BC MINISTRY OF FORESTS, OMINECA REGION

Wolf predation risk to moose in north-central British Columbia

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Executive Summary

In response to concerns about the role of wolves as potential drivers of moose population change, we investigated several aspects of predator-prey dynamics between wolves and moose in two of the Provincial Moose Research Project study sites, south of Prince George (PGS) and north of Fort St. James at the John Prince Research Forest (JPRF; Kuzyk and Heard 2014, Kuzyk et al. 2019b). The objective was to assess wolf predation risk to moose in two study areas with differing landscape disturbance: more mountain pine beetle salvage logging in the early 2000s in PGS, and less impacted/more recent pine salvage in JPRF. Predation risk is a function of wolf density, space use, habitat selection, and predation patterns (prey species and characteristics, kill rates, habitat use), and a better understanding of these factors will be key to evaluating options for moose enhancement.

We collared 33 wolves in 11 packs, six packs in PGS and five in JPRF, with an average satellite collar deployment time of 277 days before wolves dispersed or died, or collars went offline or dropped (satellite collars were anticipated to have a 2-yr lifespan; the 11 VHF collars were not regularly monitored). We recorded 9 collared wolf mortalities (3 legally harvested by trappers, 5 legally harvested by resident hunters, 1 shot when it dispersed into the area covered by the Itcha-Ilgatchuz wolf removal program for caribou recovery). Based on this small sample size, about a third of the wolf population dies annually; this is within the range of sustainable mortality rates. Based on mid-winter pack counts and home range size, wolf density is about 11-14 wolves/1000 km^2 in PGS and 7 wolves/1000 km^2 in JPRF (not including lone wolves, which are usually around 10% of the population). This is lower than the density suggested by the 2017 track survey (Anderson et al. 2017) and higher than expected based on ungulate biomass modelling (Kuzyk and Hatter 2014). Territory sizes varied from about 250 km^2 to 1100 km^2, and pack sizes ranged from 2 to 14 wolves, with PGS packs larger on average than JPRF (7 wolves per pack and 4 wolves per pack respectively).

To assess kill site and prey characteristics, we used a cluster algorithm on hourly collar locations and investigated these clusters on the ground (Knopff et al. 2009, Merrill et al. 2010). Between March 2018 and July 2022, we visited 1208 location clusters and identified 290 kills, predominantly moose in PGS (87%) and JPRF (75%). Wolves in JPRF preyed on more elk and deer than did wolves in PGS, but 10% of the kill sites we detected (n=65) were black bears. Wolves in PGS also killed deer, elk, and black bears, as well as 9 cattle (although the pack targeting cattle was subsequently removed by the BC Cattleman's Livestock Protection Program). Wolf-killed moose (n=252) did not show clear selection based on sex and the reference data to determine age selection was not available. The wolves did, however, appear to select calves, as 27% of the moose kills we found were calves while the mid-winter calf component of the population was 13-20%. Both kill sites and the midwinter calf estimate only consider these larger-bodied calves, and the calf proportion decreases through late winter when most mortality occurs, suggesting an underestimation of the selection for calves.

We determined kill rates based on complete time series of kills when we were able to visit all clusters that likely contained a kill (this varied depending on the collared wolf; some had predictable clustering behaviour around kills while others required more investigation of smaller clusters). We adjusted the

observed kill rates for the probability of attendance of a collared wolf at any of the pack's kills, based on packs with multiple collared wolves in PGS and from the same analysis on wolves in Yellowstone National Park, which provided slightly different corrected kill rates. Wolf packs in PGS killed a moose every 4-8 days in the winter and every 8-11 days in the summer (excluding neonate predation which we were not able to detect). In JPRF, wolf packs killed a moose every 7-12 days in the winter and every 19-26 days in the summer, but when we considered the number of wolves per pack in the two study areas, the kill rates per wolf were similar. Kill rates are the number of prey killed by a predator, but predation rates translate that to the effect on the prey population, typically as the proportion of the prey population lost to predation. Based on recent midwinter moose density estimates (Scheideman and Anderson 2021), these kill rates would equate to 7-20% of the moose population for PGS and 2-8% of the moose population for JPRF (excluding any neonate mortality, but this is also accounted for in midwinter density estimates). Sustainable predation rates depend on the ability of the prey population to recruit new individuals to replace those lost to predation or other causes, and the predation rates here are likely sustainable, especially given that moose populations have started to increase over the last several years (Scheideman and Anderson 2021). These predation rates may not be indicative of predation rates during the moose decline in the 2000s, so it is important to consider what mechanisms could contribute to increased or decreased kill rates.

