

Apex predators and the facilitation of resource partitioning among mesopredators

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Apex predators may influence carnivore communities through the suppression of competitively dominant mesopredators, however they also provide carrion subsidies that could influence foraging and competition among sympatric mesopredators when small prey is scarce. We assessed coyote *Canis latrans* and red fox *Vulpes vulpes* winter diet overlap and composition from scats collected in two study areas with >3-fold difference in grey wolf *Canis lupus* density due to a wolf control program. We hypothesized that differences in diet composition would be driven by the use of carrion, and tested whether 1) apex predators facilitate resource overlap, or 2) apex predators facilitate resource partitioning. We estimated the available biomass of snowshoe hares and voles based on pellet density and vole capture rates in each study area. We used molecular analysis to confirm species identification of predator scats, and used microscopic evaluation of prey remains to analyze diet composition of 471 coyote and fox scats. Ungulate carrion, voles and snowshoe hares comprised 73% of coyote and fox diet, and differences in use of carrion and microtines accounted for nearly 60% of the dissimilarity in diet among these canids. Carrion was the top-ranked item in the coyote diet in both study areas, whereas carrion use by red foxes declined >3-fold in the study area with higher wolf and small prey abundance. Diet overlap tended to be lower and diet diversity tended to be higher where wolves were more abundant, though these trends were not statistically significant. Taken together, our findings indicate that carrion provisions could facilitate resource partitioning in mesocarnivore communities by alleviating exploitation competition for small mammals.

Evidence from carnivore guilds across the globe suggests that interactions among mesopredators are moderated by the presence of apex carnivores through a cascading chain of suppression (Creel and Creel 1996, Ritchie and Johnson 2009, Levi and Wilmsers 2012, Newsome and Ripple 2015). However, facilitation by apex carnivores through carrion provisioning can supplement background resource availability, and is increasingly recognized as an important driver of community interactions and food webs (Devault et al. 2003, Wilson and Wolkovich 2011, Moleón et al. 2014, Pereira et al. 2014). Carrion provisioning could influence competition among scavengers and possibly offset the net effect of suppression cascades (Wilmsers et al. 2003a, Wilson and Wolkovich 2011). Determining how changes in apex carnivore presence and resource availability influence resource partitioning among mesopredators is needed to better understand carnivore community dynamics, especially where carnivore abundance is expected to change as a result of anthropogenic activities.

Ecological theory offers contrasting predictions about how mesopredators might respond to carrion subsidies in relation to background resource availability. Optimal foraging

theory predicts that individuals should respond to resource limitation by increasing their use of high-value resources (e.g. carrion), presumably leading to greater resource overlap, and thus increased competition (MacArthur and Pianka 1966). In contrast, competition theory predicts that when resources are limited, sympatric competitors will minimize competition by partitioning resources (Schoener 1974a). While carrion availability could be expected to increase with higher apex predator abundance, higher apex predator abundance may lead to the suppression of dominant mesopredators, which could alleviate exploitation competition between mesopredators for shared resources (Levi and Wilmsers 2012, Yarnell et al. 2013).

The grey wolf *Canis lupus*, an apex carnivore, is recolonizing parts of the western United States and Europe following substantial recovery efforts (Chapron et al. 2014, Ripple et al. 2014). Meanwhile, wolf populations are being reduced in other areas to minimize impacts on domestic livestock and threatened ungulate populations (Hervieux et al. 2014, Bradley et al. 2015). These shifts in apex carnivore distribution and abundance may have strong effects on mesopredator communities (Ritchie and Johnson 2009).

Carrion provisioning by wolves could influence diet overlap and competition among mesopredators when the abundance of small prey is limited, because background resource availability and the presence of alternative, high-value prey is expected to strongly influence competition (Oaten and Murdoch 1975, Wiens 1993).

The coyote *Canis latrans* is a widespread, generalist mesopredator that has expanded its range throughout North America and may outcompete native foxes where their ranges overlap (Ritchie and Johnson 2009). Where wolves are abundant, red foxes *Vulpes vulpes* may indirectly benefit from the suppression of coyotes (Levi and Wilmsers 2012, Newsome and Ripple 2015). Red foxes may be particularly susceptible to resource competition by coyotes, because they both prey on similarly-sized food resources and supplement their winter diets with carrion (Gese et al. 1996, Needham and Odden 2014). In temperate ecosystems, resource competition between coyotes and foxes may be reduced where there is a diverse prey base (Major and Sherburne 1987, Azevedo et al. 2006). In northern ecosystems, however, both canids rely heavily on snowshoe hares *Lepus americanus* and microtine rodents that undergo cyclic fluctuations in population density (Korpimäki and Krebs 1996, O'Donoghue et al. 1998, Prugh 2005, Dell'Arte et al. 2007). When hares are abundant, diet overlap between coyotes and red foxes can be high (Theberge and Wedeles 1989). When hare and vole populations are low, the degree of diet overlap between coyotes and red foxes, and their respective dependency on carrion as a supplemental resource, remains unknown.

In this study, we examined winter diet composition and dietary overlap of coyotes and red foxes in relation to small prey availability and grey wolf abundance in Alaska. Our study occurred during a low phase of the hare cycle, following a record peak in hare density between 2008–2010 (Krebs et al. 2013). We made comparisons between two study areas, one with an active wolf control program that has reduced wolf densities by 36–80% annually for the past decade (Alaska Department of Fish and Game 2015) and one where wolves occur at natural densities (i.e. not subject to state wolf control). We first hypothesized that variation in wolf abundance between study areas would influence coyote and red fox diet composition, and that these differences would be driven by the use of carrion. We next evaluated the influence of apex predator presence on resource partitioning between mesopredators in the context of two opposing hypotheses:

- 1) *Apex predators facilitate resource overlap.* Where wolves and carrion subsidies are abundant and small mammal resources are limited, mesopredators should increasingly exploit this highly profitable food resource as predicted by optimal foraging theory. As a result, we expect lower diet diversity and higher dietary overlap and between a dominant (e.g. coyotes) and subordinate mesopredator (e.g. red foxes).
- 2) *Apex predators facilitate resource partitioning.* Where wolves and carrion subsidies are abundant and small mammal resources are limited, use of carrion by a subordinate mesopredator should decrease in order to minimize resource competition with a dominant mesopredator, as predicted by competition theory. As a result,

we expect diet diversity of the subordinate mesopredator to increase due to inclusion of other food resources, and reduced diet overlap between a dominant and subordinate mesopredator.

Methods

Study area

This study took place in two sites in interior Alaska from January–March 2013 and 2014 (Fig. 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, tall shrubs *Salix* spp. and *Alnus* spp., and mixed deciduous forest comprised of birch *Betula* spp. and aspen *Populus tremuloides*. Moose *Alces alces*, caribou *Rangifer tarandus*, and Dall's sheep *Ovis dalli* are the sole ungulates and the primary prey for wolves. Other mesopredators in the area included Canada lynx *Lynx canadensis*, wolverine *Gulo gulo*, American marten *Martes americana*, northern river otter *Lontra canadensis*, and weasels *Mustela* spp. Five species of voles *Microtus* spp. make up the microtine community. Small mammalian prey (0.5–2 kg body mass) included snowshoe hares, red squirrels *Sciurus vulgaris*, and muskrats *Ondatra zibethicus*. Medium-sized mammalian prey (≥ 3 kg body mass) included hoary marmots *Marmota caligata*, porcupines *Erethizon dorsatum* and beavers *Castor canadensis*. Avian prey includes ptarmigan *Lagopus* spp. and spruce grouse *Falcipennis canadensis*.

The Denali study site (hereafter, 'Denali') was roughly 2000 km² overlapping the northeast corner of Denali National Park and Preserve, including 500 km² of state-managed land known as the Stampede corridor. Although wolves are subject to limited harvest in this area, harvest was not found to greatly impact wolf population dynamics within Denali and the wolf population was presumed to be naturally regulated (Borg et al. 2014). Average wolf density from 2013–2014 based on aerial tracking of radio-collared wolves in the Denali study area was estimated at 7.6/1000 km² (2013: 8/1000 km²; 2014: 7.3 / 1000 km²) equivalent to approximately 15 wolves (S. Arthur pers. comm.).

