Spring food habits of Wolverine (*Gulo gulo*) in the Colville River watershed, Alaska

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Abstract

Wolverines (*Gulo gulo*) are relatively abundant on the North Slope of Alaska, an Arctic ecosystem dominated by tundra habitats that run north from the Brooks Range across a wide coastal plain to the Beaufort Sea. The region contains a range of potential Wolverine prey species, including ungulates (Caribou [*Rangifer tarandus*], Moose [*Alces americanus*]), Arctic Ground Squirrel (*Urocitellus parryii*), and both Soricidae and Cricetidae species. The seasonal composition of these, and other prey species, in the Wolverines' diet is not well understood. We collected Wolverine scats during spring (March–May) on the North Slope while tracking animals from snowmobiles and with helicopters that visited areas identified as of interest during ground surveys or using global positioning system collared animals. We analyzed prey remains in 48 scat samples based on hair, bone, and other prey fragments. We then calculated frequency of occurrence, percentage of occurrence, and weighted percent volume for each major prey category detected. We confirmed species identity of scats as Wolverine by amplifying the control region of the mitochondrial DNA. We estimated spring diet diversity and richness based on nine major prey categories detected in scats. Ungulates and cricetids together constituted 69% of the Wolverines' spring diet, with Snowshoe Hare (*Lepus americanus*) constituting 9%, fox (*Vulpes* spp.) 6%, Arctic Ground Squirrel 2%, birds 2%, American Beaver (*Castor canadensis*) less than 1%, and unknown 6%.

Key words: Wolverine; *Gulo gulo*; diet; food habits; frequency of occurrence; percentage of occurrence; volume of occurrence; diet richness; diet diversity; Alaska

Introduction

Wolverines (*Gulo gulo*) are known as "facultative scavengers" that alternate between hunting live prey, scavenging, and consuming previously cached food to fulfill their energy requirements (Magoun 1987; Banci 1994; Dijk *et al.* 2008; Dalerum *et al.* 2009; Koskela *et al.* 2013; Mattisson 2016). In the Arctic, Wolverines generally switch from killing and consuming cached ungulate carrion (e.g., Caribou [*Rangifer tarandus*]) in the winter, to hunting small mammals (e.g., Arctic Ground Squirrel [*Urocitellus parryii*]) during the summer (Magoun 1987; Dijk *et al.* 2008). Because habitat and prey species availability differ across the Arctic and across seasons, Wolverines likely adjust their diet according to available prey sources (Churchill 1955; Mac-Donald and Cook 2009; Lenart 2015). Variation of diet composition may reflect prey availability, which in turn may influence the distribution and abundance of Wolverines. In this study, we focus on spring diet composition during the transition from winter to summer, defined here as March through May, in the Colville River watershed of the Alaskan Arctic.

Across their range, Wolverines feed on a variety of prey species comprised primarily of ungulates (Moose [*Alces americanus*], Caribou) in North America and Europe (Landa *et al.* 1997; Dalerum *et al.* 2009; Koske-la *et al.* 2013; Inman and Packila 2015). However, Wolverines also forage on small mammals, birds, and fish (Magoun 1987; Landa *et al.* 1997; Samelius *et al.* 2002; Shardlow 2013; Inman and Packila 2015). In the North American Arctic, in addition to ungulates, Wolverines feed on ptarmigan (*Lagopus* spp.), soricids (shrews), cricetids (voles, lemmings, mice), hare (*Lepus* spp.), and Arctic Ground Squirrels (Banci 1987; Mulders 2001). One study conducted on Alaska's North Slope investigated the Wolverines' seasonal diet composition in summer (May–August) and winter (September–April) near the Utukok River in the foothills of the Brooks Range, and found that Wolverines relied heavily on Arctic Ground Squirrel almost the entire year, except in midwinter (December–February) when their diet shifted to Caribou (Magoun 1987). Caribou undertake seasonal migrations and Moose reside at low densities on the North Slope of Alaska (Fancy *et al.* 1989; Carroll 2014; Tape *et al.* 2016), suggesting that Wolverines may need to rely on cached food or alternative prey sources when ungulates are scarce.

Information on the relative contribution of small prey such as cricetids, soricids, Snowshoe Hare (*Lepus americanus*), ptarmigan, and large prey in the Wolverines' diet across the Alaskan Arctic is lacking, but could contribute towards understanding how prey selection influen-

ces Wolverine survival and reproductive success (Krebs *et al.* 2004; Persson 2005; Koskela *et al.* 2013). A lack of large ungulate prey coupled with dwindling food caches during early spring may force Wolverines to switch from ungulate carrion to other prey sources (Persson 2005). Investigating the relative presence of large versus small mammals (Cricetidae, Soricidae, Sciuridae, Leporidae) in the Wolverines' spring diet is an important step in understanding how Wolverines in the Arctic address a period of high energetic demands (Magoun 1987; Landa *et al.* 1997; Dalerum *et al.* 2009).

We collected Wolverine scats on the North Slope near Umiat, Alaska to determine spring diet composition of Wolverines in the foothills of the Brooks Range and Beaufort coastal plain (Figure 1). Our objectives were to describe the spring diet composition of Wolverines in our study area and compare the portion of that period's diet made up of small mammals versus ungulate prey.

