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Wolf diet composition and kill rates

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Southern Lakes Wolf Program – wolf diet composition and kill rates

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Summary

- We used cluster modelling of wolf GPS locations to identify and investigate sites where wolves killed prey. The specific objectives of this report were to determine: 1) the diet composition of wolves, 2) the rate at which wolves kill and consume prey in the Southern Lakes in winter, 3) the length of time wolves spend consuming prey items (handling time), and 4) if handling times differ across prey species.

- We collared eight wolves among five packs and monitored daily wolf movements for an average of 80 days per pack (standard deviation [SD] = 39.5, range = 45-129), totalling 399 wolf days. Cluster modelling identified 124 potential kill sites. We visited all sites in the field and confirmed 49 ungulate kills (20 moose, 22 caribou and 7 Dall sheep).

- Kill composition varied considerably across packs. The percentage of moose killed ranged from 18-87% while caribou killed ranged from 13-57%. When averaging kill composition across packs, moose represented an average of 59% (SD = 29.8) of prey killed and were the primary prey species in three out of the five packs. Caribou represented an average of 35% (SD = 18.8) of prey killed and were the primary prey species in one out of five packs. The remaining pack relied heavily on the Whitehorse landfill as a food source, making only one kill over the study period.

- During winter, observed wolf kill rates (mean = 0.018 ungulates/wolf/day, SD = 0.006, range = 0.013 – 0.027) and biomass consumption rates (mean = 3.49 kg ungulate/ wolf/day, SD = 0.30, range = 3.30 – 3.93, n = 4), were at the lower end of the typical range observed in other Yukon and Alaskan studies (range = 3.20 – 7.89 kg ungulate / wolf / day).

- Average handling times of a moose (mean = 5 days, n = 20, SD = 2.61, range: 1.0 - 11.2 days), caribou (mean = 1.7 days, n = 21, SD = 0.78, range = 0.9 – 2.8) and Dall sheep (mean = 0.9 days, n = 7, SD = 0.36, range = 0.6 – 1.5) were longer than those observed in other Yukon and Alaskan studies. Longer times may be a function of prey density such that, where prey densities are low, wolves spend greater time with the carcass to maximize all available biomass.

- Noteworthy: Since the study by Hayes et al. (1991) in the same area, caribou have become a component of each pack's diet. However, it does not appear that wolves are preventing population growth among the herds. There is evidence that caribou have expanded their range and increased in number across the Southern Lakes (Southern Lakes Caribou Recovery Program, 2022).

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Introduction

Effective management of wolf-prey systems depends on understanding predator-prey relationships and the factors influencing them (Ballard et al. 1997, Adams et al. 2008, Fuller 1989, Hebblewhite 2005, Knopff et al. 2009). How wolf predation influences ungulate populations has been the subject of public controversy and scientific research for decades (NRC, 1997; Mech and Peterson, 2003). In naturally balanced ecosystems, wolves and ungulate populations have coexisted for millennia (Peterson and Ciucci 2003). However, research has shown that wolves can limit an ungulate population's growth (Messier 1994, Dale et al. 1994). Therefore, estimating their kill rates and the composition of their diets is important for understanding their impacts on their prey (Sand et al. 2008).

Wolf predation studies in the Southern Lakes, Yukon, were last conducted between 1983 and 1988 as part of the Coast Mountain wolf control program. The objectives of this earlier work were to determine the effects of a three-year aerial wolf control program on the demography, distribution and physical characteristics of wolves (Hayes et al., 1991).

A component of that study investigated wolf predation ecology on moose, Dall sheep and caribou at varying wolf densities. At the time, the woodland caribou populations of Carcross and Ibex herds totalled only 350 animals (Farnell 1982). As such, caribou were reported as not being an important component to the Southern Lakes wolves' diet, with only one caribou having been killed in six years (Hayes et al. 1991). Since then, the Southern Lakes Caribou Recovery Program (established 1993) has been successful in growing the Carcross, Ibex, Laberge and Atlin herds, which now total an estimated 4,000 caribou (Southern Lakes Caribou Recovery Program, 2022).

Despite this growth, local communities have expressed concern that mortalities caused by wolves may slow the caribou recovery effort. Furthermore, the situation may be aggravated by growing wolf populations that are utilizing moose as an additional food source. Given these concerns, the aim of this research was to better understand wolf predation in the Southern Lakes and determine the extent to which wolves prey on caribou within the region. The specific objectives of this study were to determine:

1. The diet composition of wolves;
2. The rate at which wolves kill and consume prey in the Southern Lakes in winter;
3. The length of time wolves spend consuming prey items (handling time); and
4. If wolf handling times differ across prey species.

Study area

The study area falls within the Coast Mountain ecoregion, which is characterized by rugged mountains that decrease in elevation as you move northward (Figure 1). The southern and western portions of the Coast Mountains are comprised of high mountain peaks (>2,000m) surrounded by rolling plateaus. About 70% of these mountains extend above the treeline. The eastern portion of this mountainous ecoregion is lower in elevation and characteristically mesic or arid.

Vegetation in the region consists of white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta)* and trembling aspen (*Populus tremuloides*). Also contained within the ecoregion is the Southern Lakes complex, which is a group of large, interconnected lakes, transecting the study area. In winter, these lakes provide important movement corridors for wolves, but they also serve as potential home range borders in the summer.

