, and we used Welch's two-sample t-test to compare pellet density and vole capture rates between study areas across years and habitat types (Zar 1999).

Prey biomass - To aid qualitative interpretation of diet composition, small mammal and wolf abundance were scaled to obtain an index of relative biomass for each prey resource. We acknowledge that converting abundance indices to available biomass introduces multiple sources of uncertainty that we were unable to account for in our biomass indices, however scaling prey abundance as a biomass index can provide a useful, albeit qualitative, standardization for comparing the relative importance of each resource, given the inherent differences in biomass per prey unit. Pellet counts are highly correlated to snowshoe hare density throughout their population cycle (Krebs et al. 2001; Murray et al. 2002), therefore hare biomass in forest and tall shrub habitat was indexed from pellet density using a conversion factor (hares/ha = pellets/m^2*0.03) and average hare body mass (1.163 kg ± 0.077 SE, n = 36) from a previous study in the central Alaska Range (Prugh 2005). To derive the index of vole biomass in spruce and meadow habitat, vole density was multiplied by the average body mass of individual voles captured during this study (19.3g ± 0.53 SE, n = 302 voles). Habitat-specific indices of hare and vole biomass were multiplied by the total hectares of each habitat type present for hares (forest + tall shrub) and voles (meadow + forest), identified from 30 m x 30 m resolution satellite imagery of land cover types in the Denali and Susitna study areas (Boggs et al. 2001, Kreig 1987). Habitat analysis was performed in ArcGIS v10.0 (Environmental Systems Research Institute, Redlands, CA).

Carrion biomass was indexed in each study area based on the best available data regarding wolf abundance and reported wolf kill rates in Northern wolf-moose-caribou ecosystems. In Denali, at least one wolf in each pack is GPS-collared and packs are regularly monitored by bi-weekly aerial monitoring. During this study, average wolf density in the Denali study area was 7.6/1,000 km^2, translating to approximately 15 wolves (S. Arthur, *personal communication*). In the Susitna site, detailed information on wolf numbers and wolf packs was not available. Therefore, we referred to reported wolf abundance from aerial snow track surveys conducted each fall and spring in the larger Game Management Unit 13 as part of the intensive management program. Because surveys were not conducted in 2014, we averaged wolf numbers for survey years 2012-2015, indicating 3.15 wolves/1,000 km^2 (ADF&G 2015b), which equates to roughly 6 wolves using the Susitna study site. This estimate concurs with observations during independent helicopter surveys conducted in winter 2013 and 2014, when a single pack of 6 wolves was observed during both years (L. Prugh, *personal observation*).

Wolf abundance in each study site was multiplied by the mean per capita wolf kill rate (0.026 kills/wolf/day) based on a sample of 16 wolf packs monitored during the winters of 1999-2001 to determine kill rates in nearby Game Management Unit 20A (McNay & Ver Hoef 2003). This estimate was within the range of published kill rates reported in similar Northern wolf-moose-caribou systems (Ballard et al. 1987; Hayes et al. 2000; Lake et al. 2013). Carrion biomass calculations were weighted by a 5:4:1 ratio of moose to caribou to Dall sheep, reflecting composition of wolf kills reported in Denali National Park (Mech et al. 1998). As in McNay & Ver Hoef (2003), live mass of ungulate prey were averaged across age classes (moose = 245 kg, caribou = 95 kg, Dall sheep = 49 kg) and multiplied by 14.6% to represent the average percent of each carcass remaining after wolf abandonment (Prugh 2005). The resulting index of wolf-provided carrion biomass available per day was multiplied by 150 days to represent total winter carrion availability from November-March.

Hunter-provided carrion was not accounted for in this study. The Denali caribou herd is protected from hunting year-round, and moose harvest only occurs on state land in the Stampede corridor in September. In Susitna, moose and caribou are hunted August-September. Winter hunts are generally not permitted, although a winter caribou hunt occurred in the larger Game Management Unit 13E during the first winter (2013) of our study. However, the location data for caribou harvested within the 20,700-km^2 subunit relative to our 1,800-km^2 Susitna study area was not available, and harvest was likely concentrated around major road corridors that did not intersect our remote study area. Although hunters provide a substantial influx of carrion resources (Wilmers et al. 2003b), it is unlikely for hunter-provided carrion from early fall to remain by winter, and there is no reasonable way to approximate what remains or what has been cached by scavengers. Furthermore, a study of carcass use in the greater Yellowstone ecosystem indicated that hunter-provided carrion was used primarily by avian scavengers, whereas mammals scavenged carrion from wolf kills more frequently than hunter kills (Wilmers et al. 2003b).

Non-predation overwinter mortality (i.e., "winter kill") for adult moose and caribou was expected to be low in both study areas and therefore not considered as an appreciable source of carrion during this study, but we acknowledge the importance of this resource during extreme environmental conditions that reduce overwinter survival. In Denali, moose and caribou herd health is currently high. Overwinter survival of radio-collared female caribou was approximately 95 and 98% during winter of 2013 and 2014 respectively, and roughly 95% for Denali moose from the 1990s-2000s (L. Adams, *personal communication*). Preliminary data from concurrent radio-tracking of moose and caribou in Susitna similarly indicated high overwinter survival, with mortality rates of 2 and 4% for moose and 9.5 and 13.6% for caribou during winter 2013 and 2014, respectively (ADF&G, *unpublished data*). Cause-specific mortality was not available for these data, however wolf predation is the major cause of moose and caribou mortality in all but the most extreme winters, and wolf control is not shown to influence overwinter survival of adult or yearling moose (Modafferi & Becker 1997; Bertram & Vivion 2002; Keech et al. 2011). During this study, winter conditions were mild overall with extremely low snow conditions during 2014 (Denali National Park and Preserve, *unpublished data*), making high overwinter mortality related to winter severity unlikely.

3.3.6 Diet analysis

Diet composition for each canid species in each study area was recorded as the frequency of occurrence of each food item in *n* scats, weighted by the visual estimation of the percent volume of each items in the scats (hereafter, "weighted percent occurrence"). Diet richness was measured as the total number of items in the diet (Krebs 1999). Niche breadth was calculated using the Shannon-Wiener diversity index (Colwell & Futuyma 1971). Percent diet overlap between coyotes and foxes was calculated using Pianka's percent overlap index, which ranges from 0, indicating no diet overlap, to 1.0, indicating complete diet overlap (Pianka 1974).

Because larger sample sizes inherently result in a greater number of expected items, we used rarefaction to assess the effect of unequal sample sizes for each species and study area on weighted percent volume and diet indices (Krebs 1999). For each sample size *n*, from 1 to the maximum number of scat samples for a given species and study area, 10,000 bootstrap samples of the weighted percent occurrence of prey items in scats were drawn, from which mean and variance was calculated for weighted percent occurrence of each prey item, Shannon-Weiner diversity, and diet richness. The resulting rarefaction curve was inspected for the sample size at which each of the diet indices reached a plateau, in order to determine if sub-sampling would be necessary to account for unequal sample sizes among species and study sites. Curves that do not plateau at the minimum sample size (i.e., continue to increase) indicate that sub-sampling from groups with larger sample sizes is necessary to make comparisons among groups. Curves that plateau indicate that sampling has adequately captured the range of resources and sub-sampling is not necessary. Means of diet indices were then re-calculated from 10,000 bootstrap samples of size *n*, with replacement (Manly 2006), based on sample size as determined by rarefaction curves (see results). Confidence intervals for mean diet indices (95%) were derived at the 0.0275 and 0.975 quantiles from the bootstrap re-sampling distribution (Efron 1982). Bootstrapping, computation of diet indices, and associated analyses were performed using the package 'bootstrap' in program R (R Core Development Team 2014).

3.4 Results

3.4.1 Scat collection and species ID

Of the total 998 carnivore scats collected in winter 2013 and 2014, 528 were identified by molecular methods as coyote or red fox (all scats encountered were collected for a concurrent study of wolf scats). Observers correctly identified 67.8% of coyote and red fox scats confirmed with molecular methods (Table 3.1). Comparison of molecular and field species identification showed that scats identified as red fox or coyote in the field with 60-75% certainty were assigned the correct ID 68.7% of the time. This increased to 70% accuracy at the 80-85% certainty criteria, and 78% at the 90-100% certainty criteria. Across all scats identified with ≥60%

certainty, 73% were correctly identified in the field (*n* = 302, Table 3.1). Based on these results, an additional 96 scats with failed molecular results and field ID recorded as coyote or red fox with ≥60% certainty were assigned the respective field species ID and included in analyses. Thus, a total of 624 coyote (*n* = 213) and red fox (*n* = 411) scats were used for diet analysis.

