WOLF PREDATION ON MOOSE IN NORTH–CENTRAL BRITISH COLUMBIA

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ABSTRACT: Moose populations declined substantially following widespread salvage logging of mountain pine beetle affected forests in interior British Columbia (B.C.) in the 2000s. The impact of wolf predation on moose was not well-understood in the context of extensive landscape change. We monitored 33 wolves across 11 packs in 2 interior B.C. study areas: Prince George South (PGS), characterized by extensive salvage logging features, and John Prince Research Forest (JPRF), also affected by salvage logging but less intensively. Because predation risk is a function of wolf density, space use, and predation patterns, we required a better understanding of these factors to develop management recommendations that could minimize predation risk to moose. Based on mid-winter pack counts and home range size, wolf density was about 10 wolves/1,000 km^2 in PGS and 5 wolves/1,000 km^2 in JPRF. We identified 290 kills made by wolves, predominantly moose in PGS (87%) and JPRF (75%). Wolves in JPRF preyed on more elk and deer than did wolves in PGS, and at 10% of the kill sites we investigated in JPRF, wolves had killed black bears. We found moose calves at 27% of the moose kill sites, compared with mid-winter estimates of standing proportions of calves in the population of 13–20%. After accounting for probability of the collared wolf attending pack kills, we calculated that wolf packs in PGS killed a moose every 4-8 days in winter and every 8–11 days in summer. In JPRF, wolf packs killed a moose every 7–12 days in winter and every 19–26 days in summer. However, when we considered the number of wolves per pack in the 2 study areas, the kill rates per wolf were similar. Based on recent midwinter moose density estimates, these kill rates would equate to 7–20% of the moose population for PGS and 2–8% of the moose population for JPRF. These predation rates may not be indicative of predation rates during the moose decline in the 2000s, so it is important to consider the mechanisms that could contribute to changing kill rates, including differential use by wolves and moose of highly modified landscapes and landscapes exposed to recent change such as widespread logging or wildfire. Based on our 2 study areas, extensive salvage logging creates habitat features that may support higher wolf densities and larger pack sizes, particularly in landscapes where moose are the dominant ungulate species.

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Key Words: *Alces alces*, *Canis lupus*, kill rate, kill site, moose, predation rate, predation risk, probability of attendance, wolf

Moose (*Alces alces*) are an important component of the ecological and sociocultural fabric of interior British Columbia (B.C., hereafter). They are a key species for consumptive and non-consumptive users, support rural and remote communities, and are critical to the

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cultural persistence of First Nations (B.C. FLNRO 2015, Gorley 2016). A mountain pine beetle (*Dendroctonus ponderosae*) outbreak in the late 1990s and early 2000s in central B.C. resulted in widespread lodgepole pine (*Pinus contorta*) mortality and subsequent salvage logging to reduce the spread and maximize utilization of dead standing pine (Alfaro et al. 2015). Moose populations declined over the same period throughout interior B.C. (Kuzyk 2016, Kuzyk et al. 2018).

In 2013, the B.C. provincial government initiated a research project to determine the effects of landscape change on moose populations (Kuzyk and Heard 2014, Kuzyk et al. 2019, Anderson et al. 2023). One of the knowledge gaps consistently identified by biologists, First Nations, and stakeholders was the role of wolf (*Canis lupus*) predation in moose declines in multi-prey, multi-predator systems (Kuzyk and Heard 2014, B.C. FLNRO 2014, Kuzyk et al. 2019). Wolves are an important cause of moose mortality (Gasaway et al. 1992, Bergerud and Elliot 1998, Hayes et al. 2003, Patterson et al. 2013, Mumma and Gillingham 2019), but several factors influence the vulnerability of moose to wolves. Many of these variables, including wolf density, pack structure, space use, and predation patterns are not well studied in interior B.C. Measuring wolf density or population trend is complicated and expensive, and relatively few wolf inventories have been done in B.C. (Kuzyk and Hatter 2014, Mowat et al. 2022). Wolves are not a species of conservation concern due to their high reproductive rates, adaptable life history, and high dispersal rates, thus inventories have not been prioritized. Instead, wolf density has been estimated provincially by an ungulate biomass index (Fuller et al. 2003, B.C. FLNRO 2014, Kuzyk and Hatter 2014).

Our objective was to determine wolf density and predation patterns in 2 study areas overlapping the provincial moose research study areas. Although we were not able to assess wolf predation during the moose declines, we were able to examine wolf predation in 2 study areas of different disturbance regimes, a spatial proxy to investigate a mechanism that could have been consistent over time.

STUDY AREA

Both study areas were in north-central B.C. on the Interior Plateau, with rolling terrain approximately 800–1,500 m elevation, and characterized by a mosaic of coniferous and deciduous forests, lakes, and wetlands. The Prince George South (PGS) study area was located from the city of Prince George west to approximately the municipality of Vanderhoof, and from Highway 16 south to the Blackwater River. The John Prince Research Forest (JPRF) study area was centered approximately over the research forest, from Fort St. James and the north shore of Stuart Lake north along the North Road to Inzana Lake in the east and Tchentlo Lake in the west. The dominant biogeoclimatic zones are Sub-Boreal Spruce, Sub-Boreal Pine–Spruce and Engelmann Spruce–Subalpine Fir at higher elevations (Meidinger and Pojar 1991). Dominant tree species varied by microsite, and included Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), hybrid white spruce (*Picea glauca x engelmannii*), subalpine fir (*Abies lasiocarpa*), trembling aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), and paper birch (*Betula papyrifera*). Summers were warm and dry (mean July temperature for study period was 16.3°C), and winters were cold (mean January temperature for study period was -6.5°C) with complete snow coverage (average maximum snow depth 55 cm) from November to March (ECCC 2024 for Fort St. James and Prince George airport weather stations).

Wildfires and forest harvesting were the dominant agents of landscape change, and the area underwent large-scale timber salvage harvesting following a mountain pine beetle outbreak in the early 2000s. We delineated study areas using the outer boundary of all wolf pack home ranges, 4,594 km^2 in PGS and 4,119 km^2 in JPRF (Figure 1). These study areas were chosen to approximate the moose study areas using the same names on a provincial moose research project (Kuzyk and Heard 2014, Kuzyk et al. 2019).

Moose were the dominant ungulate in both study areas. Rocky Mountain elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) are present in both study areas, although at higher densities in JPRF. White-tailed deer (*Odocoileus virginianus*) were also present at low densities in both study areas. Caribou (*Rangifer tarandus*) were absent from PGS but had been observed in JPRF, although infrequently. Domestic cattle (*Bos taurus*) were present on ranches and range tenures (public lands)