To examine habitat selection, we focused on using integrated step selection analysis (iSSA, Avgar et al. 2016) in PGS to investigate wolf response to the roads and cutblocks associated with salvage logging (Boucher et al. 2022). As expected, roads facilitated wolf movement. Wolves selected for new (0-8 yr old) cutblocks and moved more slowly in regenerating (9-24 yr old) cutblocks. To link wolf habitat selection and predation risk to moose, we considered the landscape characteristics at confirmed moose kill sites following a used-available logistic regression approach (Manly et al. 2002, Boucher et al. 2022). Moose kills were associated with higher proportions of new and regenerating cutblocks and were closer to water than expected at random. Deciduous-leading stands were less likely to be associated with moose kills or selected by wolves – these stands were consistently selected by cow moose in all seasons across 3 interior BC study areas, including PGS (Scheideman 2018).

The results of this project can inform habitat management to minimize predation risk to moose in areas where moose enhancement is the management objective. The well-established behaviour of wolves using roads to increase search efficiency should be considered in road construction and deactivation activities, particularly where roads connect disjunct or isolated habitat patches and could increase predation risk within those patches. Deciduous stands, which are selected by moose but not selected by wolves or associated with kill sites, should be maintained or enhanced on the landscape. Cutblock configuration should reduce sightlines, which likely contribute to wolf use of new cutblocks. Liberal wolf harvest opportunities can be maintained, although improved harvest reporting is recommended.

Introduction

Moose (*Alces alces*) are a critical component of the ecology of interior British Columbia (BC). They are also important to consumptive and non-consumptive users, ensuring the social and cultural persistence of First Nations and supporting rural and remote communities (GOABC 2016, Gorley 2016). Beginning in the early 2000s, a mountain pine beetle (MPB, *Dendroctonus ponderosae*) outbreak killed a large proportion of mature pine stands in interior BC and widespread salvage logging was undertaken to reduce the spread and maximize utilization of dead standing pine (Alfaro et al. 2015). Moose populations declined over the same period throughout interior BC (Kuzyk 2016, Kuzyk et al. 2018).

In 2013, the British Columbia Ministry of Forests, Lands and Natural Resource Operations (later Ministry of Forests, Lands, Natural Resource Operations and Rural Development; now Ministry of Forests) initiated a 5-year research project on the effects of landscape change on moose populations (Kuzyk and Heard 2014). This landscape change hypothesis predicted that moose declines were due in part to the habitat changes associated with the MPB outbreak and subsequent salvage logging, including through increased predation and hunting. Five study areas in central BC with varying levels of pine salvage were chosen where collars had been deployed in beginning in February 2012: Bonaparte (Region 3), Big Creek (Region 5), Entiako (Region 6), Prince George South (PGS; Region 7A) and John Prince Research Forest (JPRF; Region 7A). During 2015-2020, the same methods were applied to examine limiting factors for moose in the West Parsnip (Region 7A) and Moberly (Region 7B) study areas, directed by the Peace-Williston Fish and Wildlife Compensation Program (Sittler 2020). From 2016-2021, 8-month-old moose calves were also collared and monitored to test a recruitment hypothesis in the PGS and Bonaparte study areas (Procter et al. 2020).

One of the knowledge gaps consistently identified by biologists, First Nations, and stakeholders has been the role of wolf (*Canis lupus*) predation in moose declines in multi-prey, multi-predator systems (Kuzyk and Heard 2014, BC FLNRO 2014, Kuzyk et al. 2016). Research on wolf-prey dynamics is a regional priority as well, frequently brought up by stakeholders and First Nations and identified as the most significant knowledge gap in BC's Wolf Management Plan (2014). Wolves are an important cause of moose mortality (Ballard et al. 1991, Gasaway et al. 1992, Bergerud and Elliot 1998, Hayes et al. 2003, Patterson et al. 2013, Mumma and Gillingham 2019), but several factors can influence the vulnerability of moose to wolves and therefore predation rates. Many of these variables, including wolf density, pack structure, distribution and wolf use of habitat features, are not well studied in interior BC.

The objective of this project was to determine landscape features associated with higher risk of wolf predation for moose. To address this objective, we examined habitat use and movement rates in relation to landscape features, wolf density and abundance, and kill rates with particular focus on moose kills. Our study areas overlapped the PGS and JPRF Provincial Moose Research Project study areas. The project also provides baseline data for any proposed management action aimed at altering the behavior, distribution, or abundance of wolves in the BC interior.