Study Area

Our study took place in 2016 within 120 km of Umiat, Alaska in the National Petroleum Reserve-Alaska (NPR-A; Figure 1). On the southeast border of the NPR-A lies the Colville River corridor made up of flood plain with shrubs such as alder (*Alnus* spp. Miller) and willow (*Salix* spp. L.). Northwest of the Colville River are rolling hills with steep cut drainages, composed of upland tundra vegetation such as Tussock Cottongrass (*Eriophorum vaginatum* L.) and mountain avens (*Dryas* spp. L.; Viereck *et al.* 1992). Further north, the land transitions from rolling hills to a flattened terrain filled with lakes and ponds, which extends north to the coast of the Beaufort Sea. This area is considered lowland tundra, containing Water Sedge (*Carex aquatillis* Wahlenberg) and other mesic plant species (Churchill 1955). At Umiat, average temperatures range from −30°C in February to 13°C in July (NOAA 2018). Average annual rain and snow accumulation are 13.9 cm and 84.3 cm, respectively.

While large ungulates, cricetids, soricids, other small mammals (e.g., Snowshoe Hare, Arctic Ground Squirrel), and birds are available as prey to Wolverines during spring (Table 1), their relative abundance may change over time and space (MacDonald and Cook 2009). Caribou are seasonally available as they migrate through the study area in spring and fall, residing near the coast in summer, and in the Brooks Range to the south in winter (Lenart 2015). Moose and Muskox (*Ovi-*
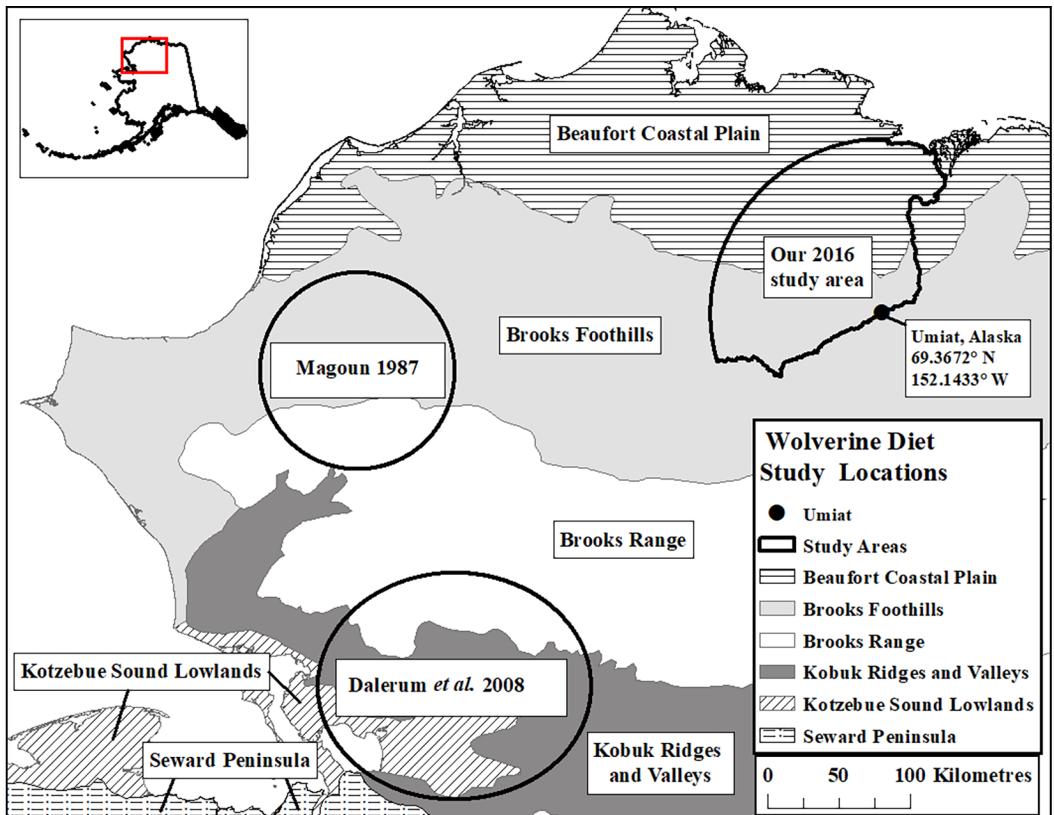

FIGURE 1. Wolverine (*Gulo gulo*) diet study areas compared to the ecoregions of northern Alaska, USA. Our 2016 study area took place within 120 km of Umiat, Alaska in the National Petroleum Reserve-Alaska.

bos moschatus) persist at low densities year-round, but Muskox only inhabit the northern portion of the study area near the Beaufort Sea (MacDonald and Cook 2009; Carroll 2014). Smaller prey that inhabit the study area year-round include: cricetids, soricids, Arctic Ground Squirrel, Snowshoe Hare, Willow Ptarmigan (*Lagopus lagopus*), and Rock Ptarmigan (*L. muta*; MacDonald and Cook 2009). Cricetids and soricids are active underneath the snow year-round, while Arctic Ground Squirrels hibernate, reducing the Wolverines access to these species in winter and early spring (Batzli and Sobaski 1980). In contrast, Snowshoe Hare and ptarmigan are available year-round. Wolverines are known to cache their prey, thus any species listed above may be consumed during winter and spring (Magoun 1987).