The Susitna study site (hereafter, 'Susitna') was 200 km southeast of Denali and included 1800 km² of land largely managed by the state, with some private in-holdings and native allotments. As part of the larger Nelchina Basin Game Management Unit (GMU) 13, the wolf population in Susitna has been periodically subject to active wolf control as a component of Intensive Management for moose since 2000. The control plan increased bag limits and extended harvest seasons for wolves, and included same-day-airborne hunts implemented in the winter of 2004 as well as aerial gunning which began in 2006. An average of 81.4 wolves per year were removed from the predator control area between 2009–2013 (Alaska Department of Fish and Game 2017). Wolf abundance in portions of GMU 13 are monitored with minimum counts conducted during aerial surveys. Although direct quantitative comparisons between the minimum count index and the telemetry-based survey methods

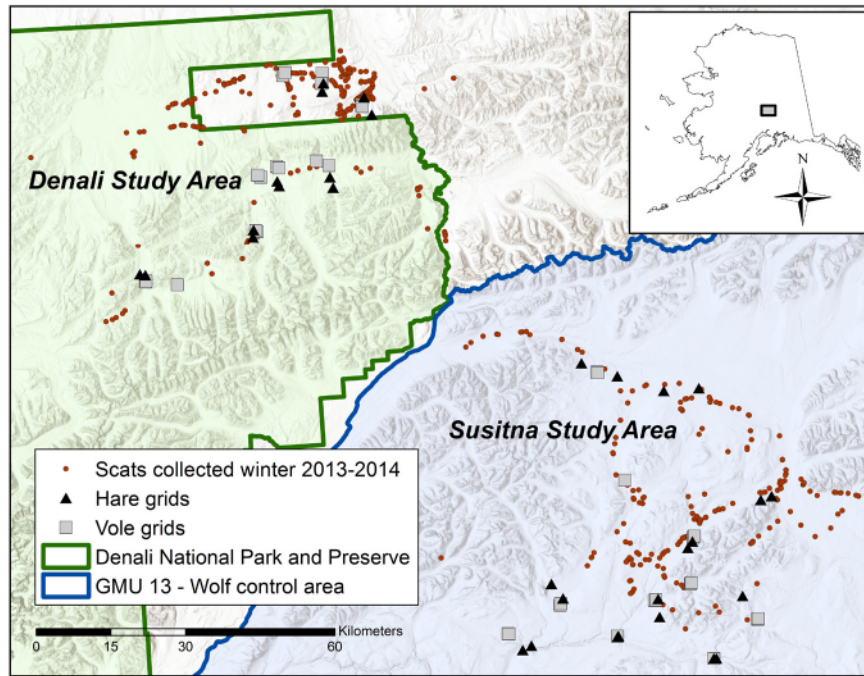


Figure 1. Locations of winter mesopredator scat collection and summer small mammal monitoring sites in Denali National Park and Preserve and Susitna River Basin, Alaska.

in Denali is problematic, the minimum counts suggest a large difference in wolf density between sites. In Susitna, minimum counts conducted in 2015 suggested a minimum density of 1.45 wolves / 1000 km² throughout GMU 13 (K. Colson unpubl.), equivalent to approximately 3 wolves total in the study area. Surveys conducted during the years of our study (2012–2014) were insufficient for a reliable minimum count, but wolf densities were likely similar or lower than they were in 2015 given the level of wolf harvest during our study (Alaska Department of Fish and Game 2015).

Differences in carrion availability between study sites were assumed to be primarily a result of differences in wolf density. Non-predation overwinter mortality for adult moose and caribou was likely low in both study areas due to mild winter conditions and generally healthy herd conditions. In Denali, overwinter survival of caribou in winters 2013 and 2014 was 95–98%; overwinter survival rates were consistently ~ 95% from the 1990s–2000s (L. Adams pers. comm.). In Susitna, preliminary data also 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 (ADF&G unpubl.). Wolf predation is the main cause of moose and caribou mortality in all but the most extreme winters, and wolf control does not affect overwinter survival of adult or yearling moose (Modafferi and Becker 1997, Bertram and Vivion 2002, Keech et al. 2011). Although big game hunting can contribute a substantial amount of carrion that sometimes exceed carrion inputs by wolves (Wilmsers et al. 2003b), the main pulse of hunter-provided carcasses occurs during the fall hunting season (August–September) and was likely consumed by scavengers prior to our winter study (January–March). There were no winter hunts in Denali. In Susitna, hunter harvest reports indicated ≤ 10 caribou harvested between January–March

2013 (ADF&G npubl.), and in 2014 there were no winter hunts.

Scat collection and identification

We collected carnivore scats daily from January–March in 2013 and 2014 while travelling along snowmobile trails, while backtracking individual coyotes and red foxes, and opportunistically at carcass sites. All carnivore scats that were encountered were collected, and we used mitochondrial DNA to confirm the field identification of each scat. Samples that failed to amplify for molecular identification were excluded from further analyses to minimize potential bias in diet analyses associated with field identified scats (Morin et al. 2016). Fecal samples were scraped with sterilized wooden craft sticks, and DNA was extracted using the Qiagen QIAamp DNA Investigator Kit. To each sample, we added 250 μ l buffer ATL, 250 μ l buffer AL, and 25 μ l proteinase k and then incubated on a shaker-incubator at 56°C for 4 h. All 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 cross-contamination between samples. Each sample was identified to species using a modification of a previously developed mitochondrial DNA fragment analysis test (De Barba et al. 2014). Primer pair DL1F and DL5R and a forward primer, Gulo1F, were combined with the primers H3R, SIDL and H16145 to amplify DNA fragments of species-specific lengths (Murphy et al. 2000, Palomares et al. 2002, Dalen et al. 2004). This method was validated using known samples obtained from the University of Alaska Museum of the North and created diagnostic fragments for brown bears *Ursus arctos*, black bears *Ursus americanus*, red foxes, coyotes, wolves, dogs, marten, and

wolverine 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.

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 H₂O, 1.26 µl TE buffer, 7.5 µl 1× 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 with no reduction in amplification success. Primer concentrations were maintained while adjusting the remaining solution volumes to 0.69 µl dH₂O, 0 µl TE buffer, 3.5 µl 1× Qiagen Master Mix, 0.7 µl 0.5× 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 min followed by 30 cycles of 95 C for 15 s, 46 C for 90 s, 72 C for 60 s with a final elongation step of 72 C for 15 min. Each sample was amplified a minimum of two times to ensure consensus identification, and was separated on an ABI 3730xl (Life Technologies, Foster City, CA). Fragment sizes were determined using GENEMAPPER 3.7 software (Life Technologies, Foster City, CA).

Diet composition

After genetic processing, individual scats were transferred to nylon bags, washed in a clothes washing machine to remove fecal material and air-dried. The contents of each individual scat were sorted and the percent of total scat volume (visually estimated) was recorded for each prey item in each scat. Prey remains were identified to the closest possible taxon 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) and a reference collection of hairs, skins and skulls on loan from University of Alaska Museum of the North. Items comprising <1% total scat volume were recorded as trace amounts and excluded from further analysis to avoid over representation of incidental items (Kamler et al. 2007). Although we were unable to identify feathers to bird species, claws and beaks indicated that avian prey were primarily ptarmigan and grouse. Occurrences of moose, caribou, and Dall sheep hairs were assumed to be a result of scavenging. In this region, coyotes and red foxes have not been documented preying on adults of these species (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. Predation of Dall sheep by coyotes is primarily limited to lambs in spring and summer, and red foxes have not been documented preying on Dall sheep (Hoefs and Cowan 1979, Arthur and Prugh 2010). For the purpose of data analysis, prey items were grouped into one of seven classes of prey categories based on size and/or type. These were: microtines (voles and shrews), birds, small mammals (0.5–1 kg: small mustelids, muskrats, and squirrels), hares (1–2 kg), medium mammals (2–3 kg: porcupines, beavers, and marmots), carrion (moose, caribou, and sheep), and 'other' (plant matter and unidentifiable remains).

Scats provide an imperfect measure of diet because of differences in digestibility among food items. We therefore based our comparisons on the percent volume of each prey

item in scats (hereafter, 'percent volume'), which provides the next best quantitative metric for addressing niche overlap in lieu of a digestibility model (Klare et al. 2011). Differences in digestibility should not influence comparisons between study areas or species. Percent volume of each dietary item *i* in coyote and red fox scats in the Denali and Susitna study areas was calculated as:

$$\% \text{ volume}_i = \frac{\sum_j^n x_{ij}}{n}$$

where *x* is the percent volume of item *i* in scat *j*, and *n* is the total number of scats in the sample. The sum of % volume across all items in the sample of each species' scats in each study area was 100% (subject to rounding error).

Diet analysis

Because larger sample sizes inherently result in a greater number of expected items, we used rarefaction to ensure that our sample sizes were sufficient for making comparisons (Krebs 1999b). For each sample size *n*, starting at 1 and ending with the maximum number of scats for a given canid species and study area, we used bootstrapping to re-sample 1000 scats (without replacement) and assess the effect of sample size on mean % volume of each prey item *i* and diversity. Rarefaction curves were inspected to determine the sample size at which the mean of each diet index reached a plateau, indicating sufficient sample size for making inferences among species and study sites. Rarefactions, bootstrapping, and calculations of diet indices were implemented in program R (< www.r-project.org >).