Study Areas

We used the same study area boundaries as the Provincial Moose Research Project in defining the wolf predation study areas in PGS and JPRF (Figure 1), although distribution of wolf collars meant there was not complete overlap. The study areas were delineated using the cumulative distribution of radio-collared moose locations, and except for on-going timber harvesting activities, there was little variation in biotic or abiotic characteristics within study areas over the course of the study. Study area–specific characteristics have been described by Kuzyk et al. (2015, 2016, 2017, 2018, 2019) and Procter et al. (2020).

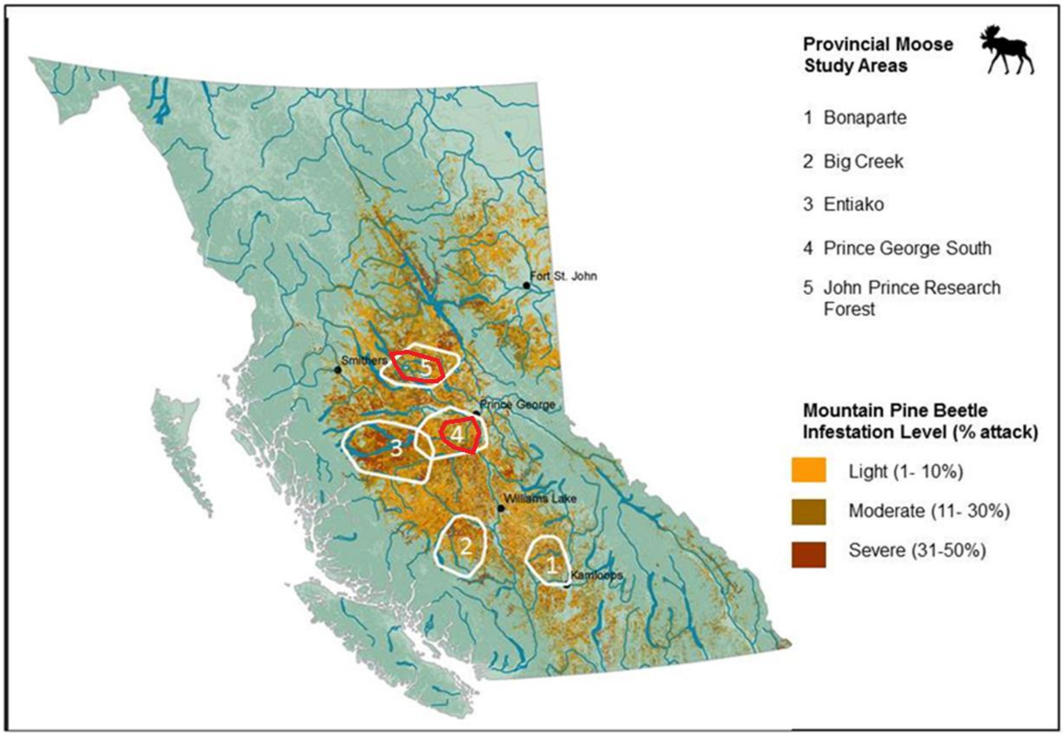


Figure 1. Provincial Moose Research Project study areas, from Procter et al. 2020. The wolf predation study areas (red) overlap the PGS and JPRF moose study areas (white).

Capture and handling

We captured wolves by aerial net-gunning and darting in winter, and by soft-catch foot-hold trapping in summer (Appendix 1, Figure 2). We used standard protocols (RISC 1998) approved by the Provincial Wildlife Veterinarian (Wildlife Act Permit PG17-272811). For helicopter captures, we immobilized wolves by aerial-delivered darts (Pneudart remote delivery system, ‘brown’ or ‘green’ charge and power setting 1 or 2) containing tiletamine-zolazepam (Telazol/Zoletil, Ballard et al. 1991) at approximately 6 mg/kg dosage. We also used a hand-held net gun to fire a net over the wolf prior to darting when possible, to ensure the wolf remained at the capture site prior to the drug taking effect. For live-trapping, we used modified steel foot-hold traps with rubberized offset jaws (Livestock Protection EZ Grip #7) and a drag hook on an 8’ chain. Traps were boiled and waxed prior to deployment in trailside sets along secondary resource roads and wolf trails around dens. Traps were checked daily and baited regularly with a combination of beaver castor, wolf gland lure, wolf urine, and fresh wolf scats from neighboring wolf pack territories. We restrained trapped wolves with a 4-6’ expanding noose pole around the neck and hand-injected tiletamine-zolazepam with the appropriate dose of immobilization drug based on the wolf’s estimated weight.

Figure 2. Winter helicopter capture (top): wolf 17-9808 darted on the Blackwater River (left) and wolf 19-1458 recovers at Graveyard Lake (right). Summer trapping (bottom): trailside trap sets (left and center) and drag mark from trapped wolf (right).