Methods

Scat collection

We followed Wolverine tracks by snowmobile 10 March–29 April 2016 to collect scats for diet analysis. We followed tracks opportunistically while maintaining a live-capture trap line, picking up scats from unknown individuals. When we encountered relatively fresh Wolverine tracks (e.g., not blown over, or covered with snow), we followed the track against the direction of travel to avoid harassing the animal. If tracks were older (e.g., blown over with snow) we followed the track in either direction. We stopped tracking when the animal travelled through terrain unnavigable by snowmobile, or when tracking conditions deteriorated. We recorded global positioning system (GPS) coordinates for each

scat collected. We recorded the location of Wolverine snow-holes encountered while tracking and returned to collect scats in late spring after the snow melted. At carcass sites, we collected all scats, but only included one randomly selected scat in our analysis to avoid pseudo-replication and the over-representation of the prey species at the carcass site (Marucco *et al.* 2008; Bacon *et al.* 2011).

We captured five Wolverines 6–26 April 2016 and affixed GPS collars (Tellus light model, Followit Sweden AB, Lindesberg, Sweden) programmed to record locations every 20 minutes. We captured three females including one juvenile and two reproductive females (with kits), one juvenile, and an adult male. Collars remained on animals until mid-summer when drop-off mechanisms were activated. In addition to scats collected while tracking unknown individuals, we collected scats from areas where collard Wolverines spent >20 minutes in an area <100 m^2, signifying an extended stay in a localized area where scat could be found (called a cluster). We returned to snow-holes and clusters on 29 May to collect scats.

We placed scats in Whirl-Packs® (Nasco, Fort Atkinson, Wisconsin, USA) and stored them at temperatures ranging from 4°C to −35°C while in the field (10 March–29 April, and 29 May). After leaving the field, we stored samples in a −20°C freezer for a maximum of 1.5 months.

We radio-tracked collared Wolverines with fixed-winged aircraft 13–22 May to observe feeding behaviour. We watched for visually identifiable prey (e.g., a

TABLE 1. List of potential prey items available in late winter and early spring to Wolverines within the National Petroleum Reserve-Alaska (MacDonald and Cook 2009).

Family	Common name	Scientific name
Bovidae	Muskox	*Ovibos moschatus*
Canidae	Gray Wolf	*Canis lupus*
	Arctic Fox	*Vulpes lagopus*
	Red Fox	*Vulpes vulpes*
Cervidae	Moose	*Alces americanus*
	Caribou	*Rangifer tarandus*
Cricetidae	Peary Land Collard Lemming	*Dicrostonyx groenlandicus*
	Brown Lemming	*Lemmus trimucronatus*
	Singing Vole	*Microtus miurus*
	Tundra Vole	*Microtus oeconomus*
	Northern Red-backed Vole	*Myodes rutilus*
Felidae	Lynx	*Lynx canadensis*
Leporidae	Snowshoe Hare	*Lepus americanus*
Mustelidae	Wolverine	*Gulo gulo*
	Ermine	*Mustela erminea*
	Least Weasel	*Mustela nivalis*
Phasianidae	Willow Ptarmigan	*Lagopus lagopus*
	Rock Ptarmigan	*Lagopus muta*
Sciuridae	Arctic Ground Squirrel	*Urocitellus parryii*
Soricidae	Cinereus Shrew	*Sorex cinereus*
	Tundra Shrew	*Sorex tundrensis*
	Barren Ground Shrew	*Sorex ugyunak*
	Holarctic Least Shrew	*Sorex minutissimus*
Ursidae	Brown Bear	*Ursus arctos*
	Polar Bear	*Ursus maritimus*

Moose carcass), and observed hunting behaviour (e.g., hunting small prey). We recorded time, location, collared animal's identity, and observed prey or behaviour.

Scat analysis

We confirmed identification of each scat as Wolverine with faecal DNA analysis, because tracking trails and clusters also had sign of other predators (e.g., foxes). We used three methods to sample faecal DNA from each scat. First, we scraped each scat using two flat-sided toothpicks and placed each into a coin envelope. Second, we removed 1 mL of faecal material from each scat and placed it into a vial. Finally, we swabbed each scat with a sterile cotton-tipped swab and placed it into a separate vial. We sent all samples to the Rocky Mountain Research Station, National Genomics Centre for Wildlife and Fish Conservation in Missoula, Montana to verify the species identity. We used the QIAGEN QIAamp Fast DNA Stool Mini Kit (QIAGEN Inc., Valencia, California, USA) following the manufacturer's instructions for DNA extraction. We amplified the control region of mitochondrial DNA (mtDNA) for species identification following Schwartz *et al.*'s (2007) methods for processing samples.