3.4.2 Resource availbility

Hare pellet density, pooled across years and habitat types, was significantly greater in Denali than in Susitna (Welch's two sample t-test, $t = 5.0258$, $df = 29.314$, $p < 0.001$; Fig. 3.2). Mean pellet density pooled across habitat types and years in Denali was 19.58 ± 2.34 SE and in Susitna was 5.51 ± 1.53 SE, with a variance of 98.82 and 42.37, respectively. Vole capture rates, pooled across years and habitat types, did not differ significantly across study areas (Welch two sample t-test, $t = 0.7143$, $df = 29.893$, $p = 0.4806$; Fig. 3.3). Mean vole captures were 2.20 ± 0.554 SE in Denali and 1.67 ± 0.49 SE in Susitna, with a variance of 5.22 and 3.57 respectively. When scaled to an index of biomass, hares made up the majority of biomass in both study sites (Denali = 48,454 kg, Susitna = 6,540 kg). Vole biomass was the second most abundant (Denali = 4,102 kg, Susitna = 1,820 kg). Carrion represented the smallest source of biomass in both study sites. Based on per capita wolf kill rates, each individual wolf can provide 0.706 kg of carrion biomass per day. Over a period of 150 days, this was calculated as 1,730 kg of carrion biomass left over from approximately 68 kills in Denali, and 649 kg of carrion biomass left over from approximately 25 kills in Susitna. The total combined biomass index (hares + voles + carrion) in Denali was 54,286 kg, versus 9,009 kg in Susitna (Fig. 3.4).

3.4.3 Diet composition

The most common prey items in coyote and red fox scats across study sites were carrion (32%), voles (29%), and snowshoe hares (11%), collectively representing over 70% of weighted occurrences. Vegetation represented just over 7% of weighted occurrences, yet it was unknown whether this was a result of intentional or incidental consumption. Of the remaining prey items, none represented more than 4% of weighted occurrences of all scat contents, further emphasizing the significance of carrion, voles, and hares as principal resources for coyotes and red foxes.

In Denali, carrion represented 39.6% and 10.1% of coyote and red fox diets, respectively (Fig. 3.5, panel a). Use of carrion in the Susitna area, where wolf density was reduced, was high for both coyotes and red foxes, comprising 62.1% and 35.2% of their diets, respectively (Fig. 3.5, panel b). Hares represented 17.6% of coyote diet and 21.9% of red fox diet in Denali, yet hares were virtually absent (<2%) from coyote and red fox diets in Susitna. Voles represented 14.6% of coyote and 48.2 % of red fox diet in Denali. In Susitna, voles represented only 4.5% of coyote diet, and 29% of red fox diet. Muskrats made up 4.9% of coyote diet in Susitna, similar in proportion to the use of voles, yet muskrat did not appear in coyote diet in Denali. Porcupine comprised 15% of coyote diet in Susitna, but was a negligible component (0.03%) of coyote diet in Denali. Birds represented 10% of red fox diet in Susitna. Although we were unable to identify feathers to bird species, presence of claws and beaks suggest that avian prey were primarily ptarmigan and grouse. Overall, the top three prey items in coyote diets in Denali ranked by use from highest to lowest were 1) carrion, 2) hares, and 3) voles, whereas for red fox prey items were ranked as 1) voles, 2) hares, and 3) carrion. In Susitna, the top three items in coyote diets were 1) carrion, 2) porcupine, and 3) vole/muskrat; whereas red fox diets were 1) carrion, 2) voles, and 3) birds.

3.4.4 Diet analyses

Diet indices- Rarefaction curves showed that diet richness increased up until sample sizes of about 60-70, after which curves approached a plateau, or exhibited a reduced slope that remained within the range of a 1-3 prey item increase (Fig. 3.6, shown for Susitna red foxes). Rarefaction curves for diet diversity increased up until a sample size of 30, after which diversity reached a plateau for all groups. The variance in percent occurrence of items in the diet tapered off greatly for both species in both study areas at sample sizes greater than 30-40 scats. We therefore sub-sampled to obtain a sample size of $n = 79$ from groups with sample sizes larger than our limiting sample size, Susitna coyotes ($n = 79$), to calculate bootstrapped estimates of diet richness and Shannon-Weiner diversity. Because the mean and variance of weighted percent occurrence of items in the diet reached a plateau for all sample size groups after 30 scats, we did not sub-sample, and drew from the full sample size to obtain bootstrapped estimates of use.

Diet overlap between coyotes and red foxes was higher in Susitna (77.1%) than in Denali (60.5%). Shannon-Weiner diet diversity ranged between 1.75 and 1.95 across all groups at a sample size of $n = 79$ (Table 3.2). Confidence intervals of bootstrapped diversity estimates indicated no difference between coyotes and red foxes in either Denali or Susitna. However, non-overlapping confidence intervals indicated that coyotes in Denali had slightly higher diet diversity (1.95) than coyotes in Susitna (1.75). Red fox diet diversity did not differ between study areas. Diet richness, i.e., number of prey items in the diet, ranged from 10.98 to 12.76 across all study areas and species. Overlapping confidence intervals indicated no significant differences in richness across any species or study area pairs (Table 3.2).

3.5 Discussion

Carrion is more than an easy meal; leftovers from top carnivores are increasingly acknowledged as having significant influences on interspecific interactions and community structure (Selva & Fortuna 2007; Cortés-Avizanda et al. 2009; Barton et al. 2013; Allen et al. 2014; Moleón et al. 2014). Where ungulate carrion is present, it is widely documented as an important supplemental resource that influences feeding behavior of coyotes and red foxes (Gibson et al. 1984; Arjo et al. 2002; Selva et al. 2003; Wilmers et al. 2003a; Switalski 2003; Helldin & Danielsson 2007; Needham & Odden 2014). However, there is a paucity of work evaluating how carrion subsidies influence diet composition, overlap and diversity in relation to large carnivore presence and small mammal prey. In this study, we observed high use of carrion by coyotes and red foxes, with reduced diet overlap and decreased use of carrion by red foxes where wolves were more abundant. Thus, as our second hypothesis suggests, carrion subsidies could minimize diet overlap, and therefore competition, among sympatric mesopredators provided there are sufficient resources for the smaller (e.g., red foxes) competitor.

The range of diet overlap (0.6-0.77) in this study was generally high in both study areas. High diet overlap (0.71-0.91) has been documented between coyotes and various fox species foraging on small mammals in numerous other North American ecosystems, yet studies either did not take place in areas with resident large carnivore populations, or scant mention of scavenging suggests carrion was not a readily available resource in those ecosystems (Theberge & Wedeles 1989; Kitchen et al. 1999; Fedriani et al. 2000; Neale & Sacks 2001; Kamler et al. 2007; Randa et al. 2009; Warsen et al. 2014). As a measure of resource utilization, diet overlap is influenced by the overall number and diversity of items in the diet (Krebs 1999). In this study, coyotes and red foxes did not vary appreciably in diversity or number of prey resources in their diet in either study area, indicating that differences in diet overlap among study areas were due to shifts in diet composition (i.e., the identity and amount of individual items in each diet) rather than changes in diversity or richness. In our study system, where a few select prey resources comprise the majority of the diet, diet overlap patterns appeared to be driven by differential response to wolves. The index of carrion biomass, assumed to scale linearly with wolf abundance, was higher in Denali. Despite the apparent differences in wolf abundance between study areas, carrion still comprised a major portion of coyote diet, whereas red foxes appeared to transition from a greater use of carrion, to reduced use of carrion. In other words, coyote diet composition was dominated by high use of carrion in both areas, whereas red fox diet composition appeared more sensitive to differences in carrion, and quite possibly, the persistent use of carrion by coyotes. On the other hand, despite greater hare pellet density in Denali compared to Susitna, both coyotes and red foxes showed reduced use of hares, dropping from 18-22% in Denali to less than 2% in Susitna. This was likely a result of coyotes using more carrion and red foxes using more voles in Susitna.

Reduced diet overlap in Denali could alternatively have been driven by difference in overall resource abundance, which based on our qualitative index of total available biomass (hares + voles + carrion), appeared to be higher in Denali. Most of this difference can be attributed to hare biomass. Statistical tests indicated that hare pellet counts were lower in Susitna, however the high variance in pellet counts indicates the uncertainty surrounding these comparisons therefore our quantitative comparison could be considered inconclusive. Nonetheless, the Susitna area is characterized by considerably less hare habitat, which is consistent with a previous assessment in the Susitna River basin that noted generally sparse, poor quality hare habitat in watersheds within our present day study area (Gibson et al. 1984). Even if differences in overall resource availability, and thus resource limitation alone, accounted for diet overlap patterns, an associated increase in diet diversity and richness in Susitna should have been evident as predators expand their diet to make up for reduced resource availability, as predicted by optimal foraging theory (MacArthur & Pianka 1966). Indeed, in a nearby study conducted during a previous hare decline, coyote diet diversity increased as hares declined (Prugh 2005). On the contrary, we observed higher diet overlap in Susitna. We observed slightly lower diet diversity in Susitna, yet these differences were negligible for coyotes and not significant for red foxes. We also observed no significant differences in diet richness between study areas. Thus, we suggest that variation in diet overlap was most likely driven by differences in biomass of wolf-provided carrion.

The high use of carrion by coyotes in both study areas indicates that coyotes maximized use of scavenging opportunities, irrespective of wolf presence, whereas carrion use by red foxes decreased 3-fold in the wolf-abundant study area. For the larger-bodied, competitively dominant coyote, carrion remained the primary resource, whereas red foxes appeared to switch from carrion to hares and voles when faced with increased competition with coyotes for carrion resources. The introduction of carrion resources by large carnivores may minimize competition among sympatric mesopredators by facilitating resource partitioning (Yarnell et al. 2013). For example, high diet overlap between black-backed jackals (*C. mesomelas*) and brown hyenas (*Parahyaena brunnea*) in South Africa was attributed to shared use of small mammals where large carnivores were absent, yet where large carnivores were present, thus introducing carrion subsidies, diet overlap declined as hyenas, the dominant mesopredator, increased specialization on carrion (Van der Merwe et al. 2009). Here, wolf presence may have similarly reduced diet overlap, and therefore competition, between coyotes and red foxes for voles, by providing sufficient scavenging opportunities such that coyotes relied more on carrion and less on voles.