After assessing anesthesia and determining the wolf was adequately sedated, we performed a complete physical examination and monitored vital signs immediately and every 5-10 minutes. We fitted each wolf with either a satellite GPS radio-collar (n=22) or a VHF radio-collar (n=11). Satellite collars were programmed to obtain positional fixes every 60 minutes. GPS positions stored on the collar but not successfully uploaded via satellite were directly downloaded from recovered collars following a mortality or recovery of a failed collar. Collars contained an internal tip switch to detect animal movement rates and were programmed to send a mortality alert via email and text message if no movement was detected for 12 hours. We retrieved collars in mortality mode but did not attempt to quantify cause-specific mortality with rapid response mortality investigations. VHF collars were deployed in packs that also had a satellite GPS collar to facilitate relocation of the pack in case of GPS collar failure. Both VHF and GPS collars were equipped with timed mechanical drop-off mechanisms to ensure collars dropped off at the completion of the study without requiring recapture of collared wolves. Wolves were also marked with a plastic ear tag for identification following timed automatic drop-off of the collar.

We examined and sampled captured wolves according to a standard protocol, including age class using tooth wear (Mech and Boitani 2003), sex, breeding status for females, body condition, standard measurements for body size, ~10 ml of blood for serological screening, 6 mm punch ear biopsy for genetics, and >30 hairs with roots to be archived (Figure 3). Breeding status was determined for males and confirmed for females based on movements and behaviour during subsequent monitoring.

Figure 3. Marking and sampling wolves captured in PGS and JPRF: applying ear tag (top left), taking measurements (top center) and blood samples (top right), checking tooth wear (bottom left) and adjusting collar fit (bottom right).

Demographic rates

Demographic rates were not a primary objective of this project, as we considered it unlikely that we would be able to monitor enough wolves for a long enough time to have precise estimates of survival, cause-specific mortality, and recruitment. Given that this information is difficult to obtain, we present what we observed based on the sample of wolves monitored between January 2018 and March 2022.

Survival rates – We applied a staggered-entry Kaplan-Meier estimator for survival (Pollock et al. 1989) with weekly entries from capture to mortality or collar failure for the duration of the study. We included all satellite-collared wolves because there was a clear date at which they could be censored from the analysis if they dispersed or if the collar went offline. One VHF-collared wolf captured in March 2018 was harvested by a hunter in November 2018 and was included in the analysis, but the other VHF collars were not monitored consistently enough to provide a date of death or censorship. Annual survival (assuming April 15 as the start of a biological year to coincide with denning) was variable and relied on a small sample size each year. About two thirds of the adult wolves appear to survive each year: survival was 0.67 (0.29-1.0 95%CI) after the first year of the project, 0.46 (0.14-0.79 95%CI) in the second, 0.32 (0.04-0.60 95%CI) in the third, and 0.17 (0-0.39 95%CI) in the fourth (Figure 4). Sample sizes were small and variance was large, making it difficult to determine any significant interannual variation in annual survival rates over the course of the study (Figure 5).