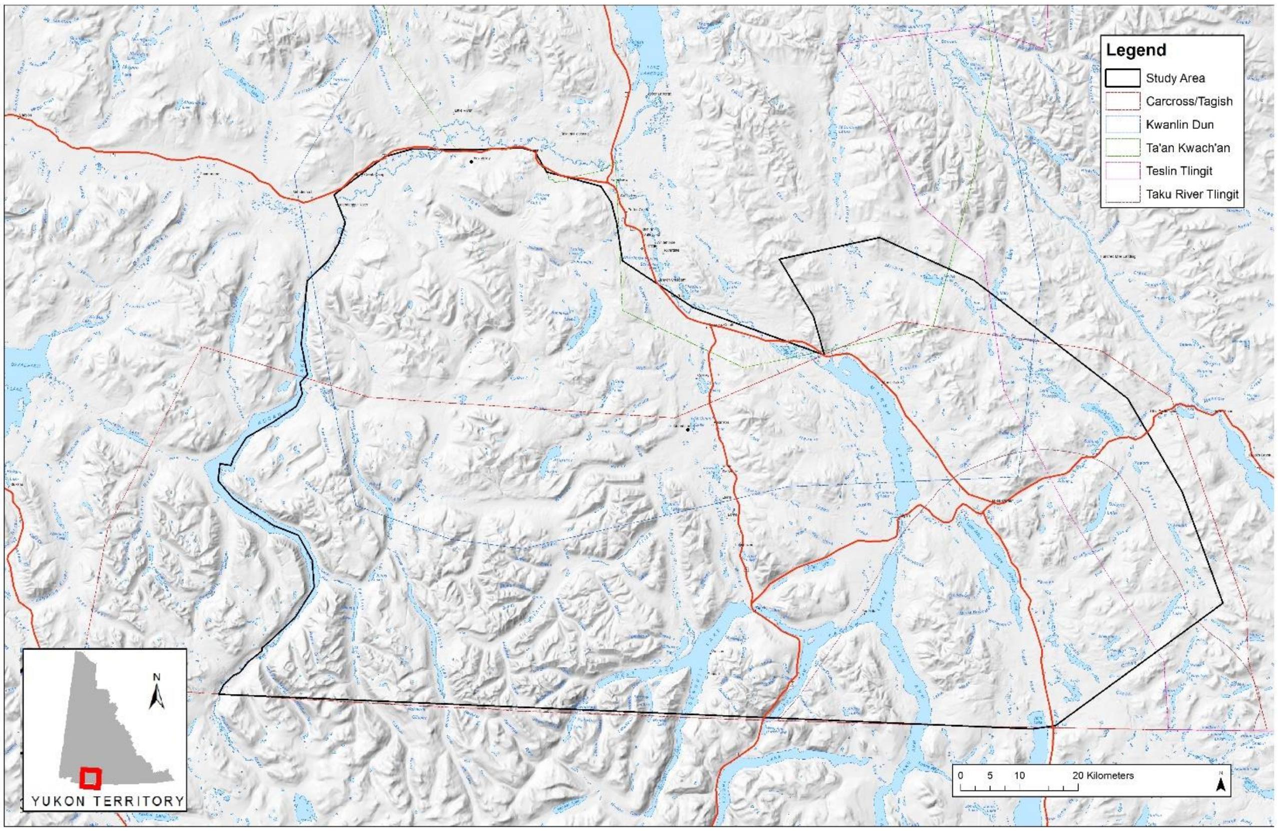

Figure 1. Study area of the Southern Lakes wolf kill site investigation (2020-2022).

Snow depths in the study area vary with latitude and elevation, with the greatest accumulation occurring at high elevations in the south and diminishing as you move northwards. Snow above the treeline is consolidated by wind and temperature fluctuations, and alpine ridges are blown free of snow throughout the winter. Snow depth in the valley floors range from 20 to 70 cm (Hayes 1991). In 2021, record snow falls were experienced with 215% of the historical median snow water equivalent (Yukon snow bulletin 2021).

Moose *(Alces alces)*, woodland caribou (R*angifer tarandus*), and Dall sheep (*Ovis dalli dalli*) occupy most of the study area. Generally, moose density is lower west of the Alaska and Atlin highways (approximately 158 moose /1,000km^2) than moose densities east of the highways (280 - 300 moose /1,000km^2) (Environment Yukon moose surveys – Jessup et *al.* 2014, Taylor et *al.* 2011, Clarke et *al.* 2013 respectively). There are two caribou populations in the study area, the Ibex and Carcross herds. Most of their winter range falls within the study area; however, in summer they disperse to cover a larger territory.

Other large carnivores present in the study area include grizzly bear (*Ursus arctos*) and black bear (*Ursus americanus)*. Smaller carnivores include the lynx (*Lynx canadensis*), wolverine (*Gulo gulo)*, coyote (*Canis latrans)* and red fox (V*ulpes vulpes fulva)*.

Our chosen study area was designed to incorporate portions of both the Carcross and Ibex caribou ranges (see Figure 2), and totalled 8,452km^2. Study boundaries were selected to follow natural home-range boundaries (e.g., lakes and high mountain ridgelines) thought to be physical barriers for wolf movements.