Following DNA sampling, we transferred individual scats into nylon mesh stockings and washed them on gentle cycle in a Haier HLP23E compact washing machine (Haier Appliances, Rapid City, South Dakota, USA). We washed scats for 2–3 cycles until the water ran clear (indicating the removal of the faecal matrix material) and air-dried samples for 48 h. We weighed each scat and identified prey remains by comparing microscopic qualities of medulla, cortex, and cuticular scale patterns of mammalian hairs to published keys (Moore *et al.* 1974; Carlee and Horelick 2011), and by comparing hair, teeth, claw, and bone fragments to reference specimens on loan from University of Alaska Museum of the North, Fairbanks, Alaska. We identified prey remains to species level or nearest taxonomic grouping if remains were highly degraded. We visually estimated the proportion of each prey type present in each scat, rounded to the nearest 5%. We also sub-sampled scats after determining the proportion of the scat belonging to each prey category. Of the scats that contained suspected cricetids and soricids, we collected 15–30 hairs to determine species identification through DNA analysis.

We used methods from Dijk *et al.* (2007) and the recommendations of Klare *et al.* (2011) to characterize Wolverine diet. Frequency of occurrence (FO) was calculated from the binary occurrence of each prey item in each scat, and represents the percentage of the total sample size containing each prey item:

$$FO_i(\%) = \frac{n_i}{N} \times 100$$

where n_i is the number of scats containing species *i* and N represents the total number of scats (Ciucci *et al.* 1996).

Percentage of occurrence (PO) is calculated from binary occurrence data that represents the percentage of the total prey occurrences containing each prey item:

$$PO_i(\%) = \frac{n_i}{\sum n_i} \times 100$$

where n_i is the number of scats containing species *i*. Finally, we calculated weighted volume (VOL) to determine the relative importance of prey in the diet in the absence of a biomass calibration (Klare *et al.* 2011).

Weighted volume is the sum of percent volume of each prey item in scats, divided by the total number of scats:

$$VOL_i(\%) = \frac{\sum v_i}{N} \times 100$$

where v_i is the proportion of each scat containing species *i*.

Scats collected while tracking individual Wolverines were treated as individual sample units. Scats collected from individual snow-holes and clusters were combined and treated as a single sample unit, because the large piles of scats collected at clusters, deposited by an unknown number of individuals, made it difficult to differentiate among individual scat samples. For scats collected at clusters, v_i was equal to the proportion of the total scat volume at a cluster.

Weighted volume was calculated for each prey item detected in scats. We then grouped prey items into one of nine major prey categories and calculated weighted volume of each major prey category in scats. The nine prey categories were: ungulate, Snowshoe Hare, Arctic Ground Squirrel, cricetids and soricids, birds (Aves), fox, American Beaver, unknown (including any unidentifiable remains), and other (consisting of vegetation, gravel, and woody debris). Items in the "other" category were expected to be incidentally ingested as a result of digging up food caches or excavating small mammal burrows. Although Wolverines have been documented to consume vegetation and berries, we assumed vegetation was incidentally ingested while feeding (Lofroth *et al.* 2007) or picked up during collection of scats. Thus we dismissed it from our analysis.

We estimated diet richness as the overall number of items in the diet, and diet diversity, which indexes heterogeneity and accounts for relative abundance of each item in the diet (Krebs 1999). We estimated diet diversity using the Shannon-Wiener diversity index (H'), whereby the higher the index value, the more evenness in use across all resources:

$$H' = \sum \hat{\rho}_i \ln \hat{p}_i$$

where p_i is the total proportion of species *i* in the sample (Colwell and Futuyma 1971). We estimated 95% CI for diet richness, diversity, and volume of each of the nine major prey categories based on 1000 bootstrap re-samplings of scat data (Manly 2006).

We used rarefaction to assess how diet diversity and richness varied with sample size (Krebs 1999). Rarefaction uses bootstrap resampling techniques to subsample from the initial dataset (without replacement) and estimate the mean and variance of the desired index (e.g., diversity, richness) for each sample size, n, from one to the maximum number of scat samples. We generated rarefaction curves based on 1000 bootstrap runs. Diet indices and bootstrapping and rarefaction analyses were calculated in Program R v 3.0.1 (R Development Core Team 2014).

Results

Scat collection

We collected 104 scat samples while tracking individual Wolverines from 10 March to 29 April ($n = 83$) and first visited GPS-identified clusters on 29 May ($n = 22$; Figure 2). We followed 64 km of tracks, collecting 83 scats during 30 tracking events. We collected 21 scats from 20 GPS-cluster sites (14 snow-holes monitored by motion-activated cameras and six clusters detected by GPS collar locations). We also collected 29 scats from near a Moose carcass.