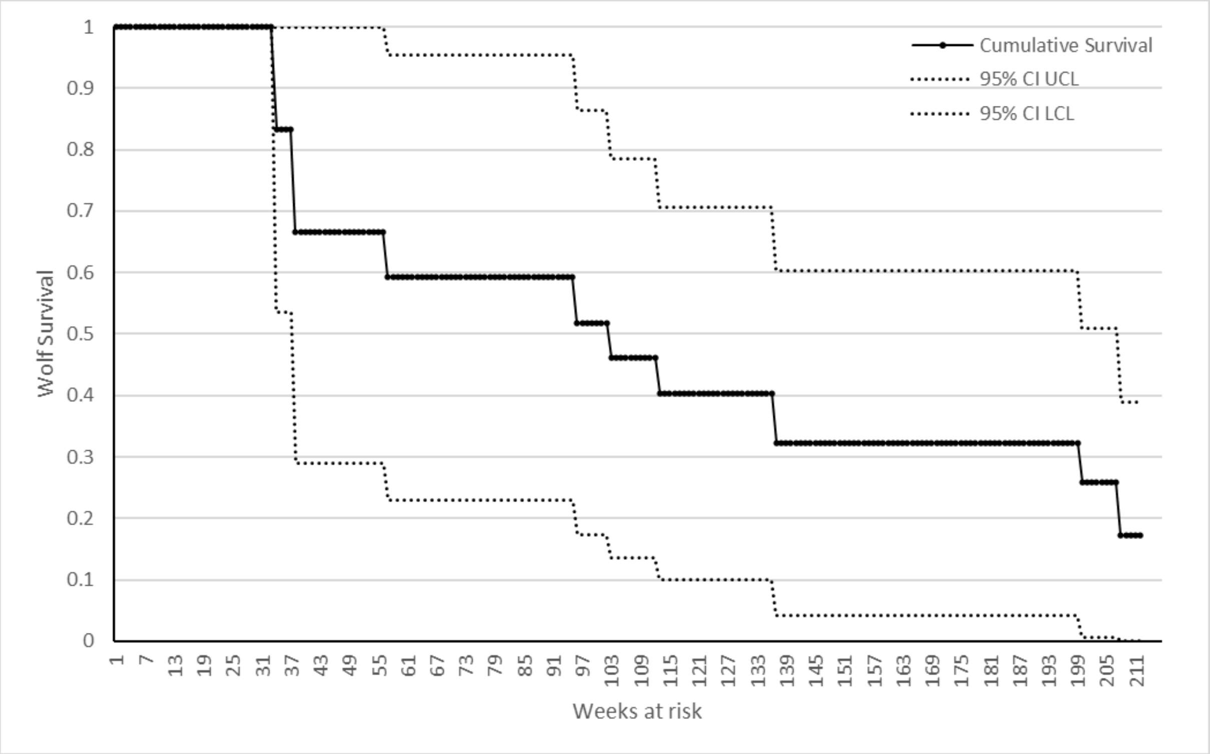


Figure 4. Staggered-entry Kaplan-Meier survival estimates for 23 wolves monitored in PGS and JPRF between January 2018 and March 2022 by satellite collar; one wolf with a VHF collar shot by a hunter in November 2018 was included, but the other VHF-collared wolves were not relocated often enough to provide a date of mortality/censorship.

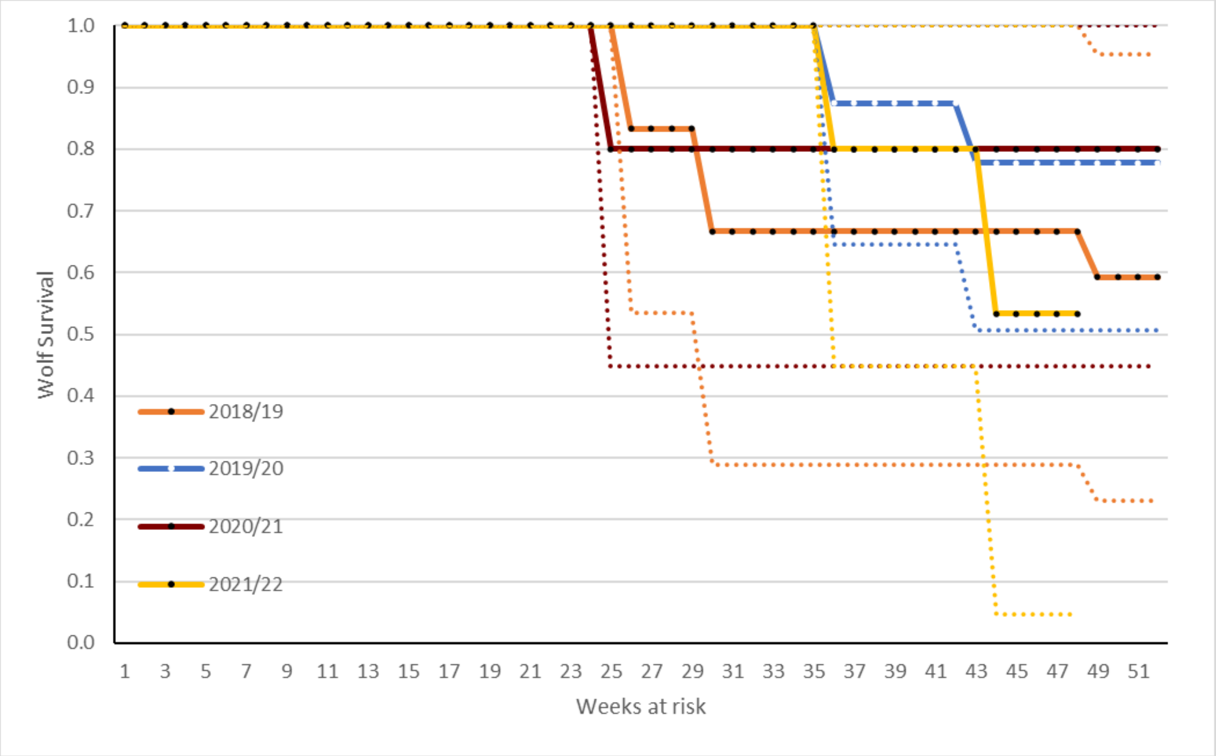


Figure 5. Annual staggered-entry Kaplan-Meier survival estimates for 23 wolves monitored in PGS and JPRF between January 2018 and March 2022 by satellite collar; one wolf with a VHF collar shot by a hunter in November 2018 was included, but the other VHF-collared wolves were not relocated often enough to provide a date of mortality/censorship. Dotted lines represent 95% confidence intervals.