Methods

Collar deployment

To monitor wolf movements and kill sites, and to determine the extent of their territories, we captured and collared wolves during the three winters between 2019 and 2022. We used a combination of ground-based trapping and helicopter net gunning to capture wolves (see Government of Yukon's wolf capture methods assessment, in prep.). Captured wolves were fitted with satellite GPS collars (Vectronics, GPS Plus Lite, Germany), programmed to record locations once every 2 or 4 hours. Humane capture protocols for both methods were approved by the Government of Yukon's Wildlife Care Committee.

Kill site identification

To determine kill site locations, we identified GPS clusters using a location data-clustering algorithm in Python (Python version 3.10.5, www.python.org) which was originally developed to identify potential kill-site (PKS) clusters from cougar data (Knopff et al. 2009), but was later modified for wolf kill sites (Webb et al. 2008).

We defined a cluster as a series of relocations wherein each relocation was within 300 m and 4 days of a previous location point. All points were included as a cluster if these two qualifications were concurrently met (Webb et al.2008). In winter 2020 - 2021 we prioritized visiting clusters where we identified at least six relocations. This ensured that an individual had spent greater than 20 hours at the site. We established this parameter based on the average handling times that similar-sized wolf packs took to consume an adult caribou (mean = 1.3 days, standard error [SE] = 0.1 days) or moose (>48 hours) (Hayes 1995). We assumed these minimal criteria would aid in identifying all adult moose and caribou killed by collared wolf packs. We acknowledge that yearling caribou or calves could be consumed at a faster rate and, therefore, all of our established kill and handling rates should be considered as minimum estimates.

In the winter of 2021-2022 we modified our consumption rate assumption by lowering our criteria for a cluster-site visitation to only 3 relocations, which approximated a wolf being onsite for approximately 10 hours. This increased the number of PKS and visitations.

Kill site Investigation

We visited PKS clusters for four wolf packs between December 2020 and March 2021, and one pack between November 2021 and March 2022. PKS clusters were visited between 5 and 45 days (mean = 14, SE = 2.1) after the first GPS location at the PKS.

Upon arrival at the PKS we searched for signs of wolf activity (bed sites, scat, tracks, and scent marking) and prey carcass remains (hair, bones, rumen, blood). A cluster was determined to be a kill site when there was strong evidence of an animal being killed by a wolf, and the remains were estimated to be of an age that matched the known dates when wolves were present (Sand et al. 2008, Webb et al. 2008). Ungulates were assumed to have been killed by wolves where observed tracks of ungulate and wolf corresponded in age and there was such an abundance of wolf tracks as to suggest wolves had remained on site. Further, the carcasses needed to be scattered and disarticulated, as opposed to being cached which would have indicated a bear kill (Logan and Irwin, 1985). It should be noted, we chose to do predation monitoring between November 25 and March 30. It was assumed bears would be denning and therefore unlikely to have killed any ungulates.

If possible, the remains were identified to species and sex, through an examination of their anatomical, skeletal and pelage characteristics (Stelfox 1993). When possible, we also assigned prey into two age classes, either adult (≥2 yr) or yearling (>1yr but <2yr). No calves or lambs were confirmed. This was accomplished by examining bone, antler or horn size, the tooth wear, and the degree of epiphysis fusion (Stelfox 1993). All kills were identified to species; however, in cases where the sex of the prey could not be identified (70%), kills were recorded as 'adult sex unknown' or 'yearling sex unknown' and where age of prey could not be identified (60%), kills were recorded as either 'moose age unknown', 'caribou age unknown' or' sheep age unknown'. Confirmed kills were assigned a date based on the first GPS location at the PKS.

Wolf prey composition

We defined prey composition in two ways. First, we defined it as the numbers of each prey species killed by wolves and, second, we calculated the percent biomass consumed for each ungulate prey species. The consumed biomass was measured in kilograms (kg).

To determine overall mean prey compositions for both metrics, we calculated the averages among packs. Estimates of weights used for prey biomass calculations are provided in Appendix, Table A2.

Wolf kill rates

We defined total kill rate as the number of ungulates killed per wolf in a pack, per day (ungulates killed / wolf / day). All wolves in a pack were included in the calculation, regardless of their age.
We divided the number of kills by the number of consecutive days the wolf pack was monitored. Kill rates for each ungulate species were also estimated; for example, the number of moose / wolf / day. To estimate an approximate number of each prey species killed over the total winter period (Oct 1 – March 31), we used species-specific kill rates timed by 182 days for each pack.

We estimated the size of each pack multiple times a season. Estimates were made, opportunistically, through track counts during ground-trapping efforts and aerial observations made during capture and kill site investigations. We also estimated pack sizes during a wolf population survey in 2022. For those wolf packs whose size changed over the monitoring period, we used the average pack size to calculate kill rates per wolf. Pack sizes are reported in Table 1.

Biomass consumption rates were defined as the amount in kg of ungulate consumed by kg of wolf in a day, (kg ungulates / kg wolf / day).
For moose and Dall sheep, we used the same weights as Hayes et al. (1991), applied in their early Southern Lakes predation study. For caribou we used sex and age specific weights based on Russell (2010) (See Appendix Table A1 for prey and wolf weights). Recognizing that bones, hide and rumen are not consumed by wolves, we chose to use an edible consumption weight of 75% of total weight following Hayes et al. (1991). We did not know the sex or age of wolf pack members and, therefore, followed wolf weights established by Hayes et al. (1991). We used 35 kg, which is the average weight of a wolf during winter.

The above measures were chosen because they are common metrics in the literature and, therefore, allowed us to make comparisons with other studies (Hayes et al.1991, Webb et al.2008, Mech and Boitani. 2003, Dale et al. 1995, Ballard et al. 1987).