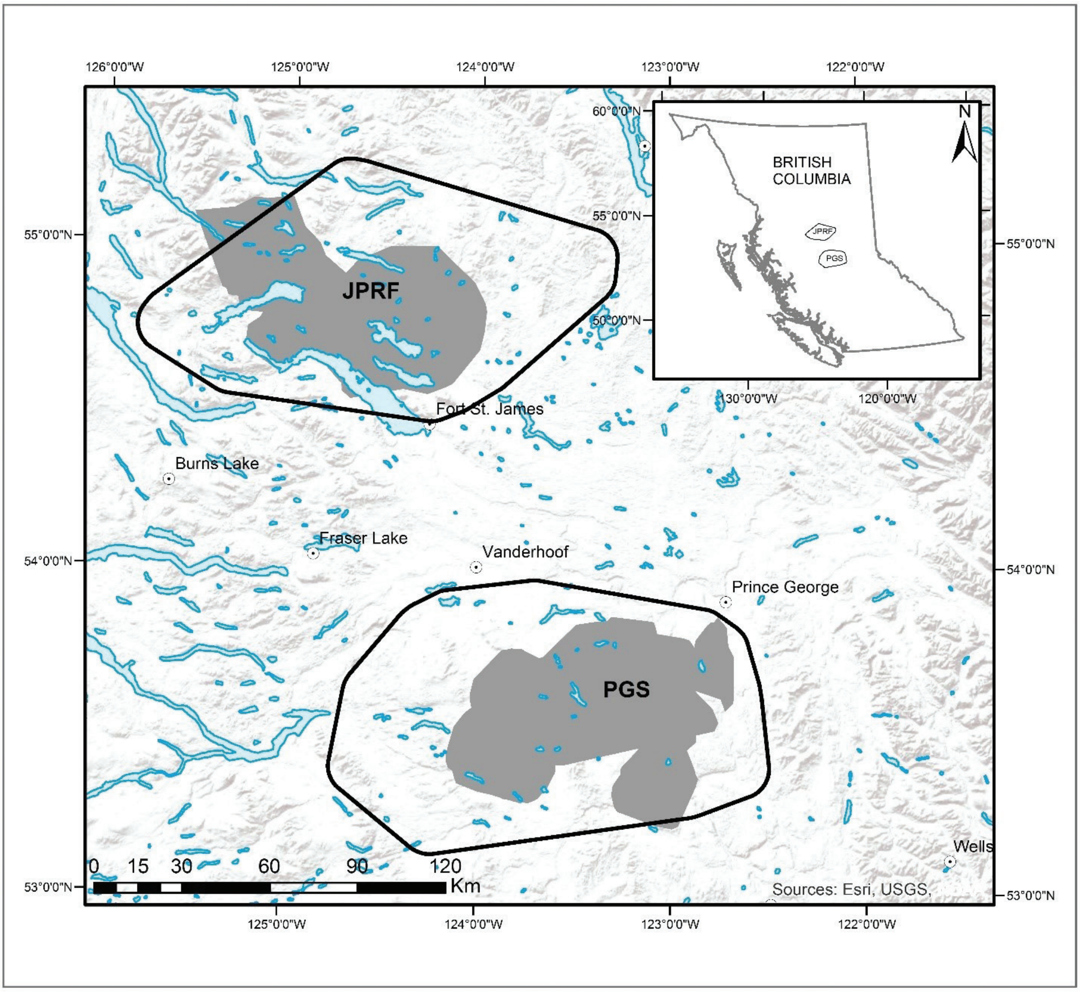

Fig. 1. Prince George South (PGS) and John Prince Research Forest (JPRF) study areas (grey shading) for wolf predation research 2018-2022. Study areas for the partner project assessing mechanisms of moose decline are indicated as well (black outline).

during the summer. Besides wolves, large carnivores included black bears (*Ursus americanus*), grizzly bears (*U. arctos*) and cougars (*Puma concolor*). There were active wolf trappers in both PGS and JPRF and a liberal licensed hunting season, but effort varied and harvest monitoring was not reliable at a fine scale (Mowat et al. 2022).

METHODS

Between June 2018 and February 2021, we captured 34 wolves with soft-catch foot-hold traps (Livestock Protection EZ Grip #7) in summer and helicopter darting or net-gunning in winter. We chemically immobilized wolves with Zoletil™ (tiletamine-zolazepam) at 6–8 mg/kg. Once immobilized, we fitted wolves with radio-collars (VHF collars, Lotek Wireless, Newmarket, ON, Canada, or satellite GPS collars, Vectronic Aerospace, Berlin, Germany). Capture protocols were approved under B.C. Wildlife Act Permit PG17-272811, and were consistent with Sikes et al. (2016). We programmed GPS collars to collect one location every hour and to activate the mortality notification after 8 hours of immobility. Contact information on the collars allowed hunters and trappers to return any encountered collars. We used VHF collars to relocate packs in case the GPS-collared wolf died or dispersed, or the GPS collar malfunctioned.

Wolf density

We relocated collared wolves 1–5 times each winter to determine pack size from visual observation of wolves, and enumerating sets of tracks where wolf trails split apart on lakes, wetlands, and clearings. Although mid-winter pack counts were the standard for wolf abundance estimates (Boitani 2003), we also set up remote cameras at den and rendezvous sites to collect minimum counts of adults and pups over the summer, especially for packs that had a collar malfunction. We defined the study area as the outer boundary of 95% minimum convex polygons (MCPs) of each collared pack calculated in R 3.6.0 (R Core Team 2024) using the *adehabitatHR* package (Calenge 2006). MCP home ranges do not account for intensity of use but have been widely implemented and can be effective for delineating home range of territorial species (White and Garrott 1990, Mech and Boitani 2003). We determined home ranges annually for summer (1 Apr – 31 Oct) and winter (1 Nov – 31 Mar), and considered the mean size of all seasonal home ranges over all years for a pack to be the overall home range size. For each pack, we determined the maximum winter pack count; for packs monitored for more than 1 year, we used the mean maximum winter pack count as the pack size. We summed the pack size for all packs in the study area and applied it to the area delineated by the pack home ranges in the study area to estimate wolf density. In some years, packs dissolved and other packs expanded into their vacant territories, so applying densities calculated for each territory separately would have effectively double-counted parts of the study areas.

Kill site investigations

GPS cluster analysis has become a well-established technique for investigating kill sites (Sand et al. 2005, Webb et al. 2008, Morehouse and Boyce 2011). We used the Find Points Cluster Identification Program v.2 (Gillingham 2009) to identify location clusters (and potentially kill sites, but see below) for each GPS-collared wolf, where a cluster was defined as a minimum of 2 locations within 100 m of each other within a 2-week (336 hours) period. We did not attempt to quantify predation on moose neonates (calves 4-6 weeks post-parturition) or other small prey, which have short handling times and are unlikely to be detected with hourly location fixes (Sand et al. 2005, Webb et al. 2008, Gable et al. 2016).

We assumed that evidence of a kill would be present at any cluster that was actually a kill site during the site investigation, which was generally weeks to months later. Kills made between November and March were rapidly buried by snow and were instead investigated after snow melt and prior to green-up in the spring. At each cluster, we searched the area for evidence of a kill (hair, rumen, and bones, often scattered over > 100 m) to determine prey species, sex (presence of antlers or antler pedicels), age (tooth wear and eruption, incisor extracted for cementum annuli aging animals > 1 year-old), and condition. To index body condition, we collected and dried marrow from intact long bones, and quantitively assessed consistency, appearance, and fat content (white waxy marrow with high fat content or red gelatinous marrow with low fat content; Mech 2008). Marrow fat is the last fat store depleted, so presence of marrow fat did not necessarily indicate an animal in good condition, but lack of marrow fat was a definitive indicator of poor condition (Mech and DelGuidice 1985). We considered < 20% fat as acute malnutrition, 20-70% fat as poor body condition, and > 70% as good body condition (Procter et al. 2020). Marrow fat levels also vary with the specific bones selected for analysis (Spears et al. 2003), and although we collected a humerus or femur when available, we were often limited by which bones were left intact at kill sites. Marrow fat is also expected to be dependent on environmental conditions, with extended exposure leading to evaporation that leads to apparent higher fat content (Lamoureux et al. 2011, Murden et al. 2017). This further limited our sample size and constrained our inference because sample collection was weeks or months after death.

Some moose identified at kill sites may have been scavenged by wolves but died from another cause. We removed obvious cases of scavenging from kill rate and predation rate analysis (e.g. cut or sawed bones at hunter kills, radio-collared cow moose confirmed killed by another proximate cause), but it remains possible that some carcasses we identified as having been wolf kills resulted from other causes.