High exploitation of carrion by coyotes could have increased the cost of foraging on carrion for red foxes by heightening risk of encountering a dominant competitor in the vicinity of carcasses. Coyotes are aggressive to red foxes and known to exclude them from carcass sites (Major & Sherburne 1987; Palomares & Caro 1999). Although competitors run the risk of encounter when foraging for small prey in shared habitat patches, carcasses are far-reaching attractants that increase the potential for interference competition between sympatric scavengers in a more concentrated area (Andelt & Hein 1996; Switalski 2003; Kamler et al. 2004; Merkle et al. 2009). Risk could be mitigated by temporal partitioning to reduce risk of encounter (Schoener 1974b), however use of other, smaller prey resources, like voles and hares, could be the preferable alternative for smaller-bodied predators, especially if and when small prey is sufficiently available. Thus, a necessary condition for carrion subsidies to reduce competition could be that sufficient resources are available to the subordinate competitor.

Our measure of the use of ungulate carrion relative to small mammal prey is susceptible to differences in digestibility. Although digestibility among small mammal species consumed by coyotes is thought to be similar (Johnson & Hansen 1979), it is not known whether coyotes and foxes differ in their digestion of various species. Moreover, little information exists regarding digestibility of small prey relative to moose and caribou carrion, as remains may be digested into unequally-sized fragments making quantitative comparisons difficult (Reynolds & Aebischer 1991). If anything, consumption of ungulate carrion may be underrepresented in coyote and fox scats, as the lower surface: volume ratio of large ungulate carrion leaves less undigested matter per kilogram of digestible meat compared to small mammals (Floyd et al. 1978). In lieu of a digestibility model, our use of weighted percent occurrence (e.g., volume) provides the next best quantitative assessment for addressing niche overlap (Klare et al. 2011). Moreover, differences in digestibility should not influence comparisons between study areas.

Interestingly, use of hares by coyotes and foxes in this study was surprisingly low, despite the biomass index suggesting that hares were the most abundant of the three resources in both study areas. Previous studies of northern coyote diets during the peak and decline phase of the hare cycle showed high use of and selection for hares (Theberge & Wedeles 1989). In one case, selection of hares increased despite a 6-fold decline in hare abundance (Prugh 2005). In our study region, hare abundance peaked from 2008-2010, crashed in 2011 (Krebs et al. 2013), and has remained low since then (C. McIntyre, unpublished data), providing insight into diet patterns after the decline phase. Hare densities may have already been low enough that hare predation was proportional to hare density, whereas predation on hares is disproportionately high during the increase and decline phases (Theberge & Wedeles 1989). When hare densities decline, hares retreat into pockets of habitat refugia in increasingly dense spruce and shrub thickets (Wolff 1980), presenting additional costs in terms of search and pursuit time (O'Donoghue et al. 1998).

Monitoring how diet overlap and composition changes during the increase phase of the hare cycle would further contribute to our understanding of the role of carrion subsidies in resource partitioning among these two canids. As hares become more abundant and more profitable, it is reasonable to expect that the use of carrion by coyotes would no longer be the optimal resource relative to hares, especially considering the inherent risk of scavenging from wolves (Merkle et al. 2009). The degree to which red foxes use hares in this particular region remains poorly known, however an earlier study of red fox diets in Susitna during a low phase of the hare cycle also documented voles and carrion as the primary diet items, with little use of hares (Gibson et al. 1984). If coyotes reduce reliance on carrion when hares are more abundant, red foxes may increase their reliance on carrion, especially when voles are scarce.

Uncertainty regarding carrion availability was a major limitation in our study. In lieu of precise estimates of kill rates in our study system, we applied the best available data to estimate carrion biomass and assumed, albeit simplistically, that carrion biomass increases linearly with wolf density. Rapid reduction in wolf density (e.g., wolf control) disrupts wolf social structure and pack dynamics leading to smaller pack sizes (Ballard et al. 1987; Borg et al. 2014). Smaller wolf packs have been found to have higher per-capita kill rates compared to larger packs (Ballard et al. 1987; Hayes et al. 2000; Lake et al. 2013), which translates to more carcass sites. Smaller packs may also leave more biomass per kill, considering individuals could become satiated and abandon their kills sooner (Giraldeau & Caraco 2000). Fewer wolves and earlier abandonment of kills could also reduce the likelihood of wolf encounters, which could entice scavengers typically wary of wolf presence to spend more time feeding at carcass sites. In addition, fewer wolves could have led to higher rates of mortality from sources other than wolves (e.g., starvation or senescence) in Susitna, despite mild winters. Future studies examining how carrion biomass varies with large carnivore density and group size would advance our understanding of carrion provisioning by large carnivores.

In conclusion, the findings of this study highlight how carrion could influence foraging patterns and resource partitioning among sympatric scavengers during a period of low prey availability. In our study area, resource competition, as opposed to optimal foraging, could be the dominant factor driving foraging patterns by red foxes. These findings suggest additional implications to food web dynamics as a result of carnivore cascades (Levi & Wilmers 2012). First, carrion subsidies from large predators could affect food web dynamics by alleviating predation by a dominant mesopredator (e.g., coyotes) on a shared food resource (e.g., voles). Second, facilitation by large carnivores could minimize competition and facilitate coexistence between sympatric mesopredators, provided there is sufficient alternative prey available to the subordinate mesopredators. Where sufficient prey is not available to the subordinate mesopredator, it is possible that that abundant carrion subsidies associated with large carnivore presence could be detrimental to smaller predators, given the risky nature of foraging for carrion.

3.6 Acknowledgements

We extend sincere thanks to all the human and canine field volunteers, community members, UAF staff, ADF&G and NPS personnel who contributed time, resources, and effort towards this project. In particular, J. Reppert, C. Bondy, and P. Baigas provided invaluable winter field assistance and volunteers from the Denali National Park Kennels assisted with scat collection. K. Colson and M. Mumma dedicated many long hours to molecular analysis of fecal samples, which is greatly appreciated. J. Rose and E. Moeller provided unending enthusiasm in picking apart canid scats. University of Alaska Museum North kindly loaned museum specimens for reference while identifying prey remains in scats. This manuscript benefitted from comments from S. Arthur, K, Kielland, and M. Lindberg. Alpine Creek Lodge, Alaska Earth Sciences, Alaska Biological Research, Inc., Murie Science Learning Center, Alaska Geographic, and Denali National Park and Preserve provided administrative and logistics support. Funding was provided by a grant from the Alaska Energy Authority (RSA # 1331) to L.R.P., a Discover Denali Fellowship to K.J.S., and a National Science Foundation Graduate Research Fellowship (#2012136814) to K.J.S.

3.7 Figures

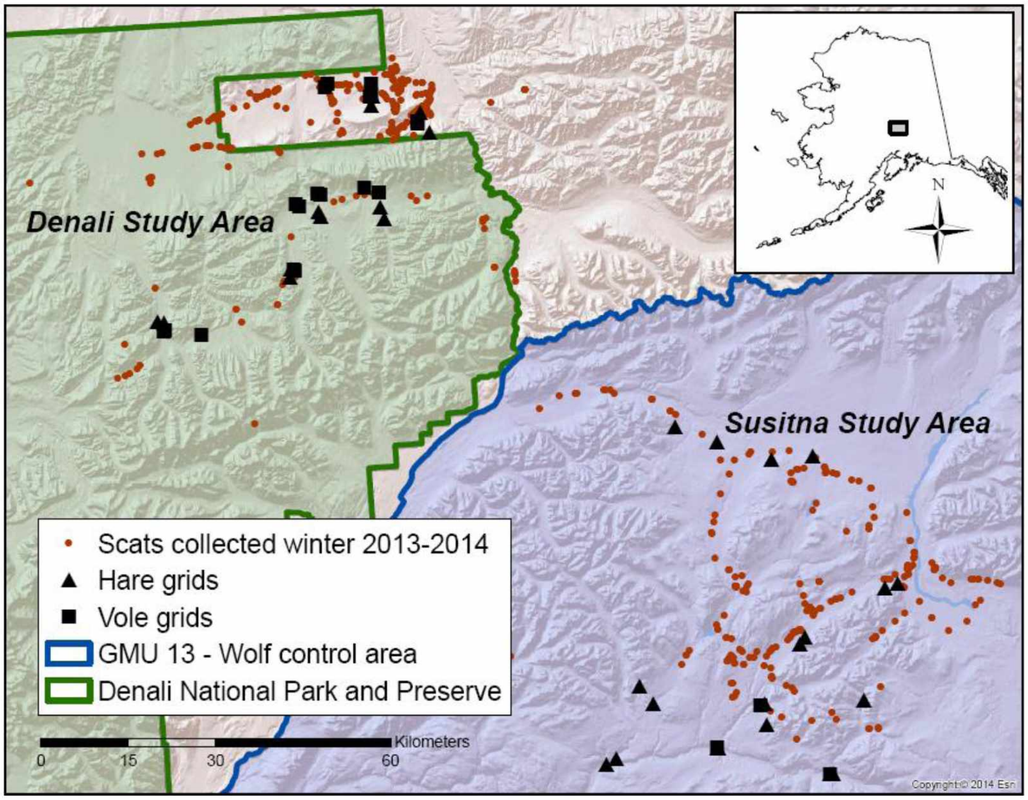

Figure 3.1 Study area map. Locations are shown of winter scat collection and summer small mammal monitoring sites in Denali National Park and Preserve and Susitna River Basin.