Handling times of ungulate prey

We evaluated the wolves handling times of prey to assess if the minimum times we used to identify potential kill site clusters were reliable.

The definition for 'handling time' includes the entire time between the first and last wolf location within 300m of the kill. This included time that wolves spent away from the carcass. As long as they returned within 4 days, we assumed returning wolves continued to obtain significant biomass from the carcass.

We estimated wolf handling times for prey using cluster analysis (Python, version 3.10.5, www.python.org). We estimated average handling times for each species by pooling all kills, across packs. We report the standard deviation (SD) and range.

Results

Over the course of this study, we collared eight wolves among five packs. We had hoped to monitor additional packs in the southern portion of the study area, but due to a combination of collar failures, wolf mortalities and logistical concerns, this was not achievable.

GPS fix rates, across the five monitored packs, averaged ≥95% (range: 90-100%). Therefore, we assumed the influence of habitat-induced GPS bias was minimal. We monitored the daily movements of five packs during December 2020 to March 2021 (four packs) and November 2021 to March 2022 (one pack). Each pack was monitored for an average of 80 days (SD = 39.5, range = 45-129). There was a grand total of 399 monitoring days.

Through cluster modelling, we identified 124 potential kill sites. We visited all locations and found 49 *ungulate* kill sites (20 moose, 22 caribou and 7 Dall sheep). Clusters that were not deemed kill sites included bedding sites (n = 18), non-descript sites (n = 36) and scavenging sites (trappers bait sites or the Whitehorse landfill) (n = 21). There was also one scavenging site where the carcass age indicated it was killed outside of our monitoring period. Scavenging sites where wolves did not make the kill were not included in the analysis because their consumption biomass could not be determined.

Where two wolves were collared in one pack, we visually compared GPS cluster data from both individuals in ArcGIS 10.7.1 and found both wolves were present at 100% of the PKS (n = 56). We therefore assumed that all pack members were present at all kill sites, no further adjustments were made.

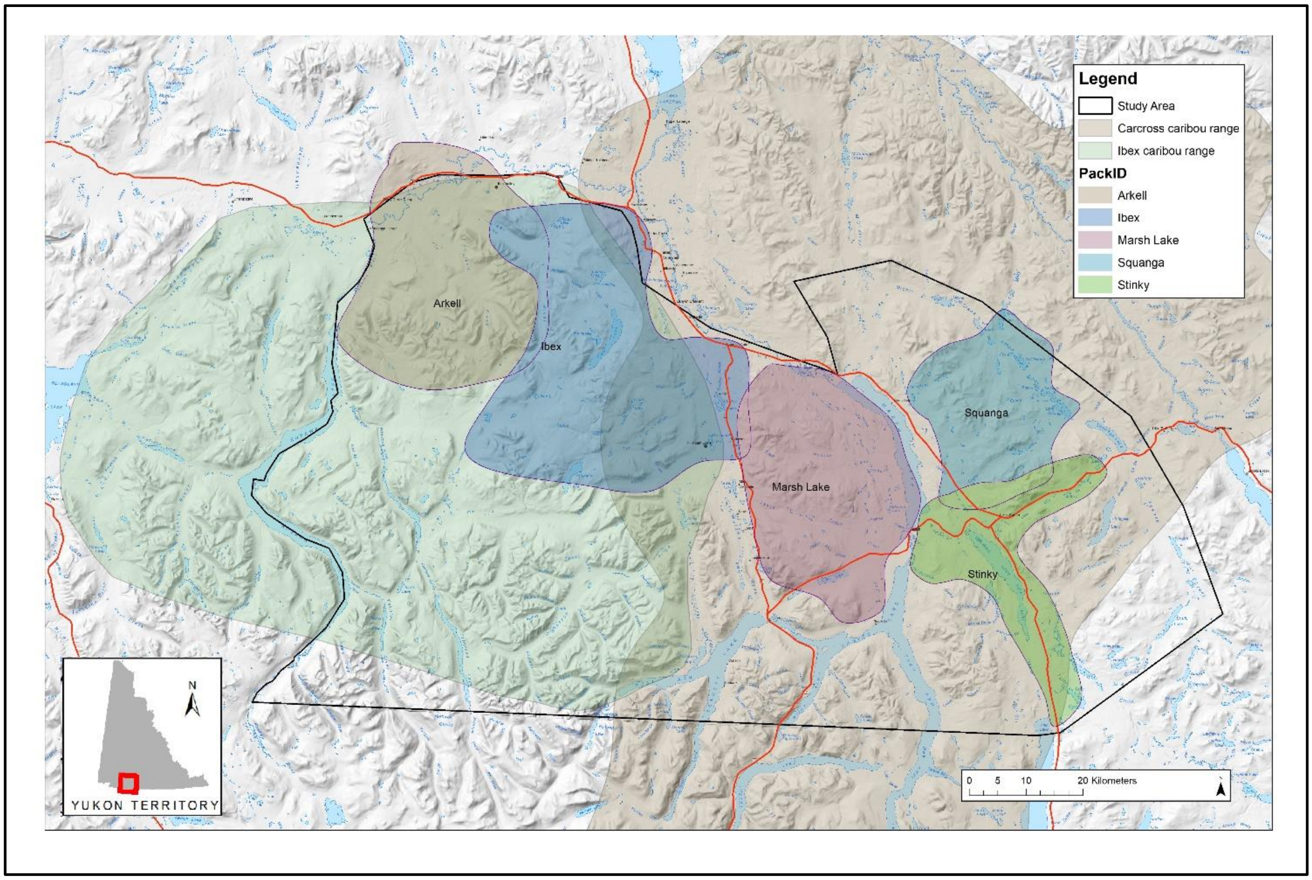

Figure 2. Home ranges of monitored wolf packs (2020-2022) showing overlap with Ibex and Carcross caribou herd ranges, Southern Lakes, Yukon.