Characteristics of wolf prey at kill sites

Determining selection requires both a measure of use, which we obtained from kill site investigations, and a measure of availability. The latter was often not available for our variables of interest. We lacked density estimates for elk, deer, or black bears in either study area, as well as data on moose population age structure (Kuzyk et al. 2020). Similarly, we had no reference data regarding condition of moose in the population, which we expected to vary seasonally and annually. We considered using vehicle strikes to represent a random sample of moose body condition and age (because neither would be expected to predispose moose to vehicle strike mortality) but lacked a sufficient sample size.

Data available to us included mid-winter stratified random block surveys that provided bull and calf ratios for both PGS and JPRF. We flew these surveys in the Prince George West (PGW; equivalent to our PGS study area) and Fort St. James (FSJ; equivalent to our JPRF study area) survey areas in December 2016 and 2020 (Klaczek et al. 2017, Scheideman et al. 2021, Table 1). Midwinter calf ratios overestimate the number of calves available to wolves throughout the entire winter because calf ratios decline over that period, and most wolf kills are in late winter and spring when calf ratios are lower (Procter et al. 2020). Calf numbers would be expected to drop by close to 30%

Table 1. Mid-winter calf and bull moose proportions for the Prince George South (PGS) and John Prince Research Forest (JPRF) study areas based on moose surveys conducted in Prince George West (PGW) and Fort St. James (FSJ) in north-central B.C. (Klaczek et al. 2017, Scheideman et al. 2021). Adjusted moose calf proportions account for 30% overwinter mortality expected between mid-winter surveys and recruitment to age 1 in late May.

	PGS (PGW)		JPRF (FSJ)	
	Calf proportion	Bull proportion	Calf proportion	Bull proportion
December 2016	0.20	0.21	0.22	0.20
Adjusted to May 2017	0.14		0.15	
December 2020	0.21	0.24	0.13	0.28
Adjusted to May 2021	0.15		0.09	

from mid-winter ratios up to recruitment at the mean birth date (May 21; Procter et al. 2020), suggesting that 13–22% of the population would be calves in December, but only 9–15% would be calves by late May. We considered the calf proportion in mid-winter and spring (midwinter adjusted to May) to examine whether wolves were selecting calves that were large enough to detect through cluster investigation. If wolves selected calves, we would expect to see a higher percentage of calves at kill sites than we see in the winter (or spring) moose population. Similarly, we would expect a higher proportion of bull moose at kill sites than in the population if wolves selected bull moose.

Kill rates

Following Vucetich et al. (2011), we defined kill rates as the number or biomass of prey killed by a predator (or biomass of a predator) over a period of time. For wolves, this means accounting for the number (and/or size) of prey killed, the pack size, and the changing size and metabolic demands of pups as they grow (Mech and Peterson 2003). Seasonality is also important due to the presence of rapidly growing neonate prey (Mech and Peterson 2003, Sand et al. 2005, Metz et al. 2011). We calculated kill rates using moose that we concluded to have been killed by wolves, excluding scavenged hunter kills and biomass intake from other sources (e.g. other large or small prey species, bait sites set by hunters and trappers, dumped livestock carcasses).

Predicting kill sites from cluster characteristics – In preliminary analyses, we used logistic regression models in R 3.6.0 (R Core Team 2024) to predict kill sites for summer, winter, both seasons, and study areas both separately and combined from cluster characteristics. All models considered the probability of a cluster being a moose kill site as dependent variables, and the amount of time spent at a cluster (number of location fixes and number of days between first and last visit to the site) and movements at the cluster (mean distance between cluster points and cluster centroid) as predictor variables. All models also incorporated individual wolf identities as random factors, and we assessed the strength of evidence for each model using Akaike's Information Criterion for small sample sizes (AICc). The low power all models had to predict kill sites led us to ultimately abandon this line of inquiry (see Results).

Assessing complete kill time series – We investigated all likely kill sites to determine the number of moose killed over a defined period (Fuller and Keith 1980, Fuller 1989, Palm 2001). We ground-truthed all clusters with more than 15 locations in the

2-week temporal window. For wolves with less predictable movement patterns at kill sites, we also visited additional clusters with fewer than 15 locations in the 2-week temporal window, especially when there was a long duration between confirmed kills. We did not include time series less than 2 weeks in duration and considered only one wolf if 2 wolves in the pack were comprehensively monitored with active GPS collars at the same time. For time series that overlapped our defined winter (1 Nov – 31 Mar) to summer (1 Apr – 31 Oct) seasons we assigned the season that was predominantly represented by the environmental conditions present.

Probability of attendance – The number of kills attended by an individual collared wolf underestimates the number of kills made by the pack because the collared wolf may not be present at all kills. To account for this, we corrected for the probability of the collared wolf not being at a kill that the other members of the pack have made. Probability of attendance varied by season, wolf age, pack size, and prey size in Yellowstone National Park (YNP, Metz et al. 2011). We considered the correction factors calculated for YNP (probability of attendance in summer = 0.68, probability of attendance in winter = 0.95, Metz et al. 2011) and created correction factors specific to our study areas using data from 3 packs in PGS with 2 wolves GPS-collared simultaneously. We used Metz et al.'s (2011) double-observer approach to estimate probability of attendance at kill sites by treating each wolf as an observer and their presence at the kill as a detection. The total number of detections was given by:

$$N_{total} = \frac{(N_A + 1)(N_B + 1)}{N_{AB} + 1} - 1 \quad (1)$$

where N_{total} was the total number of detections, N_A and N_B by pack member A or pack member B, and N_{AB} referred to detections by both pack members A and B. The probability of detection (PD) for each pack member A and B was:

$$PD_A = \frac{N_{AB}}{N_B} \text{ and } PD_B = \frac{N_{AB}}{N_A} \quad (2)$$

Predation rates

The predation rate is the proportion of a prey population killed by a predator over a specified period. We flew stratified random block surveys to estimate moose abundance in December 2020 in the PGW and FSJ survey areas (representing PGS and JPRF study areas respectively). We estimated moose densities in PGW as 0.62 (SE = 0.05) moose/km^2 and 0.84 (SE 0.12) moose/km^2 in FSJ (Scheideman et al. 2021, sightability correction following Quayle et al. 2001). These densities extrapolated to 2,849 moose (95% CI = 2,390–3,308) in the PGS study area, and 3,460 moose (95% CI = 2,531–4,388) in the JPRF study area (in both cases including 8-month-old calves). We used these population estimates and the corrected kill rates to estimate the predation rate by wolves on the moose population in each study area.

RESULTS

Wolf density

We monitored 33 wolves in 11 packs (6 in PGS, 5 in JPRF) representing contiguous wolf territories in the study areas, except for one unmonitored pack territory in PGS where wolves were seen but collars never deployed (Tables 1, 2). That area was not included in density calculations. The mean collar deployment period accounting for mortality, dispersal out of the study area, and malfunction was 277 days. Home range size of wolf packs varied from 250 to 1,100 km^2 (Table 3). Mean home range sizes of packs in the 2 study areas did not differ in summer

Table 2. Summary of wolf packs monitored in 2 interior British Columbia study areas for a study of wolf predation on moose, 2018-2022.