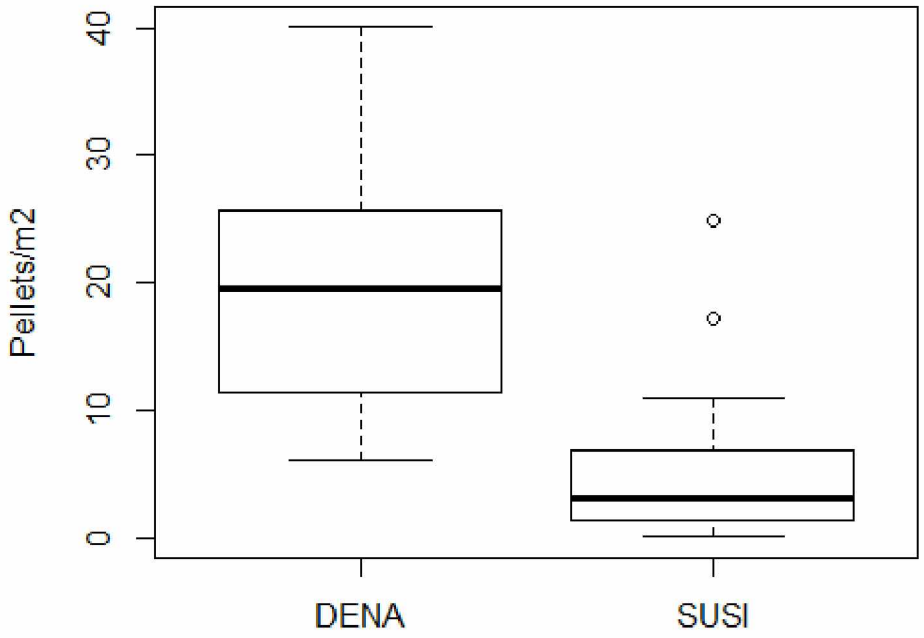

Figure 3.2 Mean snowshoe hare pellet density in Denali and Susitna. Pellet densities (pellets/m^2) estimated from annual pellet count surveys 2012-2014 in spruce and tall shrub habitat at 6 paired sites in Denali (n = 12) and 7 paired sites in Susitna (n = 14).

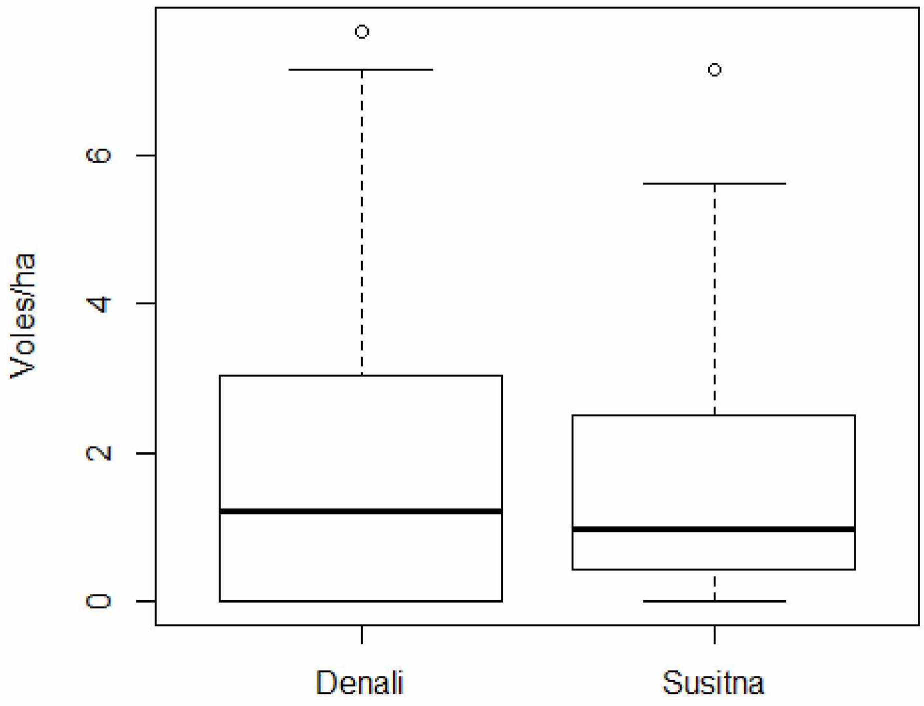

Figure 3.3 Mean vole captures in Denali and Susitna. Vole captures (voles/hectare) at trapping grids in Denali (*n* =17) and Susitna (*n* =15), 2013-2014 based on the correlation of 1st night's capture success with 5 night mark-recapture estimates at Rock Creek trapping grids, Denali National Park.

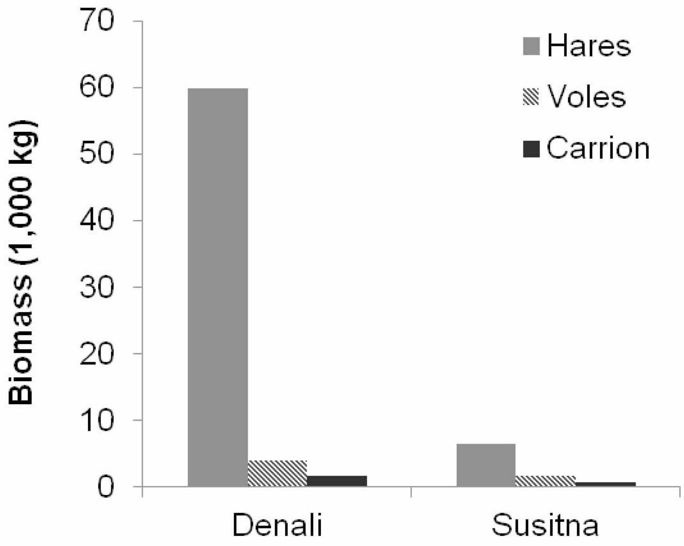

Figure 3.4 Biomass availability index in Denali and Susitna. Estimates of hare pellet density and vole capture rates were scaled by individual body mass and hectares of habitat. Wolf abundance was scaled by reported wolf kill rates, live ungulate mass, and percent biomass remaining after wolves.