To test our first hypothesis and assess the drivers and differences in diet composition between canid species and study areas, we used multivariate analyses applicable to non-normally distributed community data available in the 'vegan' package in program R (Oksanen et al. 2016, McCune et al. 2002). We conducted a permutational analysis of variance (PERMANOVA) to test for the effects of study area and canid species on diet composition. Non-metric dimensional scaling (NMDS) was used to graphically represent differences in diet composition in two dimensions of ordination space. We implemented random starts with a maximum of 200 iterations per run and considered the fit of the NMDS adequate at stress levels < 0.2 (Clarke 1993). We overlaid dispersion ellipses representing one standard deviation from average of group points to aid visualization of diet groupings (Hill et al. 2015). We used a similarity percentage analysis (SIMPER) to determine percent contribution of each prey type to the dissimilarity in diet composition among groups (Clarke 1993). All community analyses were based on a Bray–Curtis dissimilarity matrix calculated from the percent volume of each of seven prey categories. Bray–Curtis matrices are recommended for ecological data prone to zero abundance (McCune et al. 2002).

To address our second hypothesis regarding the influence of carrion subsidies on resource partitioning, we compared mean % volume of prey categories in scats, diet diversity, and diet overlap between coyotes and foxes and among study areas. We used bootstrap resampling (*n* = 10 000) to compare

mean % volume of each of the seven prey categories present in each diet grouping, based on non-overlapping 95% confidence intervals derived at the 0.025 and 0.975 quantiles from the bootstrap re-sampling distribution (Efron 1982, Manly 2006, Cumming 2009). We used the Shannon–Wiener diversity index (Colwell and Futuyma 1971, Krebs 1999a) to keep our results comparable with other coyote and fox diet studies (Dumond and Villard 2001, Kamler et al. 2007, Kozłowski et al. 2008, Prugh et al. 2008). Diet overlap was calculated using Pianka's index, which ranges from 0, indicating no diet overlap, to 1, indicating complete diet overlap (Pianka 1974). Comparisons of mean diet overlap and diversity were also based on non-overlapping 95% confidence intervals derived from bootstrap re-sampling ($n = 1000$).

Snowshoe hare and vole availability

To characterize resource availability in each study area, we used estimates of snowshoe hare and vole abundance to index their available biomass. Snowshoe hare pellet accumulation was tallied annually for three summers (2012–2014) on six spruce and six tall shrub grids in Denali ($n = 12$) and seven spruce and seven tall shrub grids ($n = 14$) in Susitna (Fig. 1). Pellet counts are highly correlated with snowshoe hare density throughout their population cycle, and dense spruce and tall shrub habitats serve as refugia for hares when populations are low (Wolff 1980, Krebs et al. 2001a, Murray et al. 2002). Each pellet grid consisted of fifty circular plots with 0.5-m radii (0.79 m²) spaced 15 m apart along linear transects. All pellets were aged, counted and removed from each plot each year following protocols described in Prugh and Krebs (2004). Hare biomass was indexed using a conversion factor (hares/ha = pellets/m² × 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).

We conducted a series of one-night live-trapping sessions for voles on trapping grids in meadow and spruce forest habitats at seventeen sites in Denali (spruce $n = 8$, meadow $n = 9$) and fifteen sites in Susitna (spruce $n = 7$, meadow $n = 8$; Fig. 1). One hundred Sherman live traps (3" × 3.5" × 9", Sherman) were spaced 10 m apart on each 90 × 90 m grid. Traps were baited with sunflower seed between 19:00–20:00 hours and checked the following morning by 09:00 hours. Upon capture, each animal was identified to genus, sexed, weighed and released. Vole biomass was estimated based on the average mass of individual voles captured (19.3 g ± 0.53 SE, $n = 302$ voles) and the relationship between the first night's capture success (N_1) and number of voles per hectare (D) estimated from five-night mark–recapture sessions from 1992–2002 in Denali National Park (L. Prugh unpubl. $D = 0.5157 \times N_1 - 0.0684$; $R^2 = 0.852$, $n = 30$ grid-years). All animal handling procedures were permitted by UAF IACUC permit no. 323540-1 and were consistent with animal welfare guidelines. Normality of pellet 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).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.b273t>> (Sivy et al. 2017b).

Results

Scat collection and identification

Of the 925 scats collected in winter 2013 and 2014, molecular species identification was successful for 791 scats (86%). Of these, 471 were identified as coyote ($n = 147$) or red fox ($n = 324$) and were retained for diet analysis. Rarefactions indicated these sample sizes of scats were sufficient for comparisons among species and study areas. Variance in mean % volume prey items stabilized for all diet groups with sample sizes > 40 scats (Supplementary material Appendix 1 Fig. A1). Diversity for each diet group stabilized with sample sizes of 30–40 scats (Fig. 2).

Diet composition

The most abundant prey items in coyote and red fox scats, pooled across both species and study sites, were ungulate carrion (34%), voles (25%), and snowshoe hares (12%), collectively representing 71% volume. Vegetation (not including berries) was the next most abundant item and represented 6% volume, yet it was unknown whether this was a result of intentional or incidental consumption. Of the remaining prey items, none represented more than 5% volume of all scat contents, which emphasizes the importance of carrion, voles and hares as principal resources for coyotes and red foxes in our study system.

In Denali, carrion (i.e. caribou, sheep, and moose) represented 40.6% and 9.8% of coyote and red fox diets, respectively (Table 1). Use of carrion in Susitna (wolf control area) was high for both coyotes and red foxes, comprising 59.5% and 34.5% of their diets, respectively. Hares represented 22.8% of coyote diet and 21.9% of red fox diet in Denali, yet were virtually absent ($\leq 3\%$) from diets of both canids in Susitna. In Denali, voles represented 12.8% of coyote and 50.7% of red fox diet. In Susitna, voles represented only 5.4% of coyote diet, but comprised 32.4% of red fox diet. Alternative prey species for each predator varied by study area, but in general coyotes consumed porcupine and muskrats, whereas red foxes consumed muskrats and avian prey (Table 1).

Diet analysis

Diet composition varied among study areas and canid species, and these factors accounted for 13% of the overall variability in scat contents (Table 2). NMDS ordination axes in Denali showed divergences between coyotes and red foxes in use of carrion and microtine prey (Fig. 3). Coyote and red fox diets overlapped in ordination space, yet coyote diets were more clustered around carrion, whereas foxes were more clustered around microtines. In Susitna, coyote diets again were centered on carrion, whereas fox diets were more diffuse from microtines to carrion along the two ordination axes (Fig. 3).

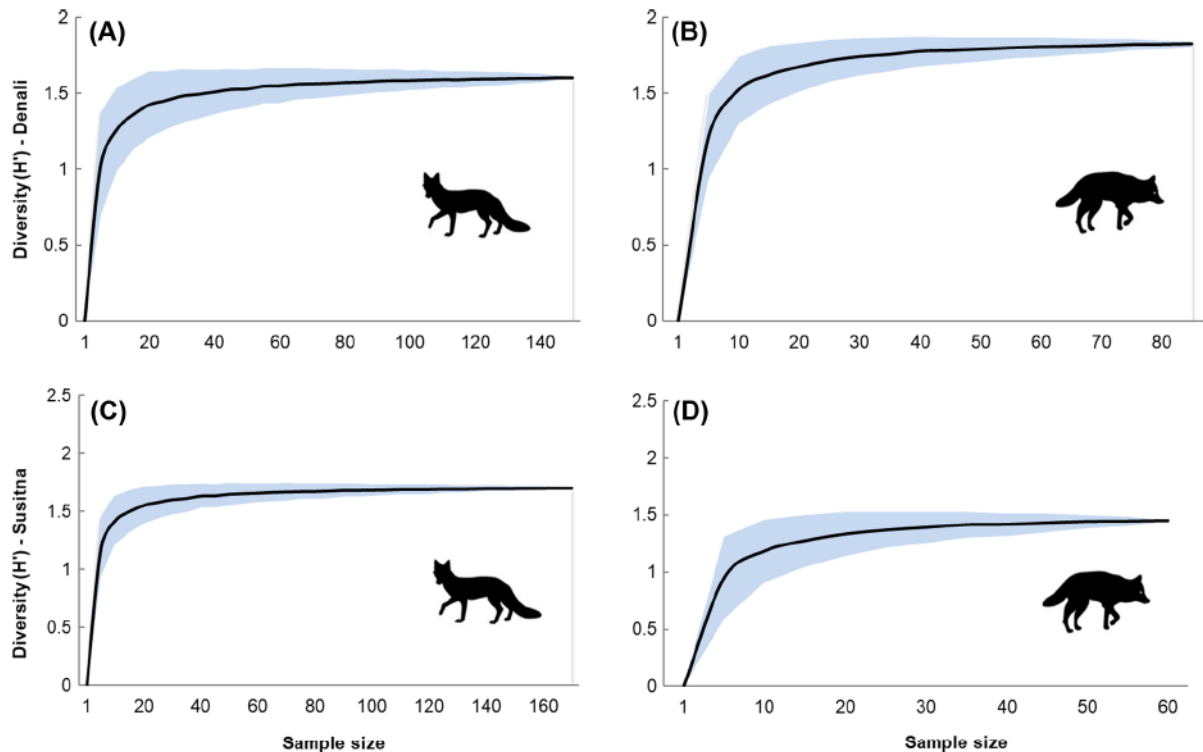


Figure 2. Rarefaction curves illustrating influence of sample size on red fox and coyote diet diversity in Denali (A, B) and Susitna (C, D). Rarefaction curves estimated from 1000 bootstrap runs for each sample size n to the maximum sample size for that group.