Study Area	Pack	GPS-collared wolves	VHF-collared wolves	Total wolf-days monitored	Monitoring Start	Monitoring End
PGS	Blackwater River	1 male	1 female	356	06 Mar 2018	25 Feb 2019
	Bobtail Mountain	2 male, 1 female	1 female	608	22 Feb 2018	11 Mar 2022
	Clear Lake	2 male, 1 female	1 male, 1 female	470	06 Mar 2018	13 Feb 2020
	Ghost Pack	1 male	1 male	88	27 Feb 2020	25 May 2020
	Grizzly Lake	2 male, 2 female	1 female	338	28 Feb 2020	19 Dec 2021
	Tagai Lake	2 male	4 female	1070	05 Jan 2019	22 Mar 2021
	Tatelkuz Lake	1 male[a]	none	97	20 Jan 2019	27 Apr 2019
JPRF	Hat Lake	1 male, 2 female	none	751	09 Jun 2018	23 Nov 2020
	Kazchek Lake	2 male	1 female	822	12 Jul 2019	07 Feb 2022
	Pinchi Lake	1 female	none	282	16 Jun 2018	25 Mar 2019
	Tachie	1 male	none	255	06 Feb 2019	19 Oct 2019
	Tanizul Lake	1 male	none	381	08 Feb 2019	24 Feb 2020

[a] This individual was collared in the Bobtail Mountain pack then dispersed to Tatelkuz Lake.

Table 3. Home range sizes based on 95% minimum convex polygon (MCP) and mean maximum midwinter pack counts for wolf packs monitored in Prince George South (PGS) and John Prince Research Forest (JPRF) in north-central B.C., 2018-2022, with density calculated at the home range scale and over the study area.

		Mean Pack Count	Range (min-max) Pack Count	Summer Range (km^2)	Winter Range (km^2)	Overall Range (km^2)	Density (wolves/ 1,000 km^2)
PGS	Blackwater	7.0	7	469	400	423	16.6
	Bobtail Mountain	10.5	7-14	1247	445	712	14.7
	Clear Lake	9.0	7-12	408	897	702	12.8
	Ghost Pack	5.0	5	315	195	255	19.6
	Grizzly Lake	7.5	6-9	424	513	454	16.5
	Tagai Lake	5.5	5-6	880	556	695	7.9
	Study area (6 packs)	44.5	37-53			4595	9.7
JPRF	Hat Lake	5.0	4-7	1006	512	723	6.2
	Kazchek Lake	3.7	3-5	1292	827	1059	3.5
	Pinchi Lake	4.7	3-8	183	410	296	15.9
	Tachie	3.0	2-4	832	574	660	4.5
	Tanizul Lake	4.5	3-6	441	340	390	11.5
	Study area (5 packs)	20.9	15-30			4119	5.1

(2-tailed test $t = -0.15$, $P = 0.88$, df = 7), winter (2-tailed test $t = 0.97$, $P = 0.35$, df = 9), or year-round (2-tailed-test, $t = 1.41$, $P = 0.19$, df = 9). We made 69 observations of pack size to determine pack counts for 28 pack-years, including 6 estimates for packs without functioning GPS collars (by locating VHF-collared wolves or den monitoring). Wolf packs were larger in PGS (7.4 wolves/pack) than in JPRF (4.2 wolves/pack) (2-tailed-test, $t = 3.26$, $P = 0.01$, df = 9). We estimated a density of 9.7 wolves/1,000 km^2 in PGS and 5.1 wolves/1,000 km^2 in JPRF, with much higher densities within some pack home ranges (Table 3). Density of monitored packs was estimated at 1.9 packs/1,000 km^2 in PGS and 1.6 packs/1,000 km^2 in JPRF.

Characteristics of wolf prey at kill sites

We investigated 1,208 clusters between March 2018 and July 2022 (908 in PGS and 300 in JPRF). The sample size difference reflected differences in collar deployment times, logistics, and how often the collared wolves made kills. In PGS, we investigated clusters a mean of 111 days after cluster formation (SD = 83 days, *n* = 892; investigation date was not recorded for some clusters) and in JPRF a mean of 97 days after cluster formation (SD = 101 days, *n* = 293; investigation date was not recorded for some clusters). We initially visited clusters regardless of the number of points in the cluster, but we consistently found no evidence of a carcass at small clusters (< 10 location fixes) and instead prioritized larger clusters with > 15 location points. Mean number of points in visited clusters was 28.1 (95% CI = 26.0–30.2); mean number of points in all clusters was 8.3 (95% CI = 8.1–8.5). Clusters were associated with dens, rendezvous sites, bed sites, old kill sites, illegal garbage dump sites, bait piles set by hunters and trappers, gut piles left by hunters, beaver (*Castor canadensis*) activity, snowshoe hare (*Lepus americanus*) activity, shed antlers that had been chewed, and kill sites. Of the 290 kill sites identified, most were moose in both PGS (*n* = 200) and JPRF (*n* = 52). Other species included elk, deer, domestic cattle (PGS only), and black bear (Table 4). The pack targeting cattle was subsequently removed by the B.C. Cattleman's Association Livestock Protection Program and a new pack moved into the vacant territory within months.

Moose kill characteristics – Of the 252 moose kill sites detected, we determined sex for 108, including 7 female calves and 6 male calves. Of 95 adult moose with sex confirmed, we found 76 cows and 19 bulls. Comparisons of the 20% bulls in the killed sample with the observed bull ratios from moose surveys (16.4% in 2016-17, *n* = 729, Klaczek et al. 2017; 20.8% in 2020-21, *n* = 1399, Scheideman et al. 2022) provided no evidence that wolves selected moose based on sex in our study areas ($\chi^2 = 0.778$, df = 1, $P = 0.38$ for 2016-17; $\chi^2 = 0.035$, df = 1, $P = 0.85$ for 2020-21).

Of the 252 moose kill sites detected, we found 69 calves, 175 adults (including 22 yearlings), and 8 moose of unknown age class. Based on our kill site investigations, 28% of wolf-killed moose were calves (95% CI = 23–34%), higher than the proportion of

Table 4. Proportion of species detected at wolf kill-sites in Prince George South (PGS, *n* = 225) and John Prince Research Forest (JPRF, *n* = 65) in north-central B.C., 2018-2022. One elk kill was detected in PGS (0% due to rounding).

Prey species	Proportion of kills, PGS	Proportion of kills, JPRF
Moose	0.87	0.75
Black bear	0.02	0.10
Deer	0.05	0.06
Elk	0.00	0.06
Domestic cattle	0.04	NA
Unknown	0.02	0.02

calves in the population (13–22% of the mid-winter population; 9–15% of the population by May).

We aged 71 wolf-killed moose > 1 year of age using cementum annuli from incisors (Figure 2). The mean age of all wolf-killed moose (not including calves) in our study was 7 years (95% CI = 6 – 8, *n* = 98, range 1–17). The mean age of wolf-killed bull moose (5 years, 95% CI = 3 – 7, *n* = 15) was lower than the mean age of wolf-killed cow moose (9 years, 95% CI = 3 – 7, *n* = 53) (2-tailed-test, *t* = 2.84, *P* = 0.006, df = 66). However, when we considered only the 9 bulls and 48 cows > 1 year of age (bulls – 8 years, 95% CI = 6 – 10, cows – 10 years, 95% CI = 9 – 11), there was no difference in age between wolf-killed bull and cow moose (2-tailed-test, *t* = 1.34, *P* = 0.19, df = 55).

We analysed marrow fat content from 31 long bones from adult moose and 4 from calves. Calf samples had a mean of 91% marrow fat (95% CI = 84 – 98%), however, the sample size was very small (*n* = 4). Adult marrow samples had a mean of 87% marrow fat (95% CI = 82 – 92%). We considered 1 moose to be acutely malnourished (8.5% marrow fat) and 2 in poor body condition (58% and 68% marrow fat). Based on 18 qualitative assessments of marrow, we noted 14 as whitish and solid (77%), 2 as pinkish red and solid (11%), and 2 as red and dried (11%). Although sample sizes were small and marrow fat percentage likely biased high even for samples collected and frozen relatively quickly, marrow fat content of wolf-killed moose was high overall.