Of the five monitored packs, one pack (Ibex pack), was found to frequent the Whitehorse landfill, consuming a high portion of their diet from that location. Of the 15 PKS identified for this pack, only one was a kill site, 11 were associated with the landfill, and 3 were non-kill sites. Due to this pack's anomalous behaviours and because only one kill site was identified during its 45-day monitoring period, we calculated its kill rates separately and chose not to include the data when reporting overall means for wolf kill rates, biomass consumption and diet composition.

When we expanded field verifications by intensifying our sampling to include all PKS where wolves had remained for ≥10 hours (winter 2021 – 2022, n = 1 pack), no moose or caribou kill sites were identified at sites where wolves spent ≤ 20 hours. This provided support that our original cluster parameter (≥ 20 hours) was appropriate, and moose and caribou kills were not underestimated from the previous winter. Nevertheless, we did find five of the seven Dall sheep kill sites were consumed in under 20 hours (See Handling times below).

Composition of prey

Prey species numbers varied considerably among the four packs (moose: SD = 29.8, range 18 – 87%; caribou: SD = 18.8, range 12.5 – 57%; Dall sheep SD = 12.5, range 0 – 25%). Yet, when we disregarded the separate packs and pooled all of their individual kills, moose were the primary prey (59%), caribou represented 35% and Dall sheep were 6%. When we converted the individual kills into biomass (weight) consumed, there was also considerable variation among the packs (moose: SD = 23.9, range: 42 - 95%, caribou: SD = 18.6 range: 5 - 47%; Dall's sheep: SD= 5.5, range: 0 – 11%). However, when all kill weights were pooled, once again, moose were the primary prey (77%), caribou represented 20% and Dall sheep were 3%.

Kill rates

Among the four packs, winter kill rates averaged 0.13 ungulates/pack/day (n = 4, SD = 0.06, range: 0.07 – 0.22). This equated to 0.018 ungulates/wolf/day (SD = 0.006, range: 0.013 – 0.027).

Daily wolf consumption rates averaged 3.49 kg ungulate/wolf/day (n = 4, SD = 0.30, range: 3.30 – 3.93). This equated to 0.10 kg ungulate/kg wolf/ day (SD = 0.01, range: 0.09 – 0.11).

The Ibex pack only killed a single caribou, resulting in a very low kill rate (0.003 ungulates/wolf/day) and consumption rate (0.01 kg ungulate/ kg wolf/ day) compared to the other packs.

For species-specific kill rates, pack average kill rates of moose were 0.009 moose / wolf / day (n = 4, SD = 0.003, range: 0.005 – 0.012), for caribou 0.007 caribou / wolf/ day, (SD = 0.006, range: 0.002 – 0.016) and Dall sheep 0.002 (SD = 0.003, range: 0 – 0.007).

If we were to assume wolves continued to kill caribou, moose and Dall sheep at these rates over the entire winter (Oct 1 – March 31), the five packs would prey on a total of 44 moose, 43 caribou and 10 Dall sheep. Based on kill rates of the Ibex pack an additional 4 caribou would also have been killed.

Handling times

The average time it took for a pack to consume a moose (handling time) was 5 days (n = 20, SD = 2.61, range: 1- 11.2 days). Average handling time for caribou was 1.7 days (n = 21, SD = 0.78, range: 0.9 – 2.8) and for Dall sheep it was 0.9 days, (n = 7, SD = 0.36, range: 0.6 – 1.5, n = 7).

Table 1. Kill rates and biomass consumption of four wolf packs during late winter 2020 – 2021 and one pack in winter 2021 - 2022, Southern Lakes study area, Yukon

Pack name	Pack size	No. days studied	No. of Kills: Moose	No. of Kills: Caribou	No. of Kills: Sheep	Predation and Consumption Rate: Total kg killed	Ungulate/ pack/day	Ungulate/ wolf/day	Kg consumed/ wolf/day	Kg consumed/ kg wolf/day[a]	# caribou killed/ winter[b]	# moose killed/ winter[b]	# sheep killed/ winter[b]
Marsh	8	66	5	2	0	2327	0.11	0.013	3.30	0.09	6	14	0
Squanga	7	45	3	2	0	1394	0.11	0.016	3.32	0.09	8	12	0
Stinky Crk	5	114	7	1	0	2990	0.07	0.014	3.93	0.11	2	11	0
Arkell	8	129	5	16	7	4691	0.22	0.027	3.40	0.10	23	7	10
Ibex[c]	7	45	0	1	0	157	0.02	0.003	0.37	0.01	4	0	0
Mean	7	80	N/A	N/A	N/A	2851	0.13	0.018	3.49	0.10	N/A	N/A	N/A
SD	1.4	39.5	N/A	N/A	N/A	1391	0.06	0.006	0.30	0.01	N/A	N/A	N/A
Totals	35	399	20	22	7	N/A	N/A	N/A	N/A	N/A	43	44	10

[a] See Appendix A2 for details of prey and wolf weights used. Unclassified moose, caribou and sheep were assumed to be adults.
[b] Calculated by multiplying daily, species specific kill rate by 182 days (October 1 – March 31).
[c] The ibex pack was not included when calculating mean kill rate and biomass consumption rates (see Methods for rationale).