Microtine rodents, followed closely by carrion, were the largest contributors to dissimilarity between coyote and fox diets in Denali, collectively accounting for 56% of this dissimilarity (Table 3, Contribution). Coyote diets were dominated by carrion, whereas fox diets were dominated by microtines (Table 3, Average abundance). Hares were the third greatest contributor (0.17) to diet dissimilarity in Denali. As in Denali, nearly 60% of the dissimilarity

between coyote and fox diets in Susitna was accounted for by carrion and microtines, and coyote diets were dominated by carrion. In Susitna, however, carrion contributed the most towards diet dissimilarity in Susitna (0.25), followed by microtines (0.17). Fox diet in Susitna was nearly equally dominated by microtines and carrion. Hares comprised a negligible (< 0.02) contribution to the dissimilarity of diets in Susitna.

Table 1. Percent volume of prey items in coyote and red fox scats collected winter 2013-2014 in Alaska.

Prey category	Prey item	Denali		Susitna	
		Coyote $n=88$	Red fox $n=154$	Coyote $n=59$	Red fox $n=170$
Microtines	shrew	0	0.4	0.9	0.6
	voles	12.8	50.7	5.4	32.4
Birds	bird	2.4	2.1	0.1	9.5
Small mammals (< 1 kg)	muskrat	–	2.2	4.9	8.4
	squirrel	1.9	1.1	–	1.6
	weasel	–	1.2	–	0.2
Hares (1–2 kg)	snowshoe hare	22.8	21.9	3.1	0.4
Medium mammals (> 3 kg)	beaver	–	–	–	0.4
	marmot	–	–	–	0.2
	porcupine	4.1	1.7	11.9	0.8
Ungulate carrion	caribou	8.5	4.1	30	19.3
	dall sheep	4.5	1.1	1.7	–
	moose	25.9	4.4	18.8	9.8
	unknown ungulate ^a	1.7	0.2	9	5.4
Other	berries	1.6	2.5	–	0.9
	vegetation	9.5	3.8	4.8	7.3
	unknown	4.3	2.1	7.9	2.8

^a – Hairs were identified as moose or caribou, but too degraded for further identification.

Table 2. Results of PERMANOVA testing for the effect of canid species and study area on coyote and red fox winter diet composition in interior Alaska, 2013–2014.

Source	df	SS	MS	F-model	R ²	p _r (>F)
Species	1	10.197	10.196	35.752	0.07	0.001
Study area	1	9.085	9.0847	31.854	0.06	0.001
Species × Study area	1	0.536	0.536	1.88	0.003	0.112
Residuals	465	132.619	0.2852		0.87	
Total	468	152.437			1	

Several key differences in prey categories used by coyotes and red foxes were apparent between study areas (Fig. 4). For coyotes, % volume of hares was the only significant difference detected between Denali ($23\% \pm 4\%$ SD) and Susitna ($3\% \pm 2\%$ SD). Carrion was more prevalent in coyote diets in Susitna ($59\% \pm 5\%$ SD) than in Denali ($41\% \pm 5\%$ SD), however the difference was only significant when comparing 90% CI. Carrion was more than three times as prevalent in red fox diet in Susitna ($34\% \pm 3\%$ SD) than in Denali ($10\% \pm 2\%$ SD). Fox diet included fewer hares ($0.3\% \pm 0.2\%$ SD) and microtines ($33\% \pm 3\%$ SD) in Susitna than in Denali (hares: $22\% \pm 3\%$ SD, microtines: $51\% \pm 3\%$ SD). Birds, although a small proportion of overall fox diet, were more prevalent in Susitna ($9\% \pm 2\%$ SD) than in Denali ($2\% \pm 1\%$ SD).

Patterns of diet overlap and diversity were consistent with the hypothesis that carrion subsidies should reduce competition, although not statistically significant. Diet diversity was 6–8% higher for both species in Denali than in Susitna (Table 4). Diet overlap among coyotes and red foxes was 23% lower in Denali (0.58 ± 0.07 SD; Table 4) than in Susitna (0.75 ± 0.05 SD).

Snowshoe hare and vole availability

Hare pellet density, pooled across years and habitat types, was nearly 4 times higher in Denali (19.58 ± 2.34 SE) than in Susitna (5.51 ± 1.53 SE; Welch's two sample t-test, $t=5.03$, $df=29.31$, $p < 0.001$; Fig. 5A). Vole capture rates, pooled across years and habitat types, did not significantly

differ between study areas (Welch two sample t-test, $t=0.71$, $df=29.89$, $p=0.48$; Fig. 5B). Mean vole density was 2.20 ± 0.55 SE voles ha^{-1} in Denali and 1.67 ± 0.49 SE voles ha^{-1} in Susitna. Hare density was indexed as 0.59 hares ha^{-1} in Denali and 0.17 hares ha^{-1} in Susitna, which corresponded to 68.3 $kg\ km^{-2}$ of hare biomass in Denali and 19.2 $kg\ km^{-2}$ in Susitna. Vole biomass was indexed as 4.2 $kg\ km^{-2}$ in Denali and 3.2 $kg\ km^{-2}$ in Susitna.

Discussion

Exploitation of ungulate carrion by coyotes and red foxes is widely documented (Arjo et al. 2002, Selva et al. 2003, Wilmers et al. 2003a, b, Switalski 2003, Helldin and Danielsson 2007, Needham and Odden 2014, Mateo-Tomás et al. 2015), however there is a paucity of work evaluating how apex carnivore presence and availability of small mammalian prey influence diet composition, diversity and overlap among these sympatric mesopredators. In this study, coyote and red fox diet composition differed among adjacent study areas characterized by a three-fold difference in wolf density. Carrion was a highly-ranked resource for coyotes and red foxes, and the differences we observed were primarily attributed to the differential use of carrion and microtine rodents. Although not significant, the trends in diet overlap and diversity where wolves (and presumably carrion) were more abundant were consistent with our second hypothesis, that apex predators might facilitate resource partitioning between sympatric mesopredators via carrion provisioning.

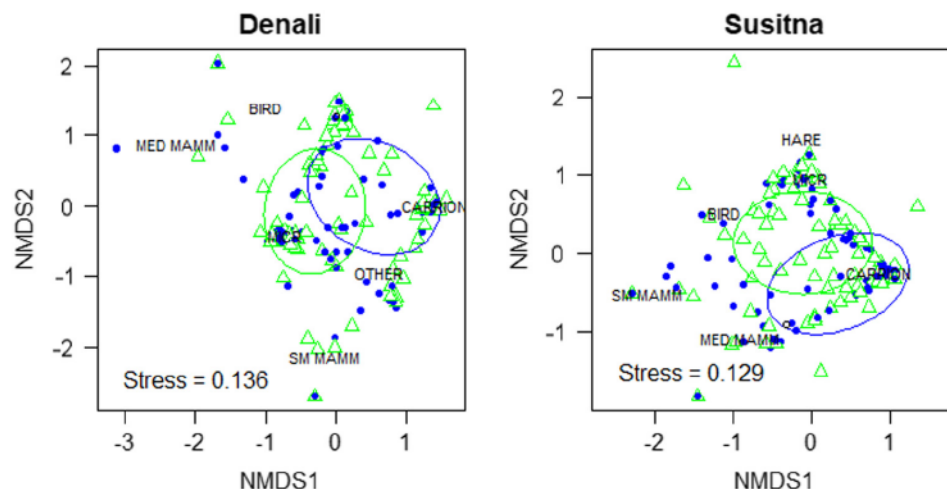


Figure 3. NMDS ordination of coyote (●) and red fox (△) winter diet composition in Denali and Susitna. Dispersion ellipses represent 1 SD of group average.

Table 3. Results of SIMPER analysis indicating the contribution of each prey item to dissimilarity in coyote and red fox diet in Denali and Susitna. Contribution=average contribution of each prey category to overall dissimilarity, SD=standard deviation of contribution, Ratio=ratio of contribution to standard deviation, Average abundance=average abundance of each prey category per diet group, Cumulative=cumulative contribution to overall dissimilarity.