Kill rates

Predicting kill sites from cluster characteristics – We considered several candidate models to predict the probability of a cluster representing a kill, but most models provided unrealistic results, especially for smaller cluster sizes. Most models suggested about a 10% probability of a cluster representing a kill if there were 2 hourly locations in the cluster, which would have generated a drastic overestimation in the number of kill sites. Wolf behaviour at kills also varied by individual, and with a mean collar deployment of 277 days, we were unlikely to have sufficient kills for individual-specific predictive models. Number of points in the cluster was consistently a significant variable in seasonal study area

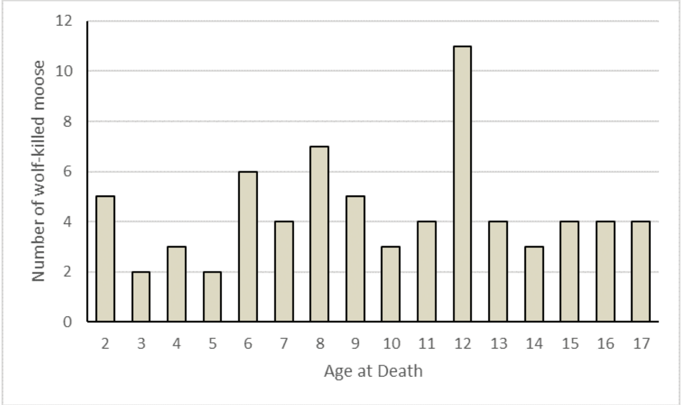

Fig. 2. Cementum annuli ages from incisor teeth collected from 71 moose 2 years or older killed by wolves in north-central B.C., 2018-2022. Calves and yearlings are not included as sample sizes for those age classes were much higher (incisors did not need to be recovered to estimate the age based on tooth eruption).

models, many of which had equivalent AICc scores for both large prey kills (Appendix 1) and moose kills specifically (Appendix 2). Clusters with more location points were more likely to represent kills, but this relationship was not as clear in summer, especially in JPRF (Figure 3); clusters in summer were often associated with rendezvous sites and dens, which obscured the relationship between persistence time at a site and likelihood of kill. We also noted considerable variability in the coefficient estimates and prediction of whether a cluster represented a kill site, even for large kill sites, compromising our ability to predict whether a cluster site represented a kill, or a moose kill specifically. Thus, we declined to extrapolate kill sites from cluster sites to subsequently determine kill rates or predation rates.

Assessing complete kill time series – We tracked 50 complete kill chronologies for PGS and 22 for JPRF, averaging about 5 weeks long and representing all collared packs. This provided a kill rate of 0.64 moose/week/pack or a moose every 12 days in PGS and 0.34 moose/week/pack or one moose every 21 days in JPRF. Seasonal kill rates for PGS were one moose every 15 days in the summer and every 8–9 days in the winter and for a pack in JPRF, one moose every 37–38 days in the summer and every 13 days in the winter.

Probability of attendance – Three packs in PGS had multiple GPS-collared wolves simultaneously: Tagai Lake pack (breeding male and a subordinate male, 25 March 2019–13 December 2019), Clear Lake pack (2 subordinate males, 21 January 2019–7 March 2019), Grizzly Lake pack (yearling female, subordinate male, and subordinate female, 23 June 2019–1 July 2021).

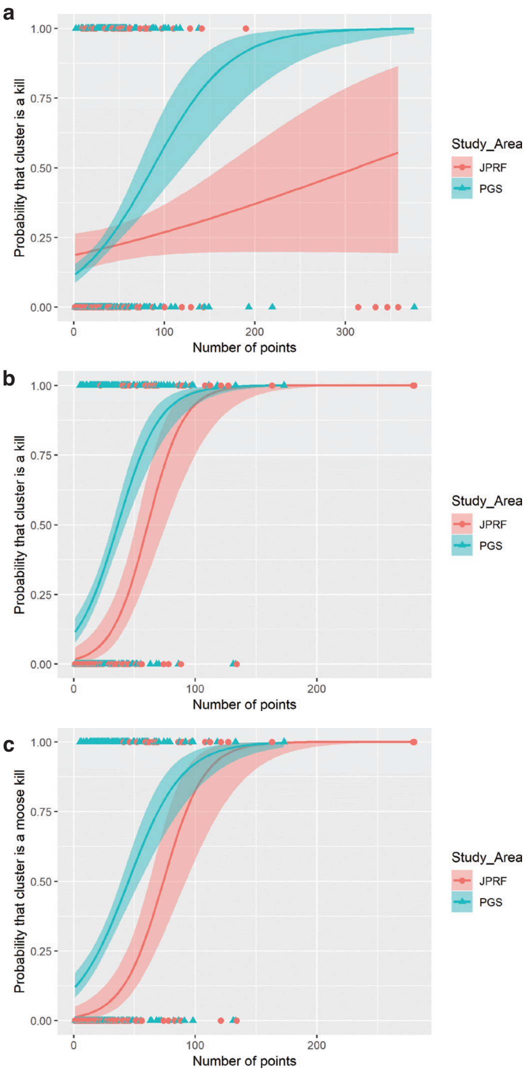

Fig. 3. Probability that location clusters represent a wolf kill site of a large prey in summer (a) and winter (b), and probability of a winter cluster representing a moose kill specifically (c), based on number of location points in the cluster for Prince George South (PGS) and John Prince Research Forest (JPRF), north-central B.C. 2018-2022. Shaded area is 95%CI.

The Tagai Lake pack's breeding wolf was present at 17 moose kills and a black bear kill, and its subordinate wolf was present at 13 moose kills. We detected 22 kills made by this pack over the 257-day period when both collars were active (PD = 0.69 for breeder, PD = 0.50 for subordinate), resulting in an estimated 26 kills (0.7 kills/week). Considering the summer season only (183 days and 16 individual kills detected, 13 by the breeder and 10 by the subordinate), PD was 0.70 for the breeder and 0.54 for the subordinate. Only 6 kills were recorded for 46 days of winter monitoring for Tagai Lake, 5 by the breeder (PD = 0.67) and 3 by the subordinate (PD = 0.40).

For Clear Lake pack, one wolf was present at 7 kills and the other at 9 kills. We documented 13 individual moose kills during the 56-day period when both collars were active (PD = 0.33 and 0.43), resulting in an estimated 21 moose killed (2.6 moose/week). We documented only a single moose kill in the short period of time in which the Grizzly Lake pack had 3 functioning collars.

We considered both the YNP seasonal probability of attendance (Metz et al. 2011) and the probability of attendance based on breeding status for the PGS wolves, assigning a probability of attendance of 0.4 to subordinate wolves and 0.7 to breeders as an approximation, realizing the sample size is low. These correction factors substantially increased the estimated kill rates for packs in both PGS and JPRF (Table 5). Kill rates per wolf were similar between PGS and JPRF, despite the differences in pack size (Table 6).

Predation rates

After adjusting for probability of attendance by the collared wolf at a kill, the predation rates on moose were 13.7% (11.8–16.4%) in PGS and 5.1% (4.0–6.9%) in JPRF year-round with higher estimates in the winter than summer (Table 7).