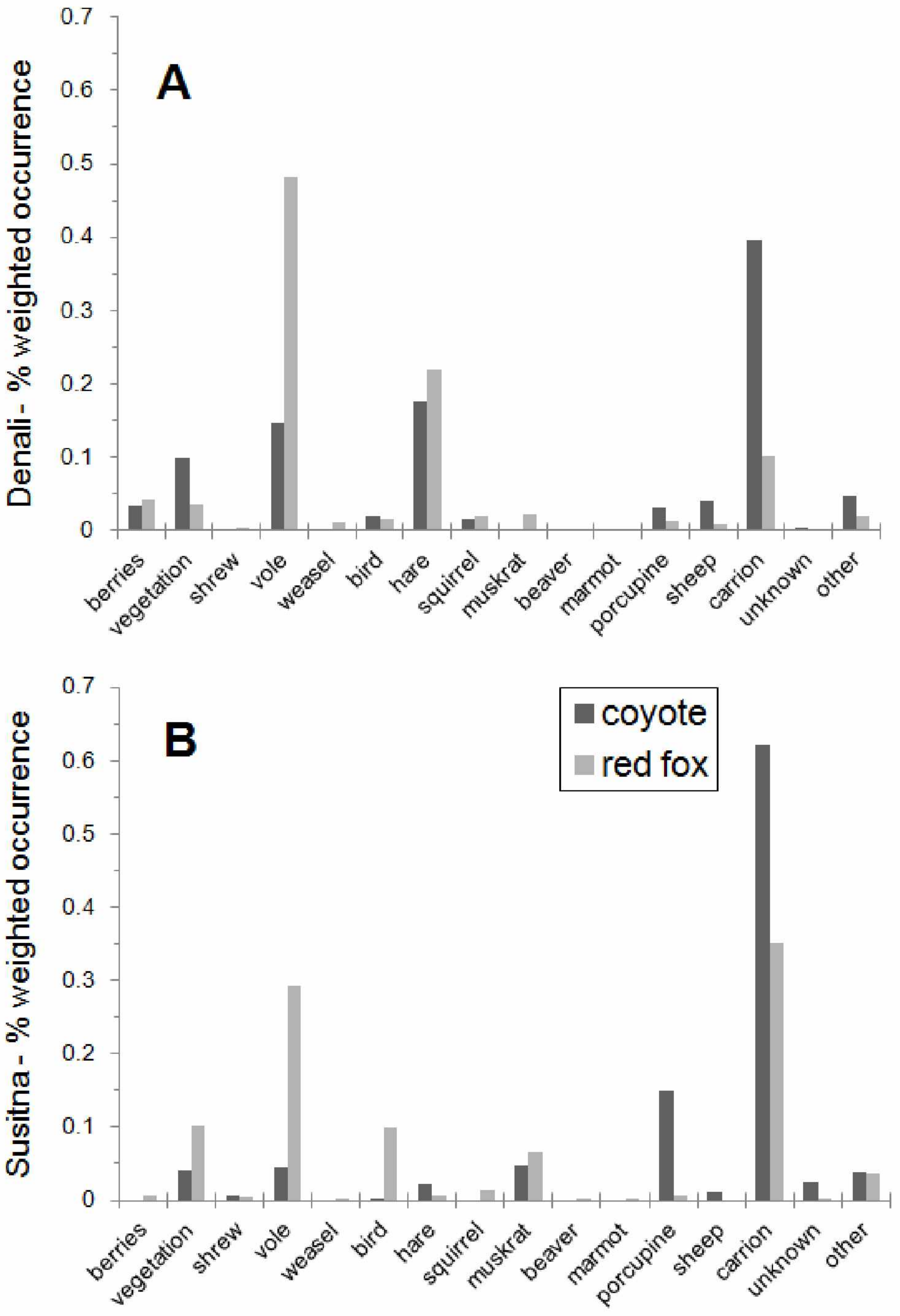

Figure 3.5 Coyote and red fox winter diet composition. Percent weighted volume (total percent volume in scats/sample size) of prey items in coyote and red fox scats collected winter 2013-2014 in Denali (panel A) and Susitna (panel B) .

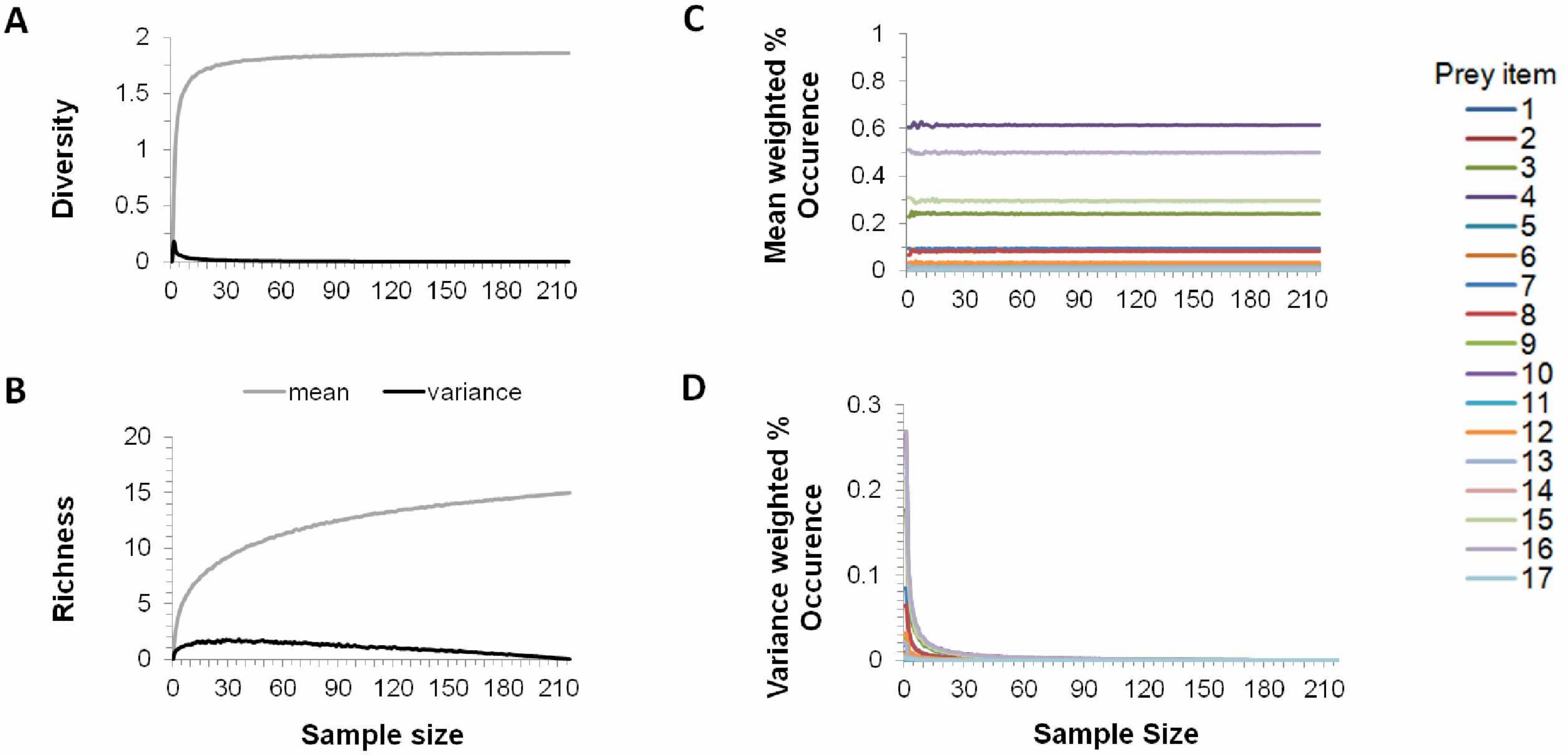

Figure 3.6 Scat rarefaction curves for red fox scats collected in Susitna (*n*=218). Panel A) Shannon-Weiner diversity, B) diet richness, C) mean weighted % occurrence, and D) variance of weighted % occurrence.

3.8 Tables

Table 3.1 Observer accuracy of field identification of coyote and red fox scats. Observer certainty is in relation to the self-rated certainty of observers in their identifications. True species identification was determined using molecular techniques.

Observer Certainty	Correct		Incorrect	
	n	%	*n*	%
all	358	0.678	170	0.322
0-55%	56	0.483	60	0.517
60-75%	110	0.688	50	0.313
80-85%	48	0.706	20	0.294
90-100%	144	0.783	40	0.217
≥ 60%	302	0.733	110	0.267

Table 3.2 Coyote and red fox winter diet diversity, richness, and percent diet overlap. Diet indices estimated from 10,000 bootstrap samples of size *n*=79.

Study Area	Species	*n*	Shannon-Wiener Diversity (95% CI)	Richness (95% CI)	Pianka's % Overlap
Denali	coyote	79	1.95 (1.86-2.03)	11.9 (10.34-13.47)	0.605
	red fox	79	1.9 (1.79-2.00)	12.76 (11.02-14.5)	
Susitna	coyote	79	1.75 (1.72-1.76)	10.98 (10.71-11.25)	0.771
	red fox	79	1.83 (1.71-1.95)	12.01 (9.74-14.28)	

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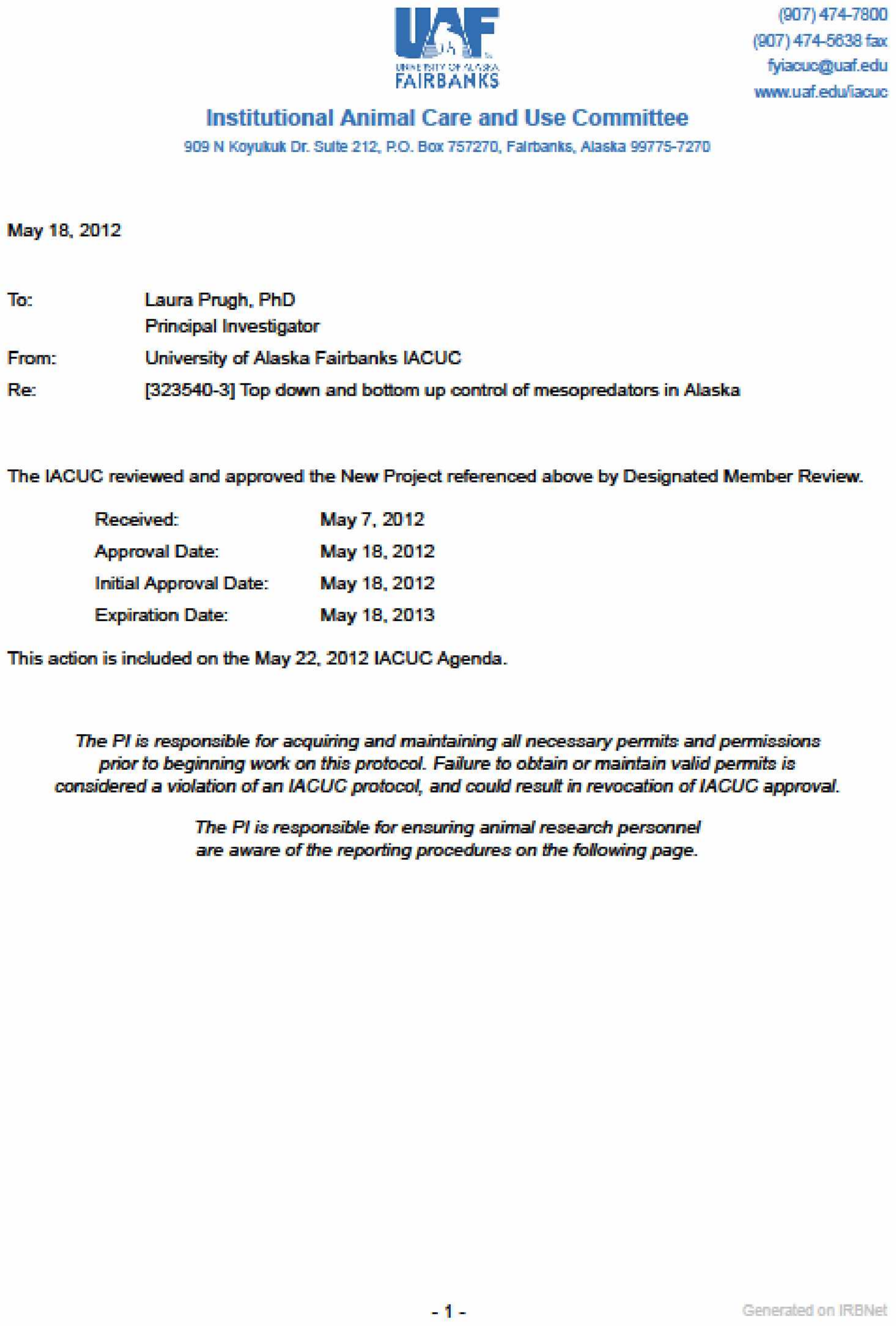
Appendices