	Prey category	Contribution	SD	Ratio	Average abundance		Cumulative
					Coyote diet	Fox diet	
Denali	microtines	0.244	0.193	1.265	0.128	0.515	0.304
	ungulate carrion	0.208	0.207	1	0.406	0.1	0.562
	hares	0.17	0.2	0.851	0.228	0.22	0.774
	other	0.1	0.156	0.645	0.154	0.083	0.899
	small mammals	0.031	0.109	0.289	0.019	0.046	0.938
	medium mammals	0.028	0.106	0.267	0.041	0.017	0.973
	birds	0.022	0.092	0.235	0.024	0.021	1
Susitna	ungulate carrion	0.248	0.181	1.373	0.604	0.346	0.347
	microtines	0.167	0.173	0.967	0.064	0.33	0.58
	other	0.099	0.144	0.688	0.129	0.11	0.718
	small mammals	0.071	0.165	0.433	0.05	0.103	0.818
	medium mammals	0.065	0.143	0.457	0.121	0.014	0.909
	birds	0.048	0.12	0.397	0.001	0.095	0.976
	hares	0.017	0.078	0.223	0.032	0.004	1

Carrion represented the largest proportion of coyote diet in both study areas, suggesting that coyotes were specializing on carrion. In a similar carnivore guild in South Africa, brown hyenas *Parahyaena brunnea* (a dominant mesopredator) specialized on carrion where large carnivores were present, which minimized diet overlap with black-backed jackals *Canis mesomelas* (Yarnell et al. 2013, Ramnanan et al. 2016). Apex carnivores could alleviate competition between mesopredators for small prey by facilitating carrion specialization by a dominant mesopredator (Yarnell et al. 2013). When background resource availability is low (e.g. hares and voles), specialization on profitable carrion subsidies could alleviate competition for a shared and limited resource base.

If coyotes were specializing on carrion, this would imply that carrion was being selected for in greater proportion to availability. Uncertainty regarding carrion availability, however, was a major limitation in our study. We assumed that carrion abundance would be positively related to wolf abundance, yet the increase in carrion use by both mesopredators where wolves were subject to removal by predator control causes us to question this assumption. Rapid reductions in wolf density can result in smaller pack sizes that could lead to higher per capita ungulate kill rates (Ballard et al. 1987, Hayes et al. 2000, Lake et al. 2013, Borg et al. 2014) and earlier abandonment of kills leaving more edible biomass (Giraldeau and Caraco 2000). A study conducted in a nearby area estimated per capita wolf kill rate as 0.026 kills wolf⁻¹ day⁻¹ (McNay and Ver Hoef 2003), which is within the range of published kill rates in similar northern wolf-caribou systems (Ballard et al. 1987, Hayes et al. 2000, Lake et al. 2013). In the Denali area, where an estimated 15 wolves were present, this could translate to approximately 35 kills over the duration of 90 days in winter, whereas in Susitna this would have translated to approximately 7 kills. Based on the average proportion of carcasses abandoned by wolves in the Alaska Range (15%; Prugh 2005), ungulate body masses, and composition of wolf kills (McNay and Ver Hoef 2003), wolves could have provided approximately 3223 kg of carrion in Denali and 553 kg of carrion in Susitna during winters 2013 and 2014. These estimates are

rough due to multiple sources of uncertainty, but indicate the likely magnitude of difference in wolf-provided carrion biomass between Denali and Susitna.

Higher rates of non-predation ungulate mortality (e.g. starvation, senescence or 'winter kill') could also explain higher use of carrion in Susitna, but winter conditions were mild and wolf control has not been shown to influence overwinter survival of ungulates in the region (Modafferi and Becker 1997, Bertram and Vivion 2002). The winter caribou hunt in Susitna during 2013, in which ≤ 10 caribou were harvested, added approximately 352 kg of carrion based on the proportion of carcasses left by hunters (40%; viscera, head, hide and lower legs) and adult male caribou body mass (225 kg; Alaska Department of Fish and Game 2014). While this hunt may have provided a substantial increase in carrion supply in Susitna in 2013, the biomass of hunter and wolf-provided carrion in Susitna was still likely several times lower than the biomass of wolf-provided carrion in Denali. In addition, the proportion of scats containing carrion in Susitna was similar in 2013 and 2014 for both coyotes and foxes, suggesting the hunter kills did not substantially affect patterns of carrion consumption (Supplemental material Appendix 1 Table A1). We strongly suggest that future work strive to quantify available carrion biomass with respect to apex carnivore density and group size to advance our understanding of carrion selection patterns by mesopredators.

Ungulate carrion and microtine rodents accounted for nearly 60% of the differences in diet composition between coyotes and red foxes. While carrion remained the primary resource for the larger-bodied, competitively dominant coyote, carrion use by red foxes decreased nearly three-fold in the wolf abundant study area (Denali). Diet overlap among coyotes and red foxes was 23% lower in Denali than in the wolf control area (Susitna). Although the difference in diet overlap was not statistically significant, high exploitation of carrion by coyotes could have increased the cost of exploiting carrion by foxes. If carrion subsidies had increased resource overlap between mesopredators, as predicted by optimal foraging, carrion should have remained a highly-used food resource for foxes in Denali. Coyotes are aggressive to red

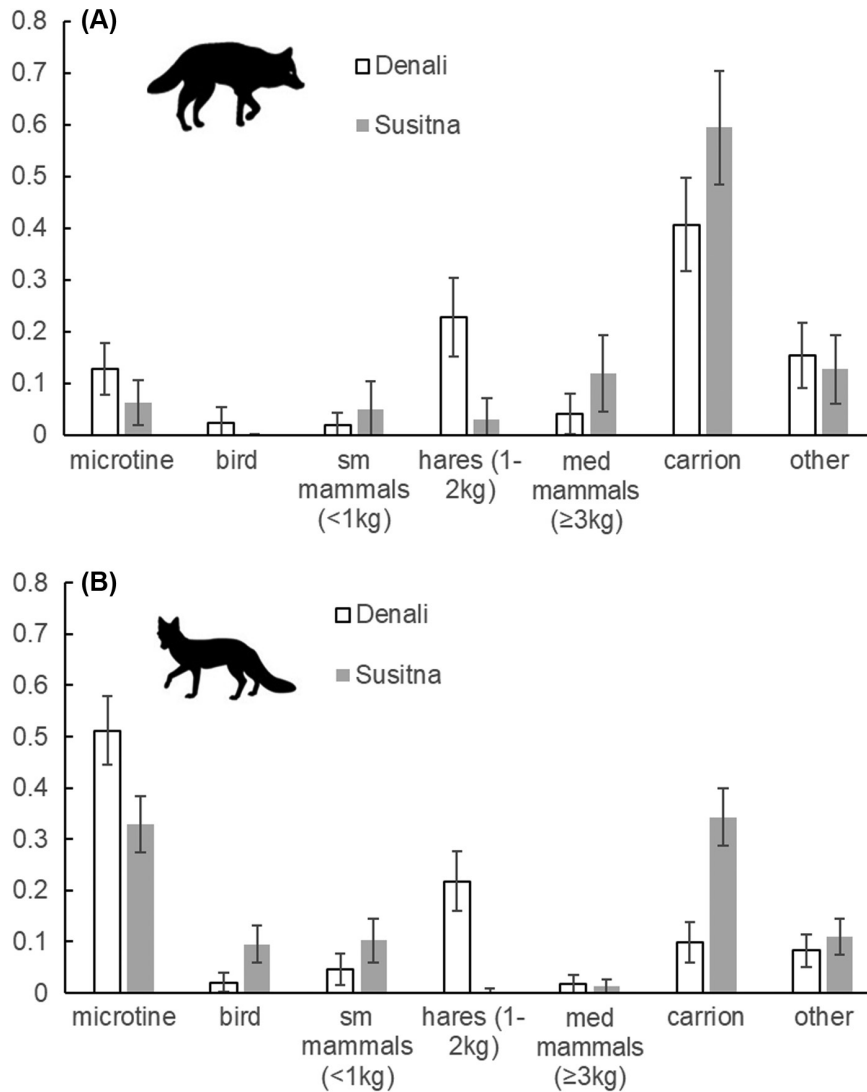


Figure 4. Percent volume of seven prey categories in coyote (A) and red fox (B) scats in Alaska. Prey categories were the combined % volume of: microtines (vole and shrew), bird, small mammals (muskrat, squirrel and weasel), medium mammals (beaver, marmot and porcupine), carrion (moose, caribou and sheep), and other (all other items). Confidence intervals (95%) estimated from 10 000 bootstrap re-samplings.

foxes and known to exclude or displace them from carcass sites (Major and Sherburne 1987, Gese et al. 1996, Palomares and Caro 1999). Foxes might also risk encountering coyotes when foraging for small prey in shared habitat patches, however carcasses are far-reaching attractants with high potential for interference competition between sympatric scavengers in a very concentrated area (Andelt and Hein 1996, Switalski 2003, Kamler et al. 2004, Merkle et al. 2009). Risk at carcass sites could be mitigated by temporal partitioning to reduce chance of encounter (Schoener 1974b), but foraging

for small prey may present a better alternative in terms of foraging costs and benefits for smaller-bodied mesopredators like foxes.