DISCUSSION

Wolf density

Across their North American range, wolves generally occur at densities from 2 to 40 wolves per 1,000 km^2 (Paquet and Carbyn 2003 and references therein). The wolf densities we calculated for PGS (10 wolves/1,000 km^2) and JPRF (5 wolves/1,000 km^2) are similar to estimates calculated from the ungulate biomass index (6.9–13.7 wolves/1,000 km^2, Kuzyk and Hatter 2014). Our density estimate would have been slightly higher had we also accounted for lone wolves, which typically make up 10–15% of the population (MN DNR 2001, Baer 2011). The wolf density in PGS and JPRF was lower than the density estimated from snow track surveys in February and March 2017 when tracking conditions were suboptimal with low snowpack and melted areas that made it difficult to follow wolf

Table 5. Kill rates adjusted for probability of attendance based on means for winter and summer calculated in Yellowstone National Park (YNP) of 0.68 in summer and 0.95 in winter (Metz et al. 2011) and based on Clear Lake and Tagai Lake packs in 2019 for subordinate wolves (0.4) and breeders (0.7). Unadjusted kill rates were based on periods of continuous monitoring 2018-2022 (JPRF *n* = 10 winter, 12 summer; PGS *n* = 17 winter, 22 summer).

		Unadjusted kill rate		PGS-adjusted kill rate		YNP-adjusted kill rate	
		Moose/pack/ week (± SE)	Days/ moose/pack	Moose/ pack/week	Days/ moose/pack	Moose/ pack/week	Days/moose/ pack
PGS	Annual	0.64 ± 0.06	11.0	1.25	5.6		
	Winter	0.87 ± 0.09	8.0	1.75	4.0	0.92	7.6
	Summer	0.45 ± 0.05	15.5	0.87	8.0	0.66	10.5
JPRF	Annual	0.34 ± 0.07	20.6	0.67	10.4		
	Winter	0.55 ± 0.12	12.7	1.08	6.5	0.58	12.1
	Summer	0.19 ± 0.06	37.5	0.38	18.6	0.28	25.5

Table 6. Kill rates per wolf adjusted for probability of attendance based on means for winter and summer calculated in Yellowstone National Park (YNP) of 0.68 in summer and 0.95 in winter and based on Clear Lake and Tagai Lake packs in 2019 for subordinate wolves (0.4) and breeders (0.7). Unadjusted kill rates were based on periods of continuous monitoring 2018-2022. Mean midwinter pack sizes were 4.2 wolves in John Prince Research Forest (JPRF) and 7.4 wolves in Prince George South (PGS), north-central B.C. Biomass assumes 297 kg/moose based on kills in the Yukon (Kaczensky et al. 2005, Hayes et al. 2000).

		Unadjusted kill rate (moose/wolf/week) ± SE	PGS-adjusted kill rate		YNP-adjusted kill rate (moose/wolf/week)	
			Moose/wolf/week	Kg/wolf/day	Moose/wolf/week	Kg/wolf/day
PGS	Winter	0.12 ± 0.01	0.24	10.2	0.12	5.1
	Summer	0.06 ± 0.01	0.12	5.1	0.09	3.8
JPRF	Winter	0.13 ± 0.03	0.26	11.0	0.14	5.9
	Summer	0.04 ± 0.01	0.09	3.8	0.07	3.0

Table 7. Estimated predation rates on moose (proportion of moose killed) 2018-2022 in Prince George South (PGS; 6 packs, mean pack size 7.4 wolves) and John Prince Research Forest (JPRF; 5 packs, mean pack size 4.2 wolves) using moose densities from winter 2020-21, north-central B.C. (Scheideman et al. 2021). The 95% CI refers to the moose population estimate; mean kill rates were applied after adjusting for probability of attendance based on PGS wolves and by values reported from wolves in Yellowstone National Park (YNP, Metz et al. 2011).

Study Area	Season	PGS-adjusted predation rate		YNP-adjusted predation rate	
		Mean	95% CI	Mean	95% CI
PGS	All	13.7%	11.8-16.4%		
	Winter	19.2%	16.5-22.9%	10.1%	8.7-12.0%
	Summer	9.5%	8.2-11.4%	7.3%	6.3-8.7%
JPRF	All	5.1%	4.0-6.9%		
	Winter	8.1%	6.4-11.1%	4.4%	3.4-6.0%
	Summer	2.8%	2.2-3.9%	2.1%	1.6-2.8%

trails, making continuous trails appear to be several separate detections (Anderson et al. 2017). This emphasized the importance of good conditions for wolf snow track surveys. Wolf density is also expected to fluctuate widely between seasons, with large litters of pups observed in both study areas during this project. Changing survival and dispersal rates for pups and adults would also change density estimates among years. Home range size (250–1,100 km^2) was within the reported values for wolf populations elsewhere in northern North America (Mech and Boitani 2003) and similar between study areas. The difference in wolf density between the 2 study areas was evidently driven by pack size rather than by the number of packs.

Pack size may be as important to predation rates as wolf density in some systems because smaller packs lose more biomass from a kill to scavengers and can therefore have a higher per wolf kill rate (Vucetich et al. 2004, Kaczensky et al. 2005). The difference in pack size had also been noted in the 2017 track surveys despite suboptimal survey conditions (5-7 wolves per pack in PGS, 3-5 wolves per pack in JPRF, Anderson et al. 2017). Below, we consider several hypotheses to explain differences in pack size between the 2 study areas.

Wolf pack size is related to prey availability and competition with other wolves. Packs tend to be larger where the primary prey is also large, because the biomass obtained from a large kill can support more wolves, and higher prey densities support larger packs (Sells et al. 2022). Large packs are also more successful than small packs at killing prey (MacNulty et al. 2012). In both study areas, moose are the primary prey and moose densities are similar, suggesting that prey availability may not be the primary driver of pack size differences. Wolf pack sizes are generally stable under low harvest but can decline under high harvest (Sells et al. 2022), and pack occupancy is generally stable even with high harvest and high turnover of individuals (Bassing et al. 2019). Without reliable harvest data (Mowat et al. 2022), we were unable to assess this as a driver for pack size between the 2 sites. When the breeding female or breeding pair is removed from a pack, the pack often dissolves (Brainerd et al. 2008, Borg et al. 2015), which can potentially increase local wolf density and number of packs (Ballard and Stephenson 1982, Mech and Boitani 2003). Harvest data was not sufficiently reliable to fully assess the impacts of harvest on wolf pack structure during our study. As wolf density increases, competition for limited resources also increases and larger packs are better at defending territories than smaller packs (Smith et al. 2010, Sells et al. 2022). Densities at which intraspecific aggression is expected to regulate wolf populations are much higher than either of our study areas (69 wolves/1,000 km^2, Cariappa et al. 2011), suggesting that the role of intraspecific competition in driving wolf pack size and population dynamics is likely overshadowed by environmental factors and food availability driving recruitment and dispersal (Fuller 1989, Bergerud and Elliot 1998, Hayes and Harestad 2000).

Characteristics of wolf prey at kill sites

Moose were the dominant prey in both PGS and JPRF as estimated using cluster searches, although wolves in JPRF consumed more elk, deer, and black bears than in PGS. Although formal inventories have been spatially limited for elk (Scheideman and Anderson 2022, 2023; Scheideman et al. 2024) and deer (B.C. Ministry of Water, Land and Resource Stewardship unpublished data), we suspect densities of these other ungulates were higher in JPRF than PGS based on discussions with local stakeholders and First Nations. Black bear density estimates were not available in either study area. We did not assess the use of small prey, but cluster sites with few (< 10) points were frequently associated with beaver dams, lodges, and foraging activity, especially in JPRF. Small prey can make up a significant proportion of wolf diets, especially in summer (Metz et al. 2012, Gable et al. 2016, Gable et al. 2018), but a more frequent fix rate and more intensive ground searches than we undertook would be needed to quantify the use of small prey in our study areas.