Appendix 3.1 Institutional Animal Care and Use Committee Permit Approval Letter, 2012



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May 18, 2012

To: Laura Prugh, PhD
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [323540-3] Top down and bottom up control of mesopredators in Alaska

The IACUC reviewed and approved the New Project referenced above by Designated Member Review.

Received:	May 7, 2012
Approval Date:	May 18, 2012
Initial Approval Date:	May 18, 2012
Expiration Date:	May 18, 2013

This action is included on the May 22, 2012 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

The PI is responsible for ensuring animal research personnel are aware of the reporting procedures on the following page.

- 1 -

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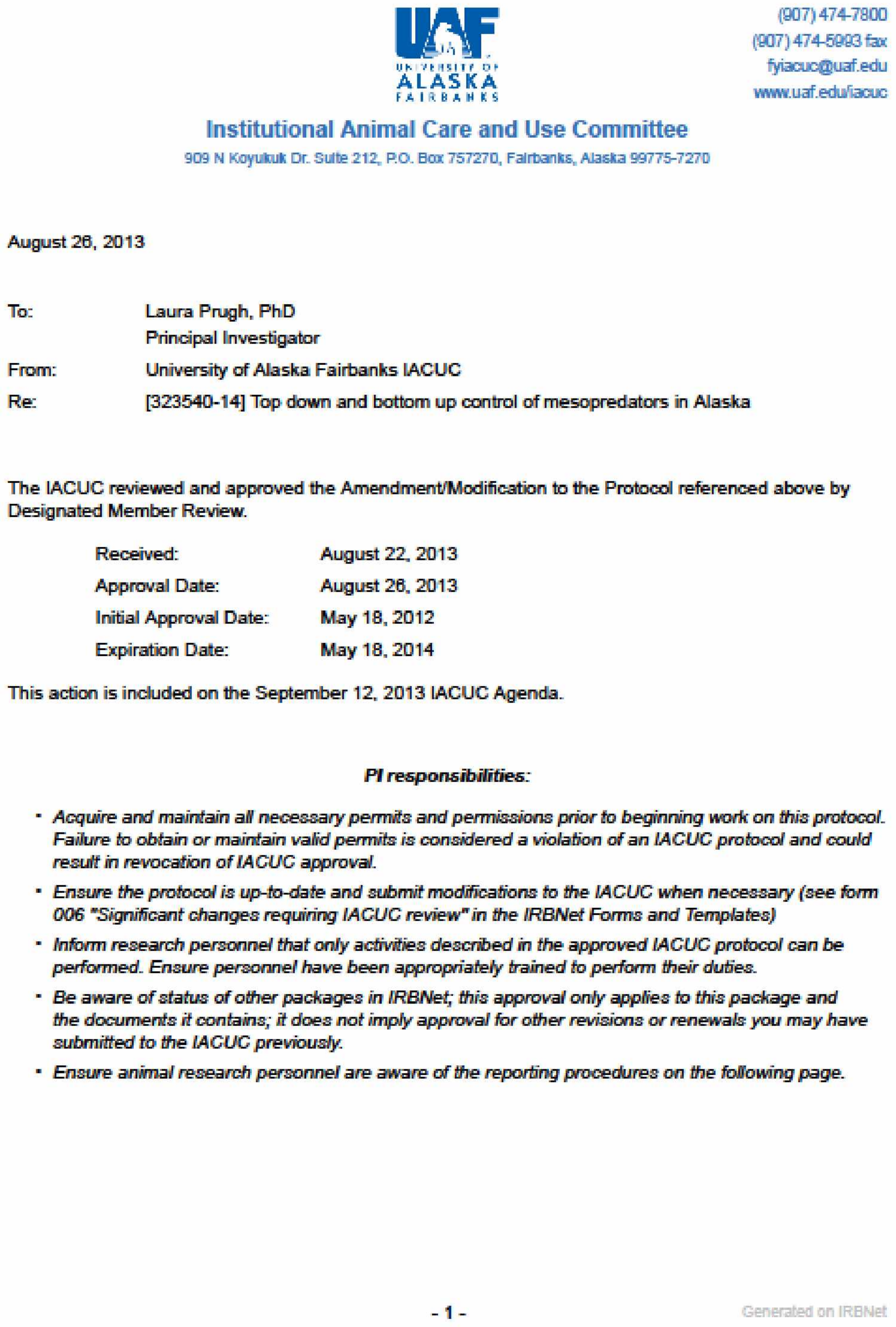
Appendix 3.2 Institutional Animal Care and Use Committee Permit Approval Letter, 2013



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August 26, 2013

To:	Laura Prugh, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[323540-14] Top down and bottom up control of mesopredators in Alaska

The IACUC reviewed and approved the Amendment/Modification to the Protocol referenced above by Designated Member Review.

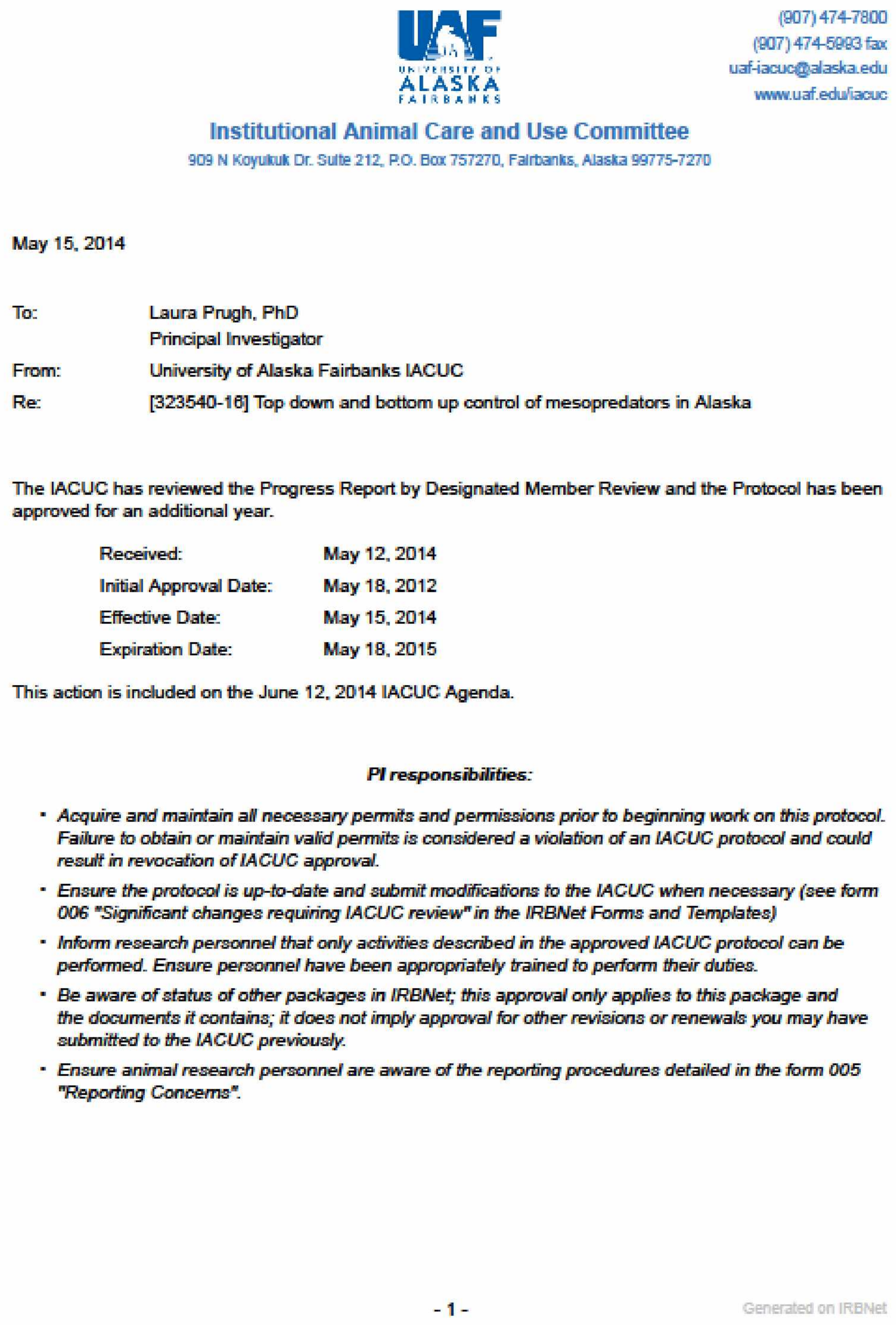
Received:	August 22, 2013
Approval Date:	August 26, 2013
Initial Approval Date:	May 18, 2012
Expiration Date:	May 18, 2014