Discussion

Diet composition

In winter, wolves in the Southern Lakes study area were killing and consuming moose, caribou and, to a lesser degree, Dall sheep. We found that caribou have become a larger proportion of the wolf's diet since they were last studied in the late 1980's, when Hayes et al. (1991) estimated the caribou population to be 350 animals (Farnell, 1982). Given the increase in availability of caribou, (approximately 4,000 caribou across 4 herds) it is not surprising wolves are killing more caribou.

It is noteworthy, the increase in caribou has occurred concurrently with the closure of the licensed hunt and the voluntary support of the First Nations, who have not been harvesting caribou since the 1990's. This increase in caribou population size occurred without predator controls.

In our study, kill composition varied considerably across packs. The percentage of moose killed ranged from 18 – 87%. The range for caribou killed was 12.5 - 57%. When averaging kill composition across packs, moose represented 59% (SD=29.8) and was the dominant prey in three out of the five packs. Caribou, representing 35% (SD = 18.8) of prey killed, was the dominant prey for one pack. The remaining pack relied heavily on the Whitehorse landfill as a food source, making only 1 kill over the study period.

In terms of biomass consumption, our study showed that moose made up 77% of the wolves' diet, caribou 20% and Dall sheep 11%. Other Yukon studies have also demonstrated similar wolf prey preference. For example, in the Finlayson area, wolves preyed upon more moose (n = 40) in comparison to caribou (n = 20) (Finlayson Study, Hayes, 1995). Further, in portions of the Finlayson area, where moose and caribou densities were relatively equal, moose comprised 89% of individuals killed and 94% of the biomass consumed (Hayes 1995). Similar findings have been observed in other North American studies (Seip 1992, Stotyn 2008, McNay 2003).

To account for this, Hayes (1995) concluded that wolves select for moose, over the more available caribou, because wolves have been entrained on moose and have developed successful hunting strategies. In general, moose demonstrate more predictable behaviours, with less seasonal range shifts than caribou, and moose, from an energetics perspective, are highly profitable.

It is possible that changes in moose and/or caribou densities may affect wolf selectivity (Hayes and Harestad 2000). For example, an increase in moose populations could create a concurrent increase in wolf numbers (Messier 1995, Hayes and Harestad, 2000). In turn, this could lead to an increase in caribou predation, because there are more wolves. This may occur even if caribou remained as the alternative prey species, a dynamic referred to as "apparent completion" (Holt 1977, Hatcher et al. 2006, Siep, 2008).

Variability in a pack's diet

The three monitored packs in the eastern portion of our study area (Marsh Lake, Stinky and Squanga packs) overlapped spatially and temporally with the Carcross caribou herd's winter range (see Figure

2). Given this ubiquitous availability, it would appear the prey composition was similar among all three packs, with caribou only representing 5 -16 % of the biomass, or 12.5 to 40% of the individual ungulates killed. Moose were clearly the primary prey for all three packs. There was one exception to this trend, the Arkell pack, located in the northwest of the study area, which overlapped with the Ibex herd's core winter range. This pack exhibited a preference for caribou. Caribou represented 57% of ungulates killed in comparison to 18% moose and 25% Dall sheep.

Significant evidence exists to support that prey composition and predation rates can vary widely even within study areas (Mech and Boitani, 2003). Variations in kill compositions may be accounted for by small-scale differences in composition and densities of prey, resulting from differences in landscape features across home ranges (Stotyn 2008). For example, the territories of the Marsh Lake, Stinky and Squanga packs all consist of mainly forested, lower elevation land, intersected by lake systems. In contrast, the home range of the Arkell pack is characterized by higher elevation alpine plateaus and mountains. A habitat that is better suited to caribou than moose. Although detailed moose density data is lacking, if lower moose densities exist, this may explain the higher proportions of caribou in the Arkell pack's diet. The vulnerability of caribou in this area may also have been a factor. For example, Dale et al. (1995) suggested that in Gates of the Arctic National Park, AK, wintering caribou utilized wind blown ridge lines that had little snow cover. He identified wolf tracks and locations of kill sites that suggested wolves were chasing caribou from these ridges into deep snow, rough terrain and relatively dense vegetation. We observed similar signs of this behaviour in the Arkell pack's territory. Conversely, caribou that overlap with the Marsh Lake, Stinky and Squanga packs' territories utilize wintering ranges that are associated with open pine forest (Jaylene Goorts, personal coms.). Locating and hunting caribou in these areas maybe more challenging.

Increasing our sample sizes and determining prey densities in home ranges are needed if we are to confirm whether the witnessed differences are consistent with variation in the kill composition of the wolf packs. Understanding prey density, specifically caribou, would allow us to determine whether the proportion of caribou killed differed relative to their availability.

A noteworthy finding occurred when examining the dietary behaviour of the Ibex pack, which denned approximately 1 km from the town of Whitehorse's landfill during summer and in winter spent most of its time in close proximity to the landfill (<3 km). This pack relied heavily on the Whitehorse landfill for food. As such, they had a kill rate that was six times lower than the other packs, and they also had a biomass consumption rate that was one tenth of the average. In comparison to the other packs, they exerted less impact on moose and caribou in their territory.