Interference competition with wolves could have affected the intensity of scavenging, as wolves are known to chase and kill scavengers (Merkle et al. 2009). If wolves suppress coyotes, coyotes might be expected to use less carrion where wolves are more abundant to avoid antagonistic encounters, just as red foxes would be expected to use less carrion where coyotes are abundant. Where coyotes are suppressed by wolves, red foxes might be expected to consume more carrion. However, we found that red foxes decreased carrion consumption where wolves were more abundant. Patterns of coyote and fox densities in Denali and Susitna, estimated from fecal genotyping in a concurrent study, were opposite of what would be expected from a mesopredator cascade in response to wolves (Pozzanghera 2015). Coyote densities were higher in Denali (1.78/100 km²) than Susitna (0.41/100 km²), whereas red fox densities in Denali were

Table 4. Coyote and red fox winter diet diversity estimated from 1000 bootstrap samples.

Species	Study area	n	Shannon–Wiener diversity (95% CI)
Coyote	Denali	88	1.92 (1.81–2.03)
	Susitna	59	1.78 (1.60–1.95)
Red fox	Denali	154	2.01 (1.93–2.10)
	Susitna	170	1.9 (1.84–1.97)

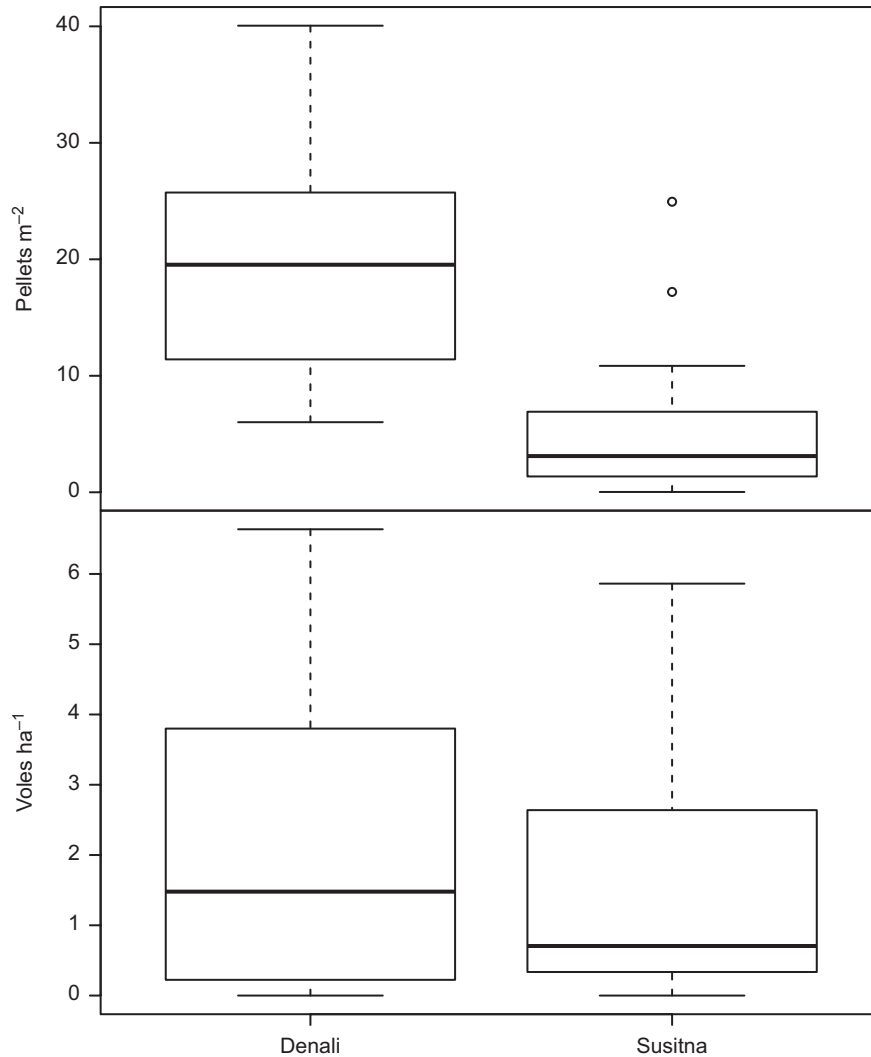


Figure 5. Mean snowshoe hare pellet density (top panel) and vole capture rates (bottom panel) in Denali and Susitna. Pellet densities (pellets m^{-2}) estimated from annual pellet count surveys 2012–2014 in spruce and tall shrub habitat at 6 paired sites in Denali ($n = 12$) and 7 paired sites in Susitna ($n = 14$). Mean vole captures in Denali and Susitna. Vole captures (voles ha^{-1}) at trapping grids in Denali ($n = 17$) and Susitna ($n = 15$), 2013–2014 based on the correlation of first night's capture success with five-night mark–recapture estimates at Rock Creek trapping grids, Denali National Park.

lower than Susitna (1.48 / 100 km^2 and 2.35 / 100 km^2 respectively). Thus, mesopredator density appears to have been influenced more by resource availability than by top-down suppression during our study. There was also little evidence in Denali and Susitna of localized avoidance of wolves by coyotes, and instead spatial patterns suggested that coyotes and red foxes were positively associating with wolves, presumably to exploit carrion (Sivy et al. 2017a). These patterns, and the generally low range of wolf densities in our two study areas, suggest that interference competition from large carnivores may not be strong enough to influence rates of scavenging by mesopredators in some systems. Higher wolf densities may be necessary for top-down suppression and interference competition to influence scavenging rates.

A necessary condition for carrion subsidies to minimize resource competition between mesopredators could be the availability of sufficient alternative resources for the subordinate competitor. Red foxes consumed less carrion and

more hares and voles in Denali, where hare pellet density and overall small mammal biomass was more abundant. The pattern of prey use with respect to available biomass suggests that relatively abundant small mammals in Denali may have facilitated avoidance of carrion (and possibly, coyotes) by red foxes. Red foxes used small mammal prey more than carrion, whereas coyotes maintained their use of carrion while also increasing use of hares in Denali. As the smaller of the two canids, small mammals may have been the optimal resource relative to carrion, given the risk of encounter with coyotes. For red foxes to consume more carrion, either the small mammal abundance would likely need to drop below some threshold, or carrion abundance may need to rise above some threshold to offset the risk. For the larger bodied coyote, small mammals may need to persist at higher densities to be an optimal resource relative to carrion. If apex carnivores increase carrion subsidies in an area with scarce small mammal prey, subordinate mesopredators may respond to resource variability by increasing their use of carrion despite

the risk of interference competition (e.g. risk-sensitive foraging, McNamara and Houston 1992).

Background resource availability may interact with carrion availability to influence resource partitioning among mesopredators, which should be considered in ecosystems exhibiting pulsed or cyclic resource dynamics (Yang et al. 2010). We acknowledge the uncertainty in our hare and vole biomass indices that we were not able to account for, however this index provides a useful aid for interpretation of relative differences in abundance when density estimates are impractical (Engeman 2005). This index allowed us to account for the influence of background prey availability on resource partitioning to some degree, however we could not examine interactive effects of small prey and apex predator densities because these factors covaried (i.e. Denali had higher wolf and small mammal abundance) and we did not have replicated or controlled treatments. Although previous work has reported the release of small mammal populations in response to mesopredator suppression by an apex predator (Ritchie and Johnson 2009), cyclic fluctuations in hare abundance result from a variety of factors including an interaction between forage availability and predation (Krebs et al. 1995). Population regulation by predation may be strongest during the peak and decline phases of the hare cycle (Krebs et al. 2001b), and densities of apex and mesopredators were likely too low during our study to affect hare abundance (Pozzanghera 2015, Sivy et al. 2017a). Rather, differences in hare abundance between Denali and Susitna were more likely due to sparse and poor hare quality habitat in Susitna (Gibson et al. 1984).