Faecal DNA analysis confirmed 70 of the 104 scats we collected as Wolverine, 23 as Red Fox (*Vulpes vulpes*), three as Arctic Fox (*Vulpes lagopus*), and eight with poor DNA quality that precluded identification. Of

the 29 scats collected at the Moose carcass, 15 were identified as Wolverine, and we randomly chose one of these scats to include in our analysis (Marucco 2008; Bacon *et al.* 2011). We combined 15 of the scats collected at clusters identified as Wolverine into eight cluster scat samples, for a final sample size of 48 (40 from tracking and eight from GPS-clusters). Of the scats containing cricetids ($n = 25$), three contained Peary Land Collared Lemming (*Dicrostonyx groenlandicus*), two Brown Lemming (*Lemmus trimucronatus*), two Singing Vole (*Microtus miurus*), and others contained hairs that were non-cricetid or had poor quality DNA, preventing species identification. No soricids were found in scats.

Scat analysis

We classified prey remains and scat contents as one of 11 categories, five of which we identified to the species level (Figure 3): unknown ungulate (too degraded to distinguish between Moose or Caribou), Moose, Caribou, unknown carnivore (too degraded to determine species), fox, American Beaver, Snowshoe Hare, Arctic Ground Squirrel, cricetids, birds, and unknown (unidentified bone and other debris). We did not attempt to identify feather remains beyond the "bird" category because the majority of feathers were too highly degraded for species identification, although we expect that they were predominantly ptarmigan based on our
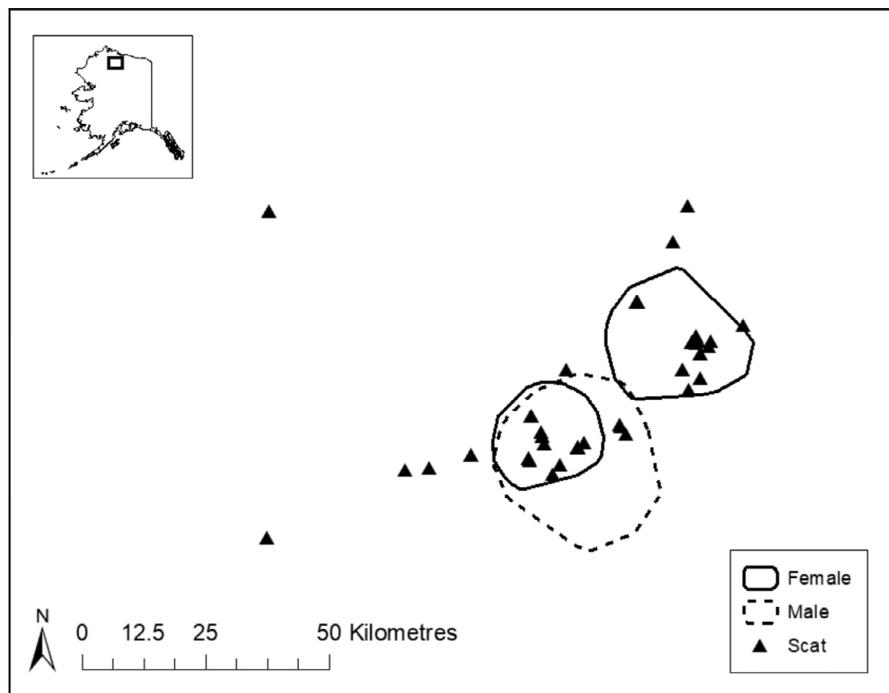

FIGURE 2. Locations of Wolverine (*Gulo gulo*) scats collected and home ranges of three Wolverines (one male, two female) near Umiat, Alaska, USA 10 March–29 April, and 29 May 2016. We collected 67 scats later confirmed through DNA analysis as Wolverine. Home ranges represent 95% minimum convex polygons. Locational details have been purposely omitted.
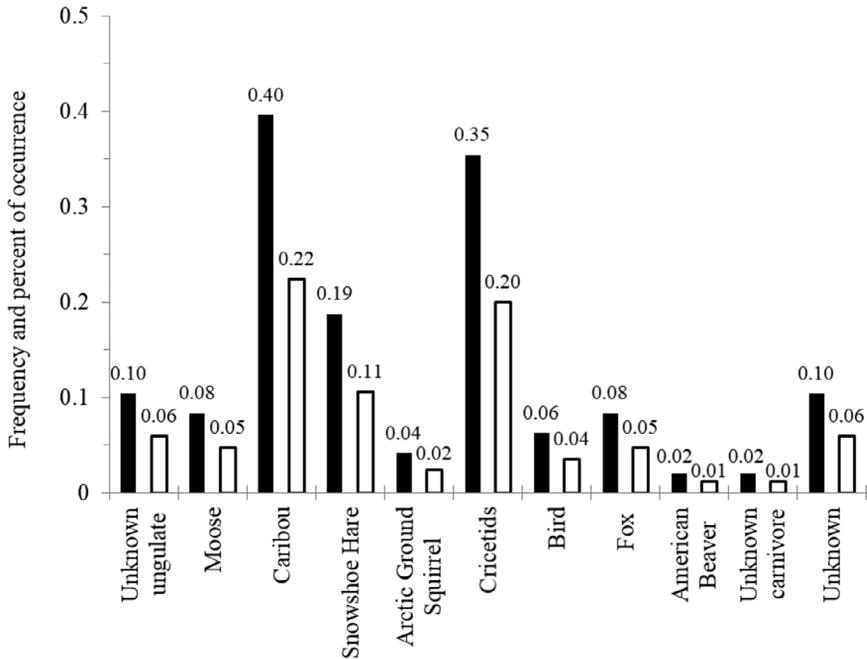
FIGURE 3. Frequency and percent of occurrence (FO and PO, respectively) of all prey species detected in combined Wolverine (*Gulo gulo*) scats (*n* = 48) collected near Umiat, Alaska, USA, 10 March–29 April, and 29 May 2016. Closed bars represent FO and open bars represent PO. Prey detected includes: unknown ungulate (Moose [*Alces americanus*], Caribou [*Rangifer tarandus*]), Moose, Caribou, Snowshoe Hare (*Lepus americanus*), Arctic Ground Squirrel (*Urocitellus parryii*), cricetids (Brown Lemming [*Lemmus trimucronatus*], Peary Land Collared Lemming [*Dicrostonyx groenlandicus*], Singing Vole [*Microtus miurus*]), bird (Aves), fox (Red Fox [*Vulpes vulpes*], Arctic Fox [*Vulpes lagopus*]), American Beaver (*Castor canadensis*), unknown carnivore (Carnivora), and unknown. Vegetation (FO = 0.25, PO = 0.14) and woody debris (FO = 0.06, PO = 0.04) not shown.