Additionally, through frequent territorial boundary forays, this pack continued to maintain a similar-sized home range as those of the other wolf packs in the Southern lakes area (1200 Km^2) (Fig.2). Based on GPS locations from the Ibex pack and the frequency of detectable kill sites in adjacent pack's territories, it can be argued, that neighbouring packs were unlikely to be killing prey within the Ibex's home range. Therefore, a quasi refuge may exist for moose and caribou within this area. Interestingly, the Ibex pack's home range covers a significant and important proportion of the Ibex caribou herds' range. Perhaps this quasi refuge has aided in the herd's recovery.

Kill rates and biomass consumption

Kill rates are an important metric to determine the impacts that wolves are having on their prey and to determine the amount of food they are consuming. That stated, it is important to recognize that in this study we only report on kill rates from late winter. These kill rates cannot be extrapolated to snow-free periods because of the influences of snow depth, seasonal pack cohesiveness, spatial arrangement of predators and prey, and changing prey vulnerabilities (Hebblewhite et al. 2003; Jedrzejewski et al. 2002; Thurber and Peterson 1993; Huggard 1993; Nelson and Mech 1986). Further, we cannot estimate the proportion of the moose and caribou populations that are removed, as density estimates for these populations are unknown. However, we are able to determine kill rates and biomass consumption of wolves in winter and then compare these values to studies across North America to determine if Yukon's rates are similar to wolf populations elsewhere.

In studying predation, the numerical kills among differing populations of wolves can vary widely due to differences in their prey's numbers, their pack handling times, the prey vulnerability and seasonal affects (Hayes 2000, Stotyn 2005, Mech and Boitani 2003). For this reason, when attempting to compare kill rates among studies, the per capita amount of biomass eaten by wolves per day is the standard (Jedrzejewski et al. 2002).

In our study, the biomass consumption rate for the four monitored packs in the Southern Lakes averaged 3.49 kg ungulate/ wolf/day (SD = 0.30, range: 3.30 – 3.93). This rate is at the lower end of a previous Southern Lakes study that found consumption rates ranging from 1.8 to 23 kg/wolf/day. (Hayes et al. 1991). Our study's rate was also lower when compared to a study done in the Finlayson Lake area which found a consumption rate ranging from 4.1 – 6.4 kg ungulate / wolf / day (Hayes et al. 2000). It is well documented that pack size can influence biomass consumption rates (Hayes et al. 2000). To determine if our packs consumption rates were on par with those from these other Yukon studies, we compared our rates to a subsample of similar-sized packs from the Hayes' (1991) study (4-8 wolves / pack, n = 7). We found that the similar-sized packs from the Hayes study had comparable consumption rates (4.15 kg ungulate/ wolf / day (SD = 1.4, range: 2.40 – 6.75).

Individual wolves require between 1.7 and 4.0 kg of food per day to survive (Peterson et al. 2003, Thurber and Peterson, 1993) and at least 3.3 kg per day to reproduce (Peterson et al. 2003). In our study, wolves met the lower range of the reproduction requirements, suggesting that wolves are just obtaining enough prey to successfully reproduce.

Our kill rate of 0.018 ungulates / wolf / day (SD = 0.006 range: 0.013 – 0.027) is lower than previously established rates by Hayes et al. (1991) for similar sized packs in the Southern Lakes (0.025 ungulates / wolf / day, SD= 0.01), but still fell within the lower end of the predicted range (range: 0.011 – 0.043 ungulates/wolf/day).

Perhaps lower kill and consumption rates in our study can be explained by the lower moose and wolf densities found in the Southern Lakes area. Based on 27 studies of moose-wolf interactions, Messier (1994), suggested kill rate was strongly related to moose density. Moose densities in the Southern Lakes are low compared to the studies used in Messier's review and, therefore, based on his models, lower kill rates would be expected.

Handling times of prey

We found that wolves utilized carcasses for a longer period than previously estimated. Handling times for both moose (5.0 days, SD = 2.61, range: 1- 11.2 days, n = 20) and caribou (1.7, SD = 0.78, range: 0.9 – 2.8 days, n = 21) were longer than those reported in other Yukon, Alaskan and Alberta studies (3.7 days per moose Hayes et al. 1991; 1.3 days per caribou Hayes et al. 2000; 2.7 days per moose, Ballard et al. 1987; 2.5 days per moose, Fuller and Keith 1980). It is likely that some of the variation in these reported handling times is the result of differences in the methods used to track wolves. For example, using high frequency (2 or 4 hour) GPS location data, we were able to detect all occurrences when a wolf left and returned to a carcass. Detections of movement in such detail, conceivably extended the handling times compared to those done by single daily aerial relocations in previous studies (Hayes 1995, Ballard et al. 1987 and Fuller and Keith 1980). In the previous studies, some handling events could have been prematurely assessed as concluded by the researcher due to the wrong determination of when wolves had left the carcass.