Previous studies of northern coyote and fox diets showed high use of hares throughout the peak and decline phase of the hare cycle (Theberge and Wedeles 1989, Prugh 2005), whereas other studies have documented carrion as a supplemental resource during small mammal declines (Jedrzejewski and Jedrzejewska 1992). In our study region, hare abundance remained low since the most recent crash in 2011 (Krebs et al. 2013). Hare density during this study was indexed between 0.17–0.59 hares per hectare, whereas densities as high as 4–6 hares per hectare have been reported in other areas of interior Alaska during the peak of the hare cycle (Kielland et al. 2010, Krebs et al. 2013). When hare densities decline, hares retreat into pockets of habitat refugia in increasingly dense spruce and shrub thickets, escalating the energetic and time costs of search and pursuit for a single hare (Wolff 1980, O'Donoghue et al. 1998). During hare lows, carrion could become a relatively more profitable food source, given the potential for substantial amounts of edible biomass at a single carcass site. As hares become more abundant through the increase phase of their population cycle, carrion may no longer be a preferred resource for large or small mesopredators, considering the inherent risks of scavenging from an apex predator (Merkle et al. 2009).

The range of diet overlap found in this study (0.58–0.75) is at the low end of the range reported by coyote and red fox studies in other North American ecosystems (0.71–0.91), yet these studies either did not take place in areas with resident large carnivore populations (Kitchen et al. 1999, Fedriani et al. 2000, Neale and Sacks 2001, Kamler et al. 2007, Randa et al. 2009, Warsen et al. 2014), or scant mention

of scavenging suggests carrion was not a readily available resource in those ecosystems (Theberge and Wedeles 1989). The effect of wolf abundance on diet overlap between coyotes and foxes in Susitna and Denali, albeit weak, indicates that large carnivore and small prey abundance may jointly influence mesopredator competition through resource partitioning. The difference in wolf abundance among our study areas may not have been large enough to significantly influence our selected measures of resource competition. As carnivore reintroduction and recovery efforts take place, determining thresholds of large carnivore densities that elicit responses in mesopredator communities will be an important area for theoretical and applied research (Newsome et al. 2017; Schmitz et al. 2017).

Conclusion

Carrion is more than an easy meal; leftovers from apex carnivores are increasingly acknowledged as having substantial influences on interspecific interactions and community structure (Selva and Fortuna 2007, Barton et al. 2013, Allen et al. 2014, Moleón et al. 2014). Our findings indicate that carrion was a highly-used food resource for mesopredators. Differences in diet composition between study areas were largely driven by the use of carrion versus microtines, suggesting that carrion provisioning and small mammal abundance could interact to drive resource partitioning. Carrion subsidies may be an optimal resource for larger-bodied, dominant mesopredators, while the reliance on carrion by subordinate mesopredators may depend on the relative availability of carrion versus small mammal biomass. The patterns of diet composition we documented suggest that carrion from top carnivores could facilitate resource partitioning between sympatric mesopredators if there are sufficient alternative resources for subordinate mesopredators. Carrion subsidies from apex carnivores could further influence food webs by alleviating predation by a dominant mesopredator (e.g. coyotes) on a shared food resource (e.g. small mammals; Levi and Wilmsers 2012). Where apex carnivores are recolonizing, the influence of carrion subsidies on resource competition among mesopredators should be considered alongside the more widely studied effects of intraguild predation.

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References

- Alaska Department of Fish and Game 2014. 2013–2014 Alaska hunting regulations. No 58. – Anchorage Printing.
- Alaska Department of Fish and Game 2015. Annual report to the Alaska board of game on intensive management for moose with wolf predation control in unit 13. – Div. of Wildlife Conservation.
- Alaska Department of Fish and Game 2017. Annual report to the Alaska board of game on intensive management for moose with wolf predation control in unit 13. – Div. of Wildlife Conservation.
- Adams, L. G. et al. 1995. Caribou calf mortality in Denali National Park, Alaska. – *J. Wildl. Manage.* 59: 584–594.
- Allen, M. L. et al. 2014. Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. – *PLoS One* 9: e102257.
- Andelt, W. F. and Hein, E. W. 1996. Coyote visitations to experimentally-placed deer carrion. – *Southwest. Nat.* 41: 48–53.
- Arjo, W. M. et al. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. – *J. Mammal.* 83: 754–766.
- Arthur, S. M. and Prugh, L. R. 2010. Predator-mediated indirect effects of snowshoe hares on Dall's sheep. – *J. Wildl. Manage.* 74: 1709–1721.
- Azevedo, F. C. C. et al. 2006. Dietary breadth and overlap among five sympatric prairie carnivores. – *J. Zool.* 269: 127–135.
- Ballard, W. B. et al. 1981. Causes of neonatal moose calf mortality in south-central Alaska. – *J. Wildl. Manage.* 45: 335–342.
- Ballard, W. B. et al. 1987. Ecology of an exploited wolf population in south-central Alaska. – *Wildl. Monogr.* 98: 3–54.
- Barton, P. S. et al. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. – *Oecologia* 171: 761–772.
- Bertram, M. R. and Vivion, M. T. 2002. Moose mortality in eastern interior Alaska. – *J. Wildl. Manage.* 66: 747–756.
- Borg, B. L. et al. 2014. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. – *J. Anim. Ecol.* 84: 177–187.
- Bradley, E. H. et al. 2015. Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho and Wyoming. – *J. Wildl. Manage.* 79: 1337–1346.
- Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. – *Science* 346: 1517–1520.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. – *Aust. J. Ecol.* 18: 117–143.
- Colwell, R. and Futuyma, D. 1971. On the measurement of niche breadth and overlap. – *Ecology* 52: 567–576.
- Creel, S. and Creel, N. M. 1996. Limitation of African wild dogs by competition with larger carnivores. – *Conserv. Biol.* 10: 526–538.
- Cumming, G. 2009. Inference by eye: reading the overlap of independent confidence intervals. – *Stat. Med.* 28: 205–220.
- Dalen, L. et al. 2004. Identifying species from pieces of faeces. – *Conserv. Genet.* 5: 109–111.
- De Barba, M. et al. 2014. Molecular species identification for multiple carnivores. – *Conserv. Genet. Resour.* 6: 821–824.
- Dell'Arte, G. L. et al. 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. – *Acta Oecol.* 31: 276–281.
- Devault, T. L. et al. 2003. Scavenging by vertebrates: behavioral, ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. – *Oikos* 102: 225–234.
- Dumond, M. and Villard, M. 2001. Does coyote diet vary seasonally between a protected and an unprotected forest landscape? – *Ecoscience* 8: 301–310.
- Efron, B. 1982. The jackknife, the bootstrap and other resampling plans. – *Soc. Industrial Appl. Math. CBMS-NSF Monogr.* Vol. 38.
- Engeman, R. M. 2005. Indexing principles and a widely applicable paradigm for indexing animal populations. – *Wildl. Res.* 32: 203–210.
- Fedriani, J. M. et al. 2000. Competition and intraguild predation among three sympatric carnivores. – *Oecologia* 125: 258–270.
- Gasaway, W. et al. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. – *Wildl. Monogr.* 120: 3–59.
- Gese, E. M. et al. 1996. Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. – *J. Mammal.* 77: 377–382.
- Gibson, P. S. et al. 1984. Furbearer Studies Phase 1 Report Update. Document 2329. – Alaska Cooperative Wildlife Research Unit.
- Giraldeau, L.-A. and Caraco, T. 2000. Social foraging theory. – Princeton Univ. Press.
- Hayes, R. D. et al. 2000. Kill rate by wolves on moose in the Yukon. – *Can. J. Zool.* 78: 49–59.
- Helldin, J. and Danielsson, A. V. 2007. Changes in red fox *Vulpes vulpes* diet due to colonization by lynx *Lynx lynx*. – *Wildl. Biol.* 13: 475–480.
- Hervieux, D. et al. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus*) in Alberta. – *Can. J. Zool.* 93: 245–247.
- Hill, A. D. et al. 2015. Diet variability of forage fishes in the Northern California Current System. – *J. Mar. Syst.* 146: 121–130.
- Hoefs, M. and Cowan, I. 1979. Ecological investigation of a population of Dall sheep. – *Syesis* 12: 1–81.
- Jedrzejewski, W. and Jedrzejewska, B. 1992. Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Białowieża National Park, Poland. – *Ecography* 15: 212–220.
- Kamler, J. F. et al. 2004. Coyote (*Canis latrans*) movements relative to cattle (*Bos taurus*) carcass areas. – *W. N. Am. Nat.* 64: 53–58.
- Kamler, J. F. et al. 2007. Dietary overlap of swift foxes and coyotes in northwestern Texas. – *Am. Midl. Nat.* 158: 139–146.
- Keech, M. A. et al. 2011. Effects of predator treatments, individual traits, and environment on moose survival in Alaska. – *J. Wildl. Manage.* 75: 1361–1380.
- Kitchen, A. M. et al. 1999. Resource partitioning between coyotes and swift foxes: space, time and diet. – *Can. J. Zool.* 77: 1645–1656.
- Kielland, K. et al. 2010. Demography of snowshoe shares in relation to regional climate variability during a 10-year population cycle in interior Alaska. – *Can. J. For. Res.* 40: 1265–1272.
- Klare, U. et al. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. – *Mamm. Rev.* 41: 294–312.
- Korpimäki, E. and Krebs, C. J. 1996. Predation and population cycles of small mammals. – *Bioscience* 46: 754–764.
- Kozłowski, A. J. et al. 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. – *Am. Midl. Nat.* 160: 191–208.
- Krebs, C. J. 1999a. Niche measures and resource preferences. – In: *Ecological methodology*. Benjamin/Cummings, pp. 597–653.
- Krebs, C. J. 1999b. Species diversity measures. – In: *Ecological methodology*. Benjamin/Cummings, pp. 532–595.
- Krebs, C. J. et al. 1995. Impact of food and predation on the snowshoe hare cycle. – *Science* 269: 1112–1115.