Wolves in both PGS and JPRF preyed on moose calves in higher proportions than they were available in the population. This, together when considering that calf kills were more likely to be underrepresented or classified as unknown due to their smaller size and more complete consumption, suggests that wolves in our study areas selected calves. Without baseline population data, we were not able to definitively show selection by wolves for moose of other age classes. Intuitively, the consistent presence of older moose at kill sites would suggest selection for older age classes (Mech et al. 1995), because they would naturally decline in abundance in the moose population. Kuzyk et al. (2020) analyzed the age of more than 2,000 hunter-killed moose from 1982–2003, 15 years prior to the beginning of our study and over a period of increasing and high moose density. They found the mean age of harvested cow moose to be 4 years old, much younger than the mean age of 10 years old for collared cow moose dying from all causes 2012–2020 in interior B.C. (n = 47, Procter et al. 2020). The difference between mean age of death identified in the 2 studies is likely due to inclusion in the latter of natural mortality that differentially affects older individuals, but the age structure may also have changed following widespread population declines. The mean age of wolf-killed, non-collared adult cow moose (> 1 yr old) from our study was similar to Procter et al.'s (2020) reported mean age of wolf-killed, collared cow moose (> 1 yr old) in the same study areas (10 yrs, 95% CI = 8.6 – 11.6, range 1–16 yrs). Additionally, we did not detect selection of wolves for either sex of moose in our study areas, although other studies have found selection for yearling or adult bulls (Fuller and Keith 1980).

We lacked data to compare the body condition of wolf-killed moose with the live moose or moose dying of other causes. We were limited to inferring body condition from marrow fat, which is only one parameter to quantify moose health. Relatively high marrow fat content of the 4 calves could be expected, as calves increase marrow fat content from birth through the fall (Spears et al. 2003) and we were sampling older calves, not neonates. Carstensen et al. (2017) found that at least 40% of the moose killed by wolves in their study had underlying health issues that may have predisposed them to predation, and poor body condition has been identified as an important mortality factor for moose in this study area and elsewhere (Mumma and Gillingham 2019, Cook et al. 2021, Anderson et al. 2023). We were unable to make any conclusions about other aspects of health that could have predisposed an animal to predation.

Kill rates

False negatives, where a kill was present but not detected by observers, may have occurred if we were unable to locate any remains due to carcasses being fully consumed or moved by wolves or by scavengers. Blecha and Aldredge (2015) used a double-observer approach to estimate a 4% false negative rate on cougar kills investigated 4–60 days after the kill in Colorado, suggesting a relatively low rate of false negatives if our study system is similar. Moose leave larger remains that are easier to detect compared to smaller species like deer which may reduce the prevalence of false negatives in our study areas.

Estimating kill rates of social carnivores requires consideration of how often members of the social group are foraging together. Under conditions when packs are not as cohesive, including for larger packs (Jedrzejewski et al. 2001), we would expect lower probabilities of attendance at kill sites. The probabilities of attendance calculated for PGS wolves were lower than those of YNP wolves, but packs in our study were smaller than the mean 13 wolves/pack in YNP. Thus, pack size would not appear to explain lower attendance in PGS. Other factors in our study areas may lead to lower pack cohesion, including active hunting and trapping of wolves which can cause pack splitting. Also, the high densities of roads and cutblocks may facilitate packs splitting up to increase search efficiency. We also did not find the same clear seasonal difference in pack cohesion as Metz et al. (2011). We would expect packs to be more cohesive in winter with individuals travelling together and therefore more likely to be at the same kills (Peterson et al. 1984); we did not detect a difference, but this may be more likely a sample size issue than a behavioural difference. The energetic efficiency of travelling as a pack in deep snow, the summer availability of small prey that can be effectively hunted by individual wolves, and behaviours associated with denning are all expected to influence pack cohesiveness and may not differ substantially between our study areas and the system examined by Metz et al. (2011).

Kill rates of moose were higher in PGS (4-11 days between moose kills) than in JPRF (8-26 days between moose kills). However, the difference in pack sizes meant that kill rate per wolf was similar between PGS (mean pack size 7.4 wolves) and JPRF (mean pack size 4.2 wolves). Differences in moose kill rates between the 2 study areas were largely due to differences in pack size. This contrasted with results from work in other wolf populations with similar pack sizes that indicated higher kill rates per wolf by smaller packs (Ballard et al. 1987, Hayes et al. 2000). This difference may have resulted from different prey availability or minimal loss to scavengers even for small packs in PGS and JPRF.

Predation rates

Fuller and Keith (1980) estimated predation rates in a wolf-moose-caribou system in northeastern Alberta as 11-12% of the adult moose population, but high calf production suggested that the moose population could sustain that predation rate. Hayes et al. (2000) estimated predation rates in the Yukon of 10-15% of all moose and 7-16% of adult moose in winter, similar to the predation rates we reported here for PGS and higher than for JPRF. Annual predation rates in both study areas appear to be within the ranges reported for stable to increasing moose populations, which is consistent with recent survey results indicating stable to increasing moose populations in both PGS and JPRF (Scheideman et al. 2021).

Other interacting factors are important to consider beyond wolf predation rates. In Alaska, moose populations declined following severe winters when exposed to predation rates of 13-34% of the winter population in addition to hunting pressure (Gasaway et al. 1983, Gasaway et al. 1992). Predation rates of 10-15% in the Yukon were observed for moose populations increasing from low to moderate density, but would be expected to vary with prey density, alternate prey availability, and prey vulnerability (Hayes et al. 2000). Wolves exploiting relatively naïve and high-density moose populations in Sweden killed 4-15% of the winter moose population, mostly calves (Palm 2001). The age classes targeted by wolves and the extent to which wolf predation is additive versus compensatory on moose populations will also influence the sustainability of any given predation rate.

The role of wolf predation in multi-prey systems has been extensively examined to determine whether or under what conditions it may be a limiting or regulating factor (Mech and Peterson 2003). Limiting factors act on populations in a density-independent manner, while regulating factors act in a density-dependent manner, i.e., they differentially affect the population based on its density. The functional response of wolves and the density and carrying capacity of moose are important considerations for the outcome of wolf predation in a given system. Messier (1994) found that wolf predation is density dependent when moose densities are < 0.65 moose/km^2 but inversely density dependent at higher moose densities. A predator pit occurs when predation on a low-density population is high enough to prevent it from expanding to a higher density equilibrium point, and can occur in systems with high carrying capacity and high predation stochasticity (Clark et al. 2021). Predator pits have been documented in moose-wolf systems in Alaska (Gasaway et al. 1983, Boertje et al. 1996, Regelin et al. 2005). However, if habitat quality is poor, low density stable states are more likely the cause of low-density populations than a predator pit (Clark et al. 2021); removal of wolf predation may result in increased prey densities, but when wolf predation is reintroduced prey densities do not remain at a high equilibrium point (Gasaway et al. 1992, Mech and Peterson 2003). Continued monitoring of interior B.C. moose population dynamics as the extensive pine beetle salvage harvest cutblocks reach successional stages selected by moose (Mumma et al. 2021) will be essential to determining whether a predator pit is a possibility. Alternatively, habitat quality may be a more important driver than predation alone in changes to moose density in our study areas, especially considering how habitat change interacts with predation. The interaction with other prey species, especially small prey that may make up a significant contribution to biomass intake (Gable et al. 2018, Anderson et al. 2025), is also unknown.