This action is included on the September 12, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix 3.3 Institutional Animal Care and Use Committee Permit Approval Letter, 2014



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May 15, 2014

To: Laura Prugh, PhD
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [323540-16] Top down and bottom up control of mesopredators in Alaska

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received: May 12, 2014
Initial Approval Date: May 18, 2012
Effective Date: May 15, 2014
Expiration Date: May 18, 2015

This action is included on the June 12, 2014 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".*

- 1 -

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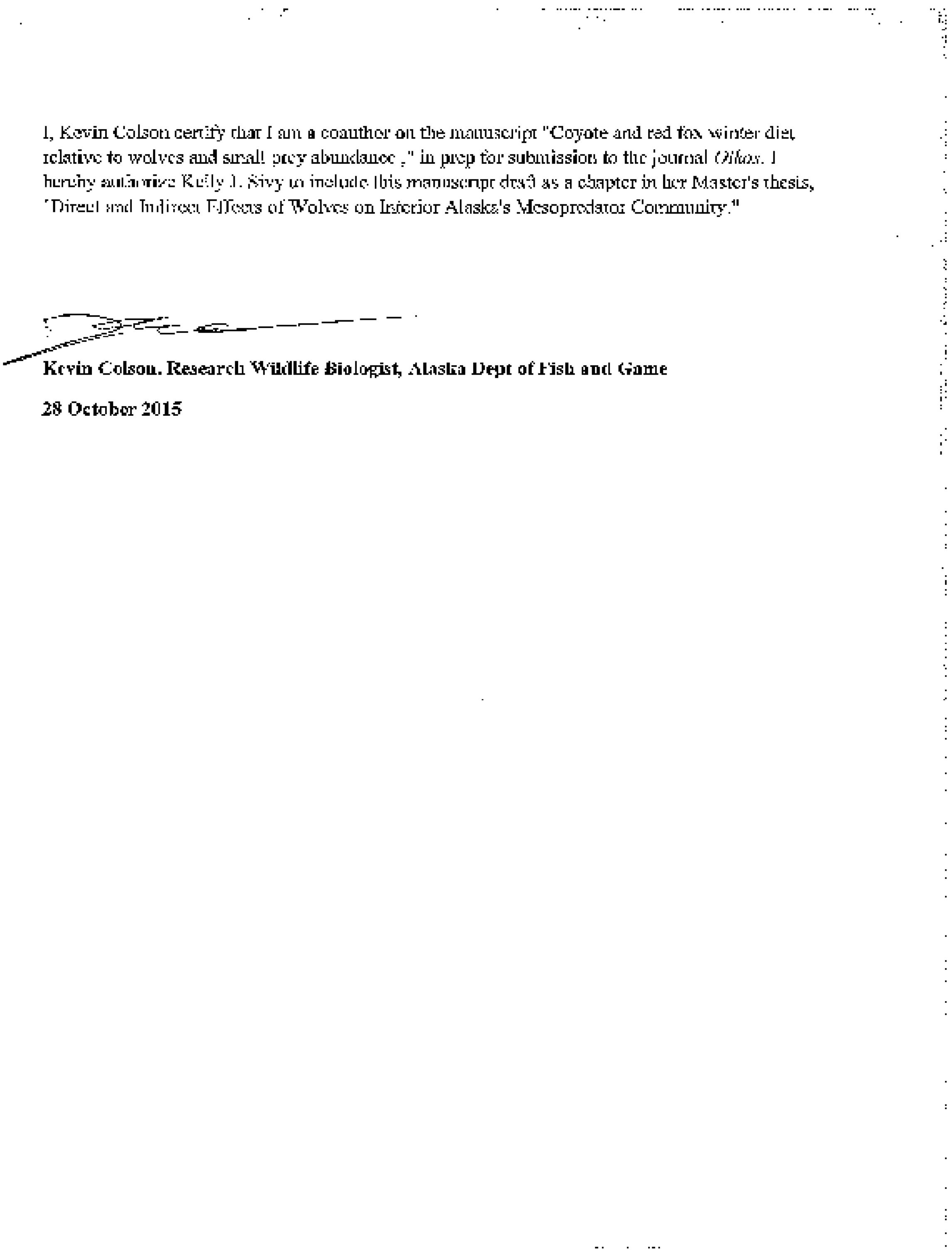
Appendix 3.4 Coauthor permission, K. Colson, Chapter 3

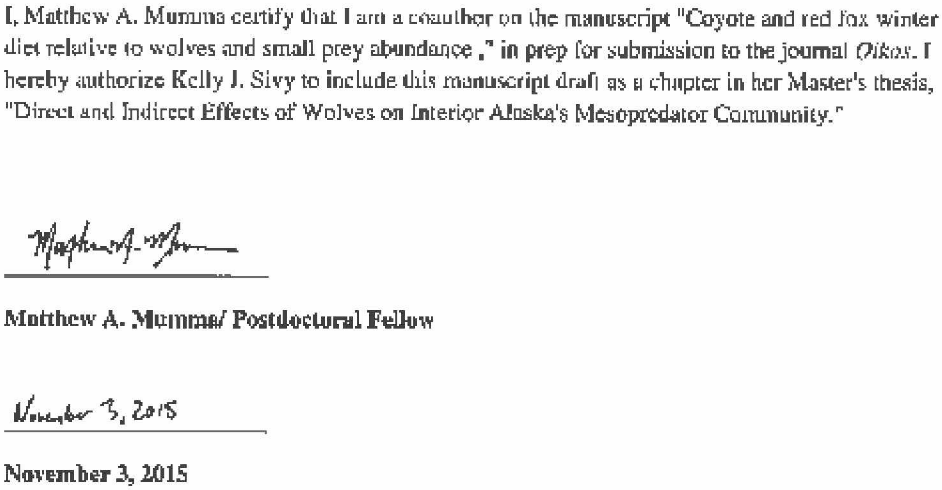


I, Kevin Colson certify that I am a coauthor on the manuscript "Coyote and red fox winter diet relative to wolves and small prey abundance ," in prep for submission to the journal *Oikos*. I hereby authorize Kelly J. Sivy to include this manuscript draft as a chapter in her Master's thesis, "Direct and Indirect Effects of Wolves on Interior Alaska's Mesopredator Community."

Kevin Colson, Research Wildlife Biologist, Alaska Dept of Fish and Game

28 October 2015

Appendix 3.5 Coauthor permission, M. Mumma, Chapter 3



I, Matthew A. Mumma certify that I am a coauthor on the manuscript "Coyote and red fox winter diet relative to wolves and small prey abundance ," in prep for submission to the journal *Oikos*. I hereby authorize Kelly J. Sivy to include this manuscript draft as a chapter in her Master's thesis, "Direct and Indirect Effects of Wolves on Interior Alaska's Mesopredator Community."

Matthew A. Mumma/ Postdoctoral Fellow

November 3, 2015

November 3, 2015

Appendix 3.6 Coauthor permission, C. Pozzanghera, Chapter 3

I, Casey Pozzanghera certify that I am a coauthor on the manuscript "Coyote and red fox winter diet relative to wolves and small prey abundance," in prep for submission to the journal *Oikos*. I hereby authorize Kelly J. Sivy to include this manuscript draft as a chapter in her Master's thesis, "Direct and Indirect Effects of Wolves on Interior Alaska's Mesopredator Community."

Casey Pozzanghera/ Graduate Student, coauthor

11-2-15

November 2, 2015

Chapter 4 General Conclusion

4.1 Overview

Large carnivores are increasingly recognized as having broad-reaching effects on ecosystem dynamics (Ripple et al. 2014). In particular, competitive interactions within the carnivore guild can result in suppression of dominant mesopredators (Ritchie & Johnson 2009). The potential for large carnivores to limit expanding populations of mesopredators, with indirect benefits to smaller predators and prey, is commonly proposed as a benefit of large carnivore restoration (Crooks & Soulé 1999; Levi & Wilmers 2012). However, large carnivores, through carrion provisioning, may also influence carnivore communities through facilitative pathways, which could vary in strength depending on environmental stress (Bruno et al. 2003; Wilmers et al. 2003a; Barrio et al. 2013). The complexities behind facilitative versus suppressive pathways can make predicting the outcomes of large carnivore-induced cascades extremely challenging. Though numerous studies have provided valuable insights gleaned through species-specific piecewise examinations of these complex interaction pathways (Ritchie & Johnson 2009), to my knowledge no study has sought to examine the response of a complete mesopredator guild to variation in large carnivore abundance. To contribute to this understanding, I examined the space use patterns of 5 mesopredators and diet composition and overlap of two competing mesocarnivores in an area where wolves are at naturally regulated densities and an adjacent area where wolves are artificially reduced by state predator control. Collectively, this research has provided the first examination of the influence of a large carnivore, the grey wolf, on the occurrence patterns and diet of a multi-species mesopredator community in Alaska.