Handling times for moose carcasses in the Southern Lakes were similar to times reported by Johnson et al. (2017) who also used a similar monitoring technique to ours. They used GPS collar data in a low-density area of north-central Alaska (4.0 days, SD=2.5, range 1-16 days). Given the low density they witnessed, they speculated that longer times at the carcass may be a function of prey density such that, where prey densities are low, wolves spend greater time with the carcass to maximize all available biomass. Long handling times may also reflect the larger effort required to secure a kill in a low prey-density system, as competition for the available food resources (carcasses) may be great. Although the current moose density for the Southern Lakes is not known, the 2010 estimate of 0.15 moose/km^2 was similar to Johnson et al. (2017) whose experimental area had a density of <0.2 moose/km^2. Lending support to this speculation, during our kill site investigations, we found that 90% of all carcasses were consumed.

Extrapolating kill rates

If we were to assume wolves continued to kill caribou and moose at the above defined rates, we estimate the four packs would predate on 44 moose, 43 caribou and 10 sheep over the entire winter (Oct 1 – March 31). There are many assumptions in estimating wolf predation in this manner, such as no change in pack size, prey vulnerability, prey availability, or climatic variation such as snow depth and ice cover (Sand et.al 2008, Knamiller, 2011, Metz et al. 2011). For these reasons we caution against extrapolating kill rates across other non-monitored packs in the study area or in other years. Following this rationale, we avoided estimating an annual predation rate for moose and caribou in this study.

Reliability of cluster model parameters

For moose, we are confident that our model parameters (≥ 20 hours) detected the majority of moose kills during the winter period. This is supported by the fact that the shortest handling time was 24 hours (n = 1), whereas all other kills were ≥ 24 hours (n = 19) and averaged 5.0 days (n = 20).

For caribou, we found the shortest handling time was 20 hours (n= 1), all other kills were ≥ 24 hours and averaged 1.7 days (n = 20).

In total, we found seven kills that were Dall sheep and each of these were consumed in under 20 hours. We did not attempt to assign potentially missed Dall sheep to the other monitored packs due to the assumptions involved. It is therefore possible that some Dall sheep kills were missed.

To improve confidence in detecting smaller bodied prey, a more conservative handling time criteria is recommended. To meet this objective, a larger budget would be required to compensate for the increased site visits.

Conclusions and recommendations

Using GPS cluster analysis, our study was successful in estimating late winter kill rates and prey compositions for five wolf packs.

We found low kill rates and longer handling times compared to other North American studies, yet our results were like low density predator – prey systems in Alaska (Johnson et al. 2017). Recently, the Government of Yukon completed population surveys for wolf (2022), moose (2021) and caribou (2019) in the Southern Lakes. These newly established estimates will help determine current population densities and population trajectories for the three species.

The Yukon Wolf Conservation and Management Plan (2012) endorses community wolf trapping programs as a management tool to reduce predation by wolves. In the future, if communities were to consider a program where the goal was to increase a caribou population, targeting wolf packs that utilize caribou as a substantial portion of their diet may help direct efforts to promote recovery.

Going forward, if the Government of Yukon were to re-establish a licenced hunt for caribou in the Southern Lakes area, careful consideration should be given to ensure the needs of both hunter and predators. Wildlife management should account for natural predation losses before adjusting harvest levels to satisfy hunting interests; otherwise, caribou and moose population instability will certainly occur (Hayes, 1991).

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APPENDIX 1

Table A 2. The weights of moose, caribou and Dall sheep prey used in Southern Lakes predation rate studies.

Species	Age [a]	Sex	Live Wt. (kg)[b]	Available kg[c]	Source
Moose	Adult	Female	400	300	Hayes 91
	Adult	Male	454	340	Hayes 91
	Adult	Unknown	427	320	Hayes 91
	Yearling	Unknown	278	209	Hayes 91
	Unknown	Unknown	352	264	our calculation[d]
Caribou	Adult	Female	135	100	Russell
	Adult	Male	180	135	Russell
	Adult	Unknown	157	118	Russell
	Unknown	Unknown	105	79	our calculation[e]
Dall sheep[f]	Adult	Female	55	41	Hayes 91
	Adult	Male	82	61	Hayes 91
	Adult	Unknown	68	51	Hayes 91
Wolf[g]	Unknown	Unknown	35	N/A	Hayes 91

[a] No moose calves, caribou yearling or calves or lambs were identified at kill sites, therefore weights are not reported.
[b] Assumed prey weights did not change over the study period (Dec- March).
[c] Assumed that 75% of live weights of all prey types were potentially available to wolves.
[d] Calculated as the average weight of adult unknown sex and yearling unknown.
[e] Calculated as the average weight of adult unknown sex and yearling unknown sex (55kg)
[f] All sheep kills were found mid winter (Dec 20 – Jan 28). Therefore, we assigned based on the average weight of early / late winter weights identified by Hayes 91.
[g] Based on average wolf weights during winter (n=135 wolves) for packs >2 (including pups, yearling and adults) (Hayes 1991)

Table A 3. Percentage of prey items killed and biomass consumed by wolves in winter (2021-2022 and 2021-2022) in the Southern Lakes wolf study area.

	% Killed prey items			% Biomass consumed		
Pack name	Moose	Caribou	Sheep	Moose	Caribou	Sheep
Marsh L	71	29	0	90	10	0
Squanga	60	40	0	81	19	0
Stinky	88	13	0	95	5	0
Arkell	18	57	25	42	47	11
Ibex	0	100	0	0	100	0
Mean[a]	59	35	25	77	20	3
SD	30	19	N/A	24	19	6

[a] The Ibex pack was not included when calculating mean kill rate and biomass consumption rates (see Methods for rationale).