The way in which wolves use salvage logging features also has implications for predation rates. Boucher et al. (2022) examined wolf movement and habitat selection in PGS to determine habitat features used and selected by wolves and where wolves were killing moose. Moose kill sites had a higher probability of occurring in areas with higher proportions of new cutblocks (0–8 yrs post-harvest, selected by wolves, but generally not by moose; Scheideman 2018, Mumma et al. 2021) and regenerating cutblocks (9–24 yrs post-harvest, not generally selected by wolves but selected by moose; Scheideman 2018, Mumma et al. 2021). This appears to represent an intersection of differing selection patterns that allows overlap between predator and prey. Moose kill sites were also less likely to occur in deciduous stands, which were generally not selected by wolves but consistently selected by moose (Scheideman 2018). Although moose habitat selection may be a trade-off between minimizing predation risk and maximizing forage intake (Francis et al. 2021), maintaining deciduous stands on the landscape may be important to moose for forage and as areas of lower predation risk. Spatial variation in wolf predation risk resulted in higher predation risk for seasonally migratory moose than for moose that remained on the same home range year-round, which can have implications for survival and recruitment (Koetke 2024). The results of this and related research underscore the importance of considering how predation dynamics could change based on widespread landscape disturbance, rather than predator or prey abundance alone.

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APPENDICES

Appendix 1. Candidate logistic regression models by season and study area predicting large prey kill sites by wolves in Prince George South (PGS) and John Prince Research Forest (JPRF) study areas in north-central B.C., 2018-2022. Top and equivalent models shown. Predictor variables are mean distance of points in cluster to the cluster centroid (Av_Dist), number of locations in cluster (Num_Pts) and number of days between first and last visits to cluster (Days). Individual wolf was a random effect in all models. Asterix denotes statistical significance at P < 0.05.

Study Area and season	Candidate model	Num_Pts Coefficient	Av_Dist Coefficient	Days Coefficient	AICc	ΔAICc
PGS+JPRF; all seasons	Num_Pts + Days	0.0326*		-0.010598*	1182.4	1.9
	Num_Pts + Days + Av_Dist	0.0323*	0.0024	-0.0111*	1180.5	0.0
PGS all seasons	Num_Pts + Days	0.0383*		-0.0102*	924.0	2.1
	Num_Pts + Days + Av_Dist	0.0376*	0.0036	-0.0110*	921.9	0.0
JPRF all seasons	Num_Pts + Av_Dist	0.0223*	-0.0123		254.6	0.7
	Num_Pts	0.0212*			254.4	0.4
	Num_Pts + Days	0.0231*		-0.0130	254.0	0.0
	Num_Pts + Days + Av_Dist	0.0236*	-0.0093	-0.0109	255.1	1.1
PGS+JPRF; winter	Num_Pts + Av_Dist	0.0658*	-0.0020		431.2	1.1
	Num_Pts + Days	0.0684*		-0.0102	432.5	2.4
	Num_Pts + Days + Av_Dist	0.0680*	0.0047	-0.0112	430.1	0.0
PGS winter	Num_Pts + Av_Dist	0.0657*	0.0060		359.6	0.0
	Num_Pts + Days + Av_Dist	0.0674*	0.0081		359.7	0.1
JPRF winter	Num_Pts + Av_Dist	0.0887*	-0.0433		66.8	0
	Num_Pts	0.0720*			67.4	0.6
	Num_Pts + Days	0.0832*		-0.0335	66.9	0.1
	Num_Pts + Days + Av_Dist	0.0962*	-0.0366	-0.0292	67.3	0.5
PGS+JPRF; summer	Num_Pts + Days	0.0191*		-0.0109*	684.0	0.0
	Num_Pts + Days + Av_Dist	0.0184*	0.0053	-0.0120*	685.1	1.1
PGS summer	Num_Pts + Days	0.0259*		-0.0134*	514.8	0
	Num_Pts + Days + Av_Dist	0.0242*	0.0082	-0.0151*	515.3	0.5
JPRF summer	Num_Pts + Av_Dist	0.0089*	-0.0147		169.2	0.5
	Num_Pts	0.0086*			168.7	0
	Num_Pts + Days	0.0097*		-0.0082	170.0	1.3

Appendix 2. Candidate logistic regression models by season and study area predicting moose kill sites by wolves in Prince George South (PGS) and John Prince Research Forest (JPRF) study areas in north-central B.C., 2018-2022. Top and equivalent models shown. Predictor variables are mean distance of points in cluster to the cluster centroid (Av_Dist), number of locations in cluster (Num_Pts) and number of days between first and last visits to cluster (Days). Individual wolf was a random effect in all models. Asterix denotes statistical significance at $P < 0.05$.

PGS+JPRF; all seasons	Num_Pts + Days	0.0303*		-0.0126*	1099.6	2.0
	Num_Pts + Days + Av_Dist	0.0307*	-0.0028	-0.0120*	1097.6	0.0
PGS all seasons	Num_Pts + Days	0.0359*		-0.0122*	876.8	1.9
	Num_Pts + Days + Av_Dist	0.0367*	-0.0029	-0.0117*	874.9	0.0
JPRF all seasons	Num_Pts + Av_Dist	0.0195*	-0.0132		215.2	0.7
	Num_Pts	0.0189*			214.8	0.3
	Num_Pts + Days	0.0208*		-0.0142	214.5	0.0
	Num_Pts + Days + Av_Dist	0.0211*	-0.0104	-0.0124	215.6	1.1
PGS+JPRF; winter	Num_Pts + Av_Dist	0.0611*	-0.0042		421.3	0.2
	Num_Pts + Days	0.0622*		-0.0102	423.0	2.0
	Num_Pts + Days + Av_Dist	0.0629*	-0.0018	-0.0099	421.1	0.0
PGS winter	Num_Pts + Av_Dist	0.0608*	-0.0013		355.5	0.0
	Num_Pts	0.0601*			357.1	1.6
	Num_Pts + Days	0.0626*		-0.0096	357.1	1.6
	Num_Pts + Days + Av_Dist	0.0629*	0.0009	-0.0098	355.5	0.0
JPRF winter	Num_Pts + Av_Dist	0.0818*	-0.0429		60.9	0.0
	Num_Pts	0.0683*			61.0	0.1
	Num_Pts + Days	0.0718*		-0.0186	62.4	1.5
	Num_Pts + Days + Av_Dist	0.0830*	-0.0397	-0.0119	62.8	1.9
PGS+JPRF; summer	Num_Pts + Days	0.0175*		-0.0137*	604.9	0.0
	Num_Pts + Days + Av_Dist	0.0171*	0.0036	-0.0145*	606.6	1.7

(*Continued*)

Appendix 2. (Continued) Candidate logistic regression models by season and study area predicting moose kill sites by wolves in Prince George South (PGS) and John Prince Research Forest (JPRF) study areas in north-central B.C., 2018-2022. Top and equivalent models shown. Predictor variables are mean distance of points in cluster to the cluster centroid (Av_Dist), number of locations in cluster (Num_Pts) and number of days between first and last visits to cluster (Days). Individual wolf was a random effect in all models. Asterix denotes statistical significance at $P < 0.05$.

PGS summer	Num_Pts + Days	0.0256*		-0.0165*	467.2	0.0
	Num_Pts + Days + Av_Dist	0.0254*	0.0011	-0.0168*	469.2	2.0
JPRF summer	Num_Pts + Av_Dist	0.0062	-0.0205		132.9	0.4
	Num_Pts	0.0063			132.5	0.0
	Av_Dist		-0.0216		134.0	1.5
	Num_Pts + Days	0.0081		-0.0134	133.0	0.5