observations while in the area and consumption by Wolverines elsewhere.

Raw measures of FO and PO indicated that the four most commonly occurring items in scats were Caribou, cricetids, vegetation (assumed to be incidentally ingested during feeding or scat collection and not considered in further analyses), and Snowshoe Hare (Figure 3). Ranking prey items by volume indicated that the three most abundant identifiable items were Caribou, cricetids, and Snowshoe Hare. Cricetids and Caribou collectively represented 55% volume of the diet (Figure 3). Bootstrapped estimates of volume (mean ± SD) of each of the nine major prey categories indicated that ungulates (0.49 ± 0.07) and cricetids (0.20 ± 0.05) were the two primary prey resources (Figure 4). Arctic Ground Squirrel (0.02 ± 0.03) made a minor contribution to the diet.

Mean diet richness was eight resource categories (8.43 ± 0.81; Figure 5a). Mean Shannon-Wiener diversity index for scats was 1.75 ± 0.11. Rarefaction curves showed that mean diet richness continued to increase up to a sample size of about 40 scats, after which the rarefaction curve began to approach an asymptote (Figure 5a). Rarefaction of mean diet diversity showed that the

diversity curve approached an asymptote after a sample size of about 20 (Figure 5b).

We observed five instances of active hunting by Wolverines between 13 and 22 May. Three events were of an adult male and two events of a single adult lactating female, exhibiting pouncing behaviour we attributed to hunting small mammals. We observed four out of five instances of hunting behaviour in tussock habitat.

Discussion

This study represents the second study of spring Wolverine diet north of the Brooks Range in Alaska (following Magoun 1987) and the first in the Colville River watershed. We documented a high prevalence of ungulates and cricetids in Wolverine scats, indicating the importance of these resources during spring. We also detected various predators (e.g., foxes), mid-size prey (Snowshoe Hare), and bird remains, documenting that Wolverines use a variety of prey types on the North Slope. Although we detected American Beaver in our scats, we attribute this to bait used by local trappers in the area as they are not a common species north of the Brooks Range of Alaska, although their range is increasing (MacDonald and Cook 2009; Tape *et al.* 2018).
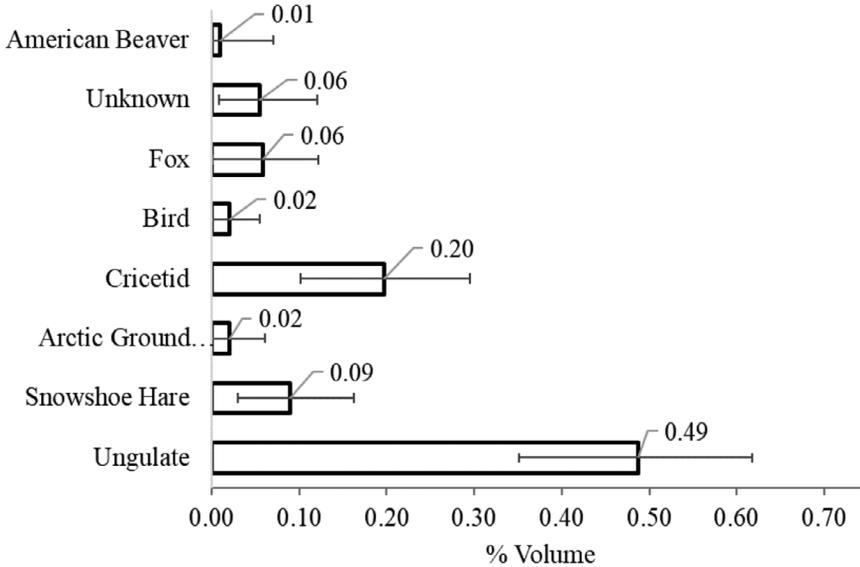
FIGURE 4. Volume and 95% CI for each of eight prey categories detected in Wolverine (*Gulo gulo*) scats collected while tracking and from GPS clusters near Umiat, Alaska, USA,10 March–29 April, and 29 May 2016. We weighed the samples then conducted an ocular estimate of the percentage of each prey item in the scat to determine percent volume. We estimated CI from 1000 bootstrap re-samplings. Prey detected includes: ungulate (Moose, [*Alces americanus*], Caribou [*Rangifer tarandus*]), Snowshoe Hare (*Lepus americanus*), Arctic Ground Squirrel (*Urocitellus parryii*), cricetids (Brown Lemming [*Lemmus trimucronatus*], Peary Land Collared Lemming [*Dicrostonyx groenlandicus*], Singing Vole [*Microtus miurus*]), bird (Aves), fox (Red Fox [*Vulpes vulpes*], Arctic Fox [*Vulpes lagopus*]), Ermine (*Mustela ermine*), American Beaver (*Castor canadensis*). Other (7%, including vegetation and woody debris) not shown.
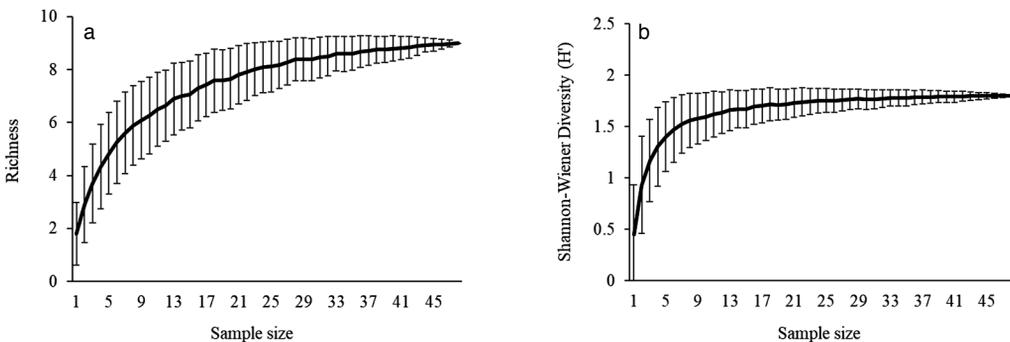