Annual survival rates estimated here are consistent with a stable wolf population, although a measure of recruitment would also be needed to determine population trajectory with any certainty. Mech (2001) suggested that annual winter harvest rates of 28-47% could be sustained by the wolf population in Minnesota. Our observed survival rates are lower than those reported for an increasing population of wolves recolonizing the northwestern US (0.75, Smith et al. 2010) but similar to the expanding Minnesota population, ranging from 0.55 to 0.87 (Chakrabarti et al. 2022). Annual survival rates of a stable wolf population around Banff National Park were 0.84 in the park and 0.44 outside the park, with low dispersal from the park (Hebblewhite and Whittington 2020). Wolves in an unhunted population with high prey density in Yellowstone National Park had much higher survival rates, around 0.80 for yearlings and adults until survival declined to around 0.63 in wolves 7+ years old (Cubaynes et al. 2014).

Cause-specific mortality - Collars were marked with contact information on a metal tag to be returned to Ministry staff and wolves were marked with an ear tag for identification after the collar dropped off. Most hunters and trappers returned collars promptly and were interested to learn about the animals they had harvested. In one case when a collar was not returned, Conservation Officers followed up to retrieve it from the hunter at their residence. There were 9 mortalities of collared wolves recorded during the study and all were human-caused: 3 wolves were legally killed by trappers, 5 wolves were legally shot by resident hunters, and one wolf dispersed to the Itcha-Ilgatchuz range and was shot during the wolf removal operations for caribou recovery there. Only one of these was a VHF-collared wolf, and it is possible that other VHF-collared wolves were killed and not reported, as we only sporadically monitored those collars. For the same reason, we may also have missed natural mortality events on VHF-collared wolves. Most of the GPS collars also did not function correctly for the expected duration of deployment – one hunter-killed wolf had an offline collar, and one trapped wolf had previously been collared but the collar had dropped (it still had an ear tag, allowing it to be identified).

Similar to this project, human-caused mortality dominates cause-specific mortality for wolves, usually a combination of vehicle strikes, hunting, and trapping (Hebblewhite and Whittington 2020, Chatrabarti et al. 2022, Hill et al. 2022). Almost 80% of wolves monitored in the northwestern US died from anthropogenic causes, but this mortality can be partially compensatory to other forms of mortality as well (Murray et al. 2010). In Yellowstone National Park, where wolves are not hunted, 30-40% of mortality was due to intraspecific aggression, and in Alaska, harvest <29% was considered largely compensatory mortality (Adams et al. 2008). High rates of human-caused mortality can be additive or super-additive (higher impact due to removal of breeders; Creel and Rotella 2010) but annual harvests of up to 35-50% have been observed with stable wolf populations (Ballard et al. 1987, Idaho Legislative Wolf Oversight Committee 2002, Montana Department of Fish, Wildlife and Parks 2003).

Recruitment – Although we did not attempt to quantify pup production or true recruitment in this study, repeated observations of the collared packs did provide some information on litter sizes, denning frequency, and occasionally the number of pups surviving until late winter (Table 1, Figure 6). We located dens by ground-truthing wolf location clusters in April and May with characteristic movement patterns associated with repeated trips to the den. Active dens were confirmed by recent excavation, fresh scat, matted vegetation in bed sites and play areas, and by the presence of pups heard or seen in the den. We set up 2-3 remote cameras (Reconyx and Bushnell) near dens to confirm pup counts and retrieved them after the denning period to reduce disturbance. Pup production was variable, with some large litters of 6-7 pups detected and some packs not producing pups every year. We would expect true recruitment to be much lower than pup production – Fuller (1989) recorded average litter sizes of 6.6 pups in Minnesota but only 3.2 pups by late November. Wolves did reuse the same den sites in multiple years, but often had several dens in their territory and were not always at dens we had located based on earlier collar locations, making it difficult to continue monitoring them after collars went offline. Over the course of the study, we observed 19 active dens or litters of 10 packs over 23 pack-years monitored, for a denning rate of 83%. However, this denning rate may be biased high because it includes 4 observations for uncollared wolves, which can be confirmed at an active den, but cannot be confirmed to not have an active den. Considering only the collared wolves for which this bias would be minimized, we recorded 15 active dens or litters of 19 pack-years, for a denning rate of 65%. Pup survival is expected to be highly variable, and the timing of litter counts varied from May (expected to approximate pup production) to late March (expected to approximate pup recruitment). We recorded four May-June pup counts (mean 5 pups 1.8 SD), two summer counts (mean 4 pups 1.4 SD), and four counts from December to March (mean 2.3 pups 2.2 SD). Pup production is expected to be higher than what we observed because of early den failures and early pup mortality.