- Krebs, C. J. et al. 2001a. Estimating snowshoe hare population density from pellet plots: a further evaluation. – *Can. J. Zool.* 79: 1–4.
- Krebs, C. J. et al. 2001b. Ecosystem dynamics of the boreal forest: the Kluane project. Vol. 1. – Oxford Univ. Press.
- Krebs, C. J. et al. 2013. Synchrony in the snowshoe hare (*Lepus americanus*) cycle in northwestern North America, 1970–2012. – *Can. J. Zool.* 91: 1–11.
- Lake, B. C. et al. 2013. Wolf kill rates across winter in a low-density moose system in Alaska. – *J. Wildl. Manage.* 77: 1512–1522.
- Levi, T. and Wilmers, C. C. 2012. Wolves–coyotes–foxes: a cascade among carnivores. – *Ecology* 93: 921–929.
- MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. – *Am. Nat.* 100: 603–609.
- Major, J. T. and Sherburne, J. A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. – *J. Wildl. Manage.* 51: 606–616.
- Manly, B. F. 2006. Randomization, bootstrap and Monte Carlo methods in biology. – CRC Press.
- Mateo-Tomás, P. et al. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. – *Divers. Distrib.* 21: 913–924.
- McCune, B. et al. 2002. Analysis of ecological communities. – MjM Software Design, Gleneden Beach, OR, USA.
- McNamara, J. and Houston, A. 1992. Risk-sensitive foraging: a review of the theory. – *Bull. Math. Biol.* 54: 355–378.
- McNay, M. E. and Ver Hoef, J. M. 2003. Predation on moose and caribou by a regulated wolf population. – *Fed. Aid Wildl. Restor. Proj.* W-27-4 to W-33-1, Proj. 14.19
- Merkle, J. A. et al. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. – *Can. J. Zool.* 87: 56–63.
- Modafferi, R. D. and Becker, E. F. 1997. Survival of radio-collared adult moose in lower Susitna River valley, southcentral Alaska. – *J. Wildl. Manage.* 61: 540–549.
- Moleón, M. et al. 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. – *Biol. Rev. Camb. Phil. Soc.* 89: 1042–1054.
- Moore, T. et al. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. – Wyoming Game and Fish Dept.
- Morin, D. J. et al. 2016. Bias in carnivore diet analysis resulting from misclassification of predator scats based on field identification. – *Wildl. Soc. Bull.* 40: 669–677.
- Murphy, M. A. et al. 2000. Quantitative evaluation of fecal drying methods for brown bear DNA analysis. – *Wildl. Soc. Bull.* 28: 951–957.
- Murray, D. L. et al. 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. – *Can. J. Zool.* 781: 771–781.
- Neale, J. C. C. and Sacks, B. N. 2001. Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats. – *Can. J. Zool.* 79: 1794–1800.
- Needham, R. and Odden, M. 2014. Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. – *Acta Theriol.* 59: 391–398.
- Newsome, T. M. and Ripple, W. J. 2015. A continental scale trophic cascade from wolves through coyotes to foxes. – *J. Anim. Ecol.* 84: 49–59.
- Newsome, T. M. et al. 2017. Top predators constrain mesopredator distributions. – *Nat. Commun.* 8: 154–169.
- O'Donoghue, M. et al. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. – *Ecology* 79: 1193–1208.
- Oaten, A. and Murdoch, W. W. 1975. Switching, functional response, and stability in predator–prey systems. – *Am. Nat.* 109: 299–318.
- Oksanen, J. et al. 2016. Vegan: community ecology package. – R package ver. 2.3-5. <<http://CRAN.R-project.org/package=vegan>>.
- Palomares, F. and Caro, T. M. 1999. Interspecific killing among mammalian carnivores. – *Am. Nat.* 153: 492–508.
- Palomares, F. et al. 2002. Faecal genetic analysis to determine the presence and distribution of elusive carnivores: design and feasibility for the Iberian lynx. – *Mol. Ecol.* 11: 2171–2182.
- Pereira, L. M. et al. 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. – *Mamm. Rev.* 44: 44–55.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. – *Proc. Natl Acad. Sci. USA* 71: 2141–2145.
- Pozzanghera, C.B. 2015. Non-invasive methods for obtaining occupancy probabilities and density estimates of interior Alaska's mesocarnivore populations. – MS thesis, Univ. of Alaska, Fairbanks, AL.
- Prugh, L. R. 2005. Coyote prey selection and community stability during a decline in food supply. – *Oikos* 110: 253–264.
- Prugh, L. R. and Krebs, C. J. 2004. Snowshoe hare pellet-decay rates and aging in different habitats. – *Wildl. Soc. Bull.* 32: 386–393.
- Prugh, L. R. et al. 2008. Use of faecal genotyping to determine individual diet. – *Wildlife Biol.* 14: 318–330.
- Ramnanan, R. et al. 2016. Resource partitioning between black-backed jackal and brown hyaena in Waterberg Biosphere Reserve, South Africa. – *Canid Biol. Conserv.* 19: 8–13.
- Randa, L. et al. 2009. Prey switching of sympatric canids in response to variable prey abundance. – *J. Mammal.* 90: 594–603.
- Ripple, W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. – *Science* 343: 1241484.
- Ritchie, E. G. and Johnson, C. N. 2009. Predator interactions, mesopredator release and biodiversity conservation. – *Ecol. Lett.* 12: 982–998.
- Schoener, T. 1974a. Resource partitioning in ecological communities. – *Science* 185: 27–39.
- Schoener, T. W. 1974b. The compression hypothesis and temporal resource partitioning. – *Proc. Natl Acad. Sci. USA* 71: 4169–4172.
- Schmitz, O. J. et al. 2017. Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. – *Ecology* 98: 2281–2292.
- Selva, N. and Fortuna, M. A. 2007. The nested structure of a scavenger community. – *Proc. R. Soc. B* 274: 1101–1108.
- Selva, N. et al. 2003. Scavenging on European bison carcasses in Białowieża Primeval Forest (eastern Poland). – *Ecoscience* 10: 303–311.
- Sivy, K. J. et al. 2017a. Fatal attraction: intraguild facilitation and suppression among predators. – *Am. Nat.* 190: 663–679.
- Sivy, K. J. et al. 2017b. Data from: Apex predators and the facilitation of resource partitioning among mesopredators. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.b273t>>.
- Switalski, T. A. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. – *Can. J. Zool.* 81: 985–993.
- Theberge, J. B. and Wedeles, C. H. R. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. – *Can. J. Zool.* 67: 1285–1290.
- Valkenburg, P. et al. 2004. Calf mortality and population growth in the Delta caribou herd after wolf control. – *Wildl. Soc. Bull.* 32: 746–756.
- Warsen, S. A. et al. 2014. Isotopic investigation of niche partitioning among native carnivores and the non-native coyote (*Canis latrans*). – *Isotopes Environ. Health Stud.* 50: 414–24.
- Wiens, J. A. 1993. Fat times, lean times and competition among predators. – *Trends Ecol. Evol.* 8: 348–349.

- Wilmsers, C. C. et al. 2003a. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. – *J. Anim. Ecol.* 72: 909–916.
- Wilmsers, C. C. et al. 2003b. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. – *Ecol. Lett.* 6: 996–1003.
- Wilson, E. E. and Wolkovich, E. M. 2011. Scavenging: how carnivores and carrion structure communities. – *Trends Ecol. Evol.* 26: 129–135.
- Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. – *Ecol. Monogr.* 50: 111–130.
- Yang, L. H. et al. 2010. A meta-analysis of resource pulse–consumer interactions. – *Ecol. Monogr.* 80: 125–151.
- Yarnell, R. W. et al. 2013. The influence of large predators on the feeding ecology of two African mesocarnivores: the black-backed jackal and the brown hyaena. – *S. Afr. J. Wildl. Res.* 43: 155–166.
- Zar, J. H. 1999. *Biostatistical analysis*. – Prentice Hall.

Supplementary material (available online as Appendix oik-04647 at <www.oikosjournal.org/appendix/oik-04647>). Appendix 1.