FIGURE 5. Rarefaction curves exhibiting the influence of sample size (x-axis) on Wolverine (*Gulo gulo*) diet richness (a) and diversity (b) estimated for scats collected near Umiat, Alaska, USA, 10 March–29 April, and 29 May 2016. Error bars show one SD estimated from 1000 bootstrap re-samplings of data.

Ungulates made up the largest portion of the Wolverines' diet based on our scat frequency and percentage of occurrence, and volume, which is similar to previous studies in North America and Fennoscandia (Lofroth *et al.* 2007; Dalerum *et al.* 2009; Koskela *et al.* 2013; Inman and Packila 2015). Moose contributed to diets of Wolverines in our study area, however due to their low abundance they likely are not a reliable prey source. The only Moose carcass we found provided an abundance of food for local Wolverines, but Caribou provide more overall biomass when available. Another Wolver-

ine diet study in the southwestern Brooks Range (Dalerum *et al.* 2009), also found that Wolverines mainly subsisted on Caribou throughout the winter, despite the Western Arctic Caribou Herd's only seasonal availability (Lenart 2015). Dalerum *et al.* (2009) found that Caribou made up >50% of stomach and colon contents in Wolverine carcasses. Because winter Caribou distribution on the North Slope is inconsistent between years (Dau 2015; Lenart 2015), access to Caribou in the winter can be supplemented from food caches. We were unable to determine whether prey remains were from cach-

ing their own prey, scavenging other predator kills (such as from Gray Wolf [*Canis lupus*]), or from actively hunting. Obtaining this information would help reveal how Wolverines in our study area manage seasonally abundant ungulates compared to other prey sources (e.g., Arctic Ground Squirrel) that are less accessible in late winter. Similar to other studies basing diet inference on scats, only hair, bone, and feathers are available to determine FO and PO. This may underestimate a large prey item where large amounts of muscle are digested yielding a potentially smaller proportion of hair to biomass consumed. Other items, such as bird eggs may not be identified, but are known to be eaten by Wolverines (Magoun 1987; Samelius *et al.* 2002).

Although ungulates represent a significant portion of the Wolverines' diet in our and other studies (e.g., Mulders 2001; Dalerum *et al.* 2005, 2009; Lofroth *et al.* 2007; Inman and Packila 2015), cricetids are clearly another important prey. Cricetids composed the second highest frequency and percentage of occurrence, and volume for overall diet in our study. We also observed behaviour in spring consistent with hunting small prey, highlighting their potential significance as a spring food resource. Cricetid populations are irruptive and fluctuate over various temporal and spatial scales influencing their availability to Wolverines (Krebs and Myers 1974). The high proportion of cricetids detected in our Wolverine scats may reflect an abundance of cricetids throughout the study area. Wolverine scats could also contain a large proportion of cricetids because Wolverines preferentially selected them (Manly *et al.* 2002). Wolverines could increase their use of cricetids when snow begins to melt in the spring exposing subnivean prey at a time when the tundra tussock habitat is flooding with meltwater (as observed for the animals we saw hunting). However, without a measure of small mammal and ungulate abundance, it is unclear if Wolverines select for these prey resources on the North Slope, or adjust their intake based on availability alone during spring.