Table 1. Denning activity and pup counts for wolf packs in PGS and JPRF. Den activity was based on sign found at dens and movements of collared wolves, summer pup counts were based on remote camera detections, and winter pup counts were based on observations during aerial surveys and captures.

Study Area	Pack	Summer 2018	Summer 2019	Summer 2020	Summer 2021
PGS	Blackwater	3 (in May)	7 (in May)	Not monitored	Not monitored
	Bobtail Mountain	No den found	Not monitored	Not monitored	Active den
	Clear Lake	Active den	No den found	Not monitored	Not monitored
	Ghost Pack	Not monitored	Not monitored	No den found	Not monitored
	Grizzly Lake	Not monitored	Not monitored	5 (in July)	Active den
	Tagai Lake	2-3 (in Mar 2019)	4 (in June)	No den found	Not monitored
JPRF	Hat Lake	Active den	Active den	Active den	Not monitored
	Kazchek Lake	Not monitored	Active den	3 (in July)	Active den
	Pinchi Lake	1 (in Mar 2019)	Not monitored	5 (in Dec)	Not monitored
	Tachie	0 (in Feb 2019)	Active den	6 (in June)	Not monitored
	Tanizul Lake	Not monitored	Active den	Not monitored	Not monitored

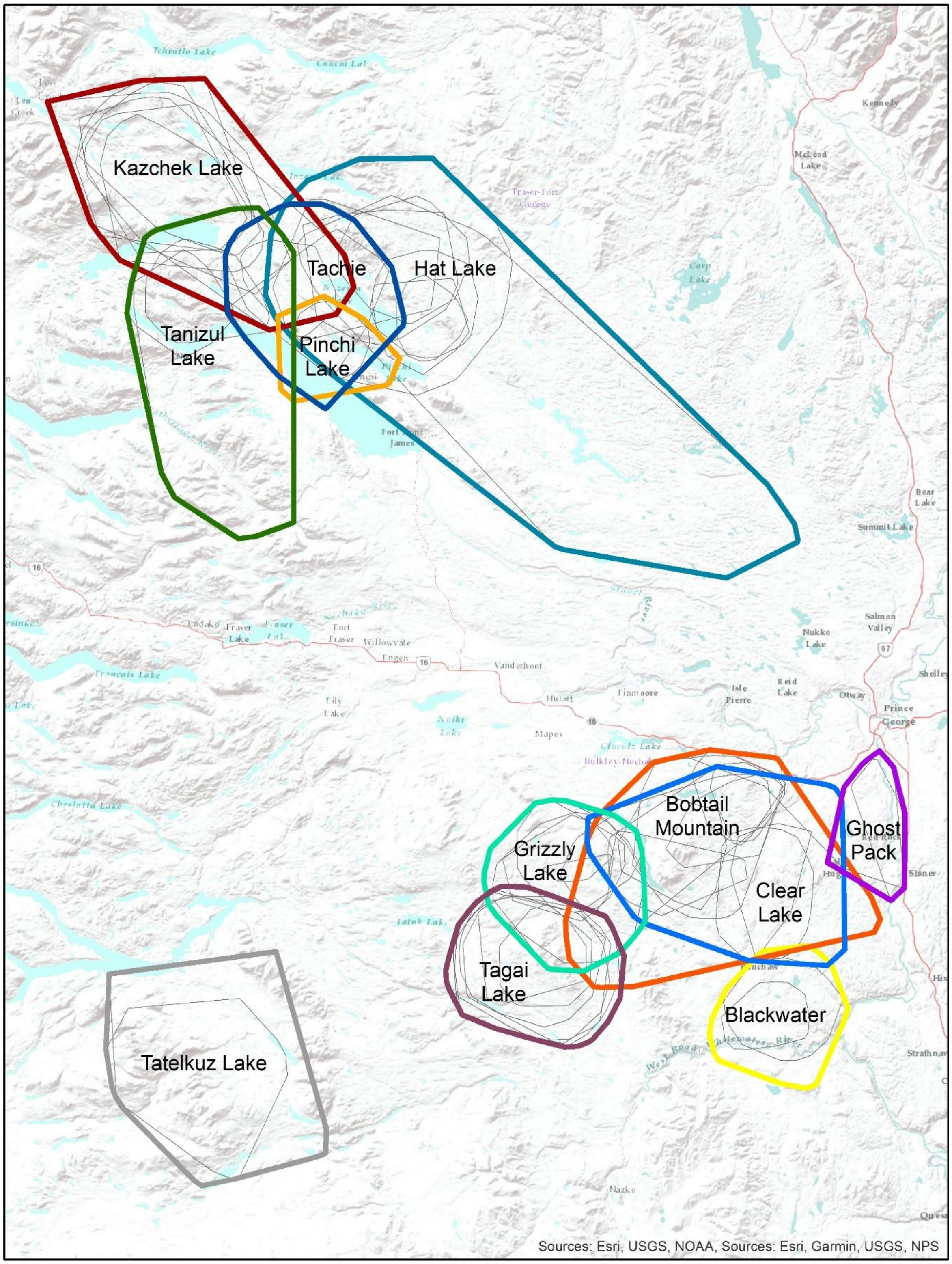
Figure 6. Typical wolf dens used by PGS and JPRF packs under trees (Bobtail Mountain pack, top left; Blackwater pack, top right) and dug into banks (Hat Lake pack, bottom left; Blackwater pack, center right). The largest litters we recorded were 6 pups in the Tachie pack (center left) and 7 pups in the Blackwater pack (bottom right).