In chapter 2, I quantified the relative strengths of hypothesized direct and indirect interaction pathways, accounting for moderating factors of prey availability and snowpack, to assess the strength and direction (positive or negative) to which wolf presence elicits coyote-mesopredator cascades. In Chapter 3, I examined winter diet composition, prey selection, and diet overlap by coyotes and red foxes in these two areas differing in wolf management.

4.2 Key findings

1) The patterns of wolf-mesopredator occurrences did not support either hypothesis of a suppression-induced or facilitation-induced cascade through coyotes. Wolves exerted a strong influence on coyote occurrence, however coyotes were a poor predictor of lynx, red fox, and marten occurrence. I concluded that during a period of reduced abundance of small mammal prey, coyotes exerted minimal influence on the space use patterns of other mesopredators, suggesting that competitive interactions among these species were likely a weak driver of community composition.

2) The relative strength of top-down versus bottom-up effects in this study system indicated that during a period characterized by low small mammal abundance, wolves were the strongest predictor of canid and mustelid occurrence, while lynx presence remained most strongly predicted by prey.

3) Wolf presence appeared to elicit a guild-wide response that could vary by spatial scale. All mesopredators, except marten, responded positively to localized wolf presence within both study areas, whereas comparisons at a landscape scale across study areas indicated

lower probability of occupancy for all mesopredators in the study area where wolves were more abundant. My hypothesis to explain these observations is that local scale facilitation by large carnivores could lead to landscape scale patterns of suppression by large carnivores, which could provide a key link between abundance patterns and the structure of carnivore communities at different spatial scales relevant to conservation and management.

4) Carrion, voles, and snowshoe hares collectively represented the majority (over 70%) of coyote and red fox diets across study areas, highlighting the importance of these prey resources. In particular, carrion was a heavily used resource by coyotes and red foxes. Where wolves were abundant, carrion constituted 40% of coyote diet and 10% of red fox diet; whereas where wolf abundance was reduced, carrion constituted 62% and 35% of coyote and red fox diet, respectively.

5) The index of total available biomass of hares, voles, and carrion was higher in Denali, which was largely attributed to differences in hares and voles between study areas.

6) Diet overlap was highest in the study area where wolves, and small prey, were less abundant. Although wolf abundance and small mammal abundance appeared to co-vary in each study area, diet diversity and richness was similar between study areas, suggesting that coyotes and red foxes likely also adjusted foraging in response to carrion availability, as opposed to resource limitation alone. While coyotes, the larger, competitively dominant mesopredator, maintained use of carrion as a primary resource,

red foxes appeared to switch from carrion to small prey where small prey was more abundant. I concluded that carrion subsidies from large carnivores could minimize resource competition between sympatric mesopredators in our study area, provided that there are sufficient resources for the smaller mesopredators.

4.3 Recommendations for future study and management implications

This study provided the first examination of the effect of artificially reduced wolf densities on an entire mesocarnivore community. Carnivore management has been, and will likely continue to be, a contentious issue. Alaska's complex history of predator control is riddled with controversy, further ignited with the passing of the 1994 Intensive Management Law that mandates predator control in game management units of concern (Rawson 2001). Although a substantial body of work has sought to determine the efficacy of this practice for increasing ungulate populations (Boertje et al. 1996; Keech et al. 2011), the impact of manipulating large carnivore densities on Alaska's diverse mesocarnivore community has remained unknown.

Our study was conducted during the low phase of the snowshoe hare cycle, which allowed for an examination of carnivore interactions in an environment characterized by low resource abundance. Although we did not detect a negative association between coyotes and other mesopredators, it is possible that the strength of indirect mesopredator cascades could be dependent on densities of mesopredators and their prey resources in our study area. Monitoring how interaction strengths and foraging patterns among carnivores change during the increase, peak, and decline phases of the hare cycle would provide valuable insights into the role of productivity in mediating intraguild interactions among carnivores. Mesopredator densities may fluctuate 6-7.5 fold throughout the hare cycle, therefore species interactions are expected to intensify with increased density due to increased probability of encounter (Polis et al. 1989; O'Donoghue et al. 1997). As hares become abundant, I would predict interactions among mesopredators to intensify as coyote densities also increase. As predator densities peak and hares then begin to decline, coyote-mesopredator cascades could become evident with the onset of resource competition among mesocarnivore populations at high density. The heavy reliance on carrion as an alternative to snowshoe hares would also be expected to change during the hare cycle. As hares become more abundant, I expect that reliance on carrion would decrease significantly because the risk of foraging for this resource would likely outweigh the reward, relative to foraging for abundant hares.

All of the species examined in our study are managed as furbearers, and some species (e.g., marten, lynx, wolverine) are important subsistence resources throughout the state. The positive association between wolves and mesopredators we detected within each of our study sites suggests that wolves may promote mesopredator occurrence, and influence diet overlap between sympatric mesopredators during low phases of the hare cycle, which could be a consideration for intensive management programs in cases where ensuring furbearer harvest opportunity is a priority. Although our finding of a negative effect of wolves on mesopredators across a landscape scale lacked the spatial replication and random assignment of treatments to conclude that wolf presence alone accounted for differences in overall mesopredator occupancy across our two study areas, the patterns observed nonetheless prompt the hypothesis that wolves may exert contrasting, scale-dependent influences on mesopredators. If so, widespread wolf control could further influence distribution of mesopredators across landscape or regional scales, and these responses may be guild-wide, rather than species-specific. In particular, increased resource availability as a result of carrion provisioning by wolves to mesopredators at local scales could benefit individual survival and reproduction and translate to elevated dispersal rates of mesopredators between neighboring populations. However, the degree to which direct mortality and aggression between wolves and mesopredators drives actual density patterns is unclear, considering wolf-caused mortality may disproportionately impact transient individuals unlikely to contribute to population growth (Berger & Gese 2007). Thus, evaluating whether scavenging related mortalities contribute to landscape-scale patterns of density will be an important area of future work. The mosaic of wolf density resulting from predator control programs that presently reduces wolf densities by 50-80% across 8 management units throughout Alaska provides an ideal framework for examining these dynamics with strong inference across multiple spatial scales. Such studies could help managers better understand the dynamics of carnivore communities and predict the consequences of predator management on furbearer populations.

Defining the scale over which facilitation versus suppression dominates carnivore community interactions and structure could greatly benefit management and conservation planning. Each of these processes could be representative of an "ecological domain," which refers to a distinct area characterized by a suite of dominant ecological processes (Wiens 1989). Ecological domains can be disrupted by the presence of geographical and physiological barriers (Caughley et al. 1988; Newsome & Ripple 2015), and this framework could aid in predicting how management interventions pertaining to large carnivores might impact ecological processes and communities. This concept can similarly be extended to consider how anthropogenic impacts, such as management and conservation actions, act as barriers for ecological domains. As anthropogenic impacts become ever more tangible across the landscape, habitat fragmentation, politics, and limited budgets often define the scale of conservation and management actions. With respect to these findings, indentifying ecological domains, and the dominant processes that define them, could help practitioners better predict what is truly being affected relative to conservation and management actions, and interventions could be scaled appropriately for the desired outcome.

Finally, I acknowledge that the strength of inference of this study is limited due to lack of spatial replication and the potential for additional confounding factors (Hurlbert 1984). With two, adjacent comparison study areas characterized primarily by differences in wolf management spanning more than a decade, this study design yielded greater internal validity and experimental control than an observational study, however the strength of internal validity was less than if we had been able to conduct a manipulated field experiment (Rosenbaum 2002). However, replication and rigorous study design presents considerable logistical and financial challenges for ecological study of wide-ranging carnivores, and natural or quasi-experiments present a viable alternative with proper forethought (Hargrove & Pickering 1992). To strengthen inferences in this study related to study area, where data from randomized and replicated landscape-scale experiments were not available, we considered factors most likely to influence the patterns and processes of interest, and developed and tested a priori hypotheses relevant at a smaller (e.g., local) scale in order to infer patterns at a broader scale (Hargrove & Pickering 1992). We observed strong effects along a gradient of interest (wolf abundance), for which the most likely proposed causes and mechanisms (mesopredator release, facilitation, and suppression) are well supported in the literature, thus providing qualitative measures that further support the internal validity of our findings (Rosenbaum 2002). We applied statistical methods designed to test a priori hypotheses pertaining to multivariate data, and by developing a network hypothesis based on a priori knowledge and testing expectations using SEM, we drew inferences by adopting a hypothetico-deductive approach (Bareinboim & Pearl 2015) and presented relevant interpretations with support from other studies.

4.4 Conclusion

Carnivores at all levels of the dominance hierarchy have the potential to adversely, and favorably, influence valued resources and ecosystem characteristics. Although the potential for large carnivores to "restore balance" to degraded ecosystems in commonly cited as a benefit of carnivore conservation, this research highlights that the influences of large carnivores are not easily simplified. As conservation groups increasingly look towards large carnivores as a promising restoration tool, and wildlife managers seek to mitigate impacts of carnivore restoration on prey populations, it is important to consider community-wide implications of the direct, and indirect effects, of management and conservation actions related to large carnivore communities.

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