Cricetids, Snowshoe Hare, and Arctic Ground Squirrel collectively constitute 30% volume of spring Wolverine diet in our study. However, the role of small prey in Wolverine population dynamics is poorly understood and could be significant given the timing of availability relative to reproduction (Inman *et al.* 2012). Small mammal abundance in our area contributes to the diets of reproducing female Wolverines, when ungulates are only seasonally available, or as cached carrion. The availability and use of ungulates versus small mammals could influence Wolverine survival and reproductive success (Krebs *et al.* 2004; Persson 2005; Koskela 2013; Petersen 2014). Access to prey is particularly important when females are under increased energetic stress in late winter through summer while nursing and provisioning young with prey (Inman *et al.* 2012; Koskela 2013).

Future studies would benefit from determining diet composition of individual Wolverines to compare diet among home ranges. For example, a Wolverine that has an established territory in a riparian area may exclude another individual from access to a Moose carcass, thereby forcing the individual to find other prey sources. Our satellite collared Wolverines (R.D. unpubl. data), along with other radio tracking studies (Dawson *et al.* 2010; Persson *et al.* 2010), showed that Wolverines exhibit intrasexual territoriality, which likely precludes individuals of the same sex from accessing resources in neighbouring territories. Differences in diet among individual Wolverine territories could provide useful information on small-scale controls of population dynamics among habitat types, sex and age classes, and seasons.

Our work in the spring does not allow us to make inferences about summer diet. However, cricetids and Arctic Ground Squirrel may both be easier to hunt in summer months due to lack of snow cover and could be an important resource for Wolverine kits. In southern Norway, an abundance of cricetids in summer increased Wolverine kit survival (Landa *et al.* 1997). In addition, Arctic Ground Squirrel was an important diet resource for Wolverines on the western portion of the North Slope (Magoun 1987). Future studies would benefit from documenting summer Wolverine diets for kits and adults across a broader area, to determine the reliance on cricetids and Arctic Ground Squirrel, and their relation to Wolverine population dynamics.

Arctic Ground Squirrel represented only a small portion of the spring Wolverine diet in our study area, which differs from Magoun's (1987) findings, but may be confounded with the timing of our sampling. Near the Utukok River in the western portion of the North Slope, Wolverines fed on Caribou in mid-winter (December–February), but primarily fed on Arctic Ground Squirrel the rest of the year (Magoun 1987). Scats collected at the same time also contained large quantities of soil, likely from Wolverines digging up cached or hibernating Arctic Ground Squirrels (Magoun 1987). We observed negligible soil in the scats we sampled. However, the low frequency and percentage of occurrence and volume of Arctic Ground Squirrel in our analysis compared to Magoun (1987) could also relate to a difference in Arctic Ground Squirrel abundance and emergence dates between study areas. Our study area contains well drained soils preferred by Arctic Ground Squirrels, but their abundance is unknown (Barker and Derocher 2010). Assessing Arctic Ground Squirrel abundance and emergence throughout the area could aid interpretation of differences in the reliance on ground squirrels according to their activity and availability. This may be particularly important given the progressively earlier spring melt and potentially earlier availability of ground squirrels and cricetids through reduced snow pack (IPCC 2013). Furthermore, ground squirrels may increase in density in some well-drained

areas as permafrost thaws in these northern ecosystems (Wheeler and Hik 2013).

To our knowledge, no other studies have used the Shannon-Wiener diversity index to calculate Wolverine diet diversity. We have no basis for comparing heterogeneity in resource use on the North Slope to other areas but monitoring how diet diversity changes over time or compares between areas could indicate differences in foraging strategies over time or among Wolverine populations. Future studies might consider adding this metric to their analysis to quantify how differences in resource use vary with the number of prey types in the diet. According to our rarefaction analysis, our sample size for diet richness may have been inadequate to provide accurate estimates of the average number of resources used by Wolverines. Future diet studies on the North Slope should consider increasing sample size to determine the full range of resources used by Wolverines.

A quantitative assessment of use versus availability would also provide improved insights into factors driving Wolverine prey selection, such as increased cricetid abundance, decreased ungulate abundance, or by the snowpack conditions affecting how cricetids and Arctic Ground Squirrels are accessible as the snowpack melts. Increased food availability corresponded with increased reproductive success of female Wolverines in Sweden (Persson 2005), thus, changes in food availability that influences reproductive success is a mechanism that could ultimately influence Wolverine abundance.

Author Contributions

Writing—Original Draft: R.D., K.S., and M.R.; Writing—Review & Editing: R.D., K.S. M.R., T.G., and K.P.; Conceptualization: R.D., M.R., and K.S.; Investigation: R.D., T.G., K.S., and K.P.; Methodology: K.S., R.D., and T.G.; Formal Analysis: K.S. and K.P.; Funding Acquisition: M.R.

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