Wolf abundance

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). Seasonal and interannual variation can also be high. High wolf density areas of BC, including PGS and JPRF, likely represent 5-15 wolves/1000 km^2 (BC FLNRO 2014). Measuring wolf density or population trend is a complicated and expensive exercise, and relatively few wolf inventories have been done in the province (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, so most inventories were done to better understand wolf predation on caribou (van Oort et al. 2010, Serrouya et al. 2015, Bird et al. 2016, Gill and van Oort 2017, White 2018, Anderson and Klaczek 2019), deer (Hatter and Janz 1994) or moose (Bergerud and Elliot 1998, Anderson et al. 2017). Instead, wolf density has been estimated provincially by an ungulate biomass index (Fuller et al. 2003, BC FLNRO 2014, Kuzyk and Hatter 2014). When collared animals are available, the combination of territory delineation and pack counts can provide more reliable multi-year population estimates. Other non-invasive methods are being developed as well, but often provide presence/absence data or measures of relative abundance, rather than absolute abundance estimates.

Home range size

We considered a 95% kernel density estimate (KDE) and a 95% minimum convex polygon (MCP) estimate calculated in R Studio using R 3.6.0 in the *adehabitatHR* package (Calenge 2021). KDE home ranges consider the intensity of use within the home range in the estimator; MCP home ranges do not account for intensity of use, but have been widely implemented, especially prior to high fix rate GPS collars, and can be effective for delineating home range of territorial species. We determined home ranges annually for summer (April 1-October 31) and winter (November 1 – March 31; Figure 6) and considered the average size of all seasonal home ranges for a pack to be the overall home range size. We used ArcGIS 10.8 (ESRI, Redlands, CA) to delineate the outer boundary of all MCPs to define the study area for density calculations (study areas were 4594 km^2 in PGS and 4119 km^2 in JPRF; we excluded the off-territory movements in Hat Lake and Tanizul Lake in winter 2020, Figure 7). Home range size varied from around 250-1100 km^2 (Table 2). This is within the reported values for wolf populations elsewhere in northern North America (Mech and Boitani 2003). There was no significant difference between the average home range sizes of packs in PGS and JPRF for summer or winter (t-test, $p>0.05$).



Sources: Esri, USGS, NOAA, Sources: Esri, Garmin, USGS, NPS

Figure 7. Seasonal home ranges (95% MCP) for wolf packs monitored 2018-2022 in PGS and JPRF (thin grey lines) and minimum convex hull of aggregate seasonal home ranges (thick colored line) – this includes some off-territory movements in Tanizul Lake and Hat Lake, and incorporates shifting home ranges between Clear Lake and Bobtail Mountain.

Pack size

Wolf density is generally presented based on mid-winter pack counts. Mid-winter pack counts are the standard for reporting wolf densities because packs are more cohesive, counts have historically been easier to obtain, and the estimates account for early pup mortality. We determined pack counts over the 5 years of the study when possible – if collars were offline, packs could not always be reliably located. In winter, we based pack counts off observations during wolf captures and other fieldwork in the study areas (moose and elk surveys, calf-at-heel surveys, moose captures), and reports from trappers and guides. This included counts of the wolves as well as track counts where the pack split apart on frozen lakes or in cutblocks. Wolves in the same pack are not always travelling together even in winter, so we attempted to get multiple observations. The number of winter pack estimates in a given year varied from one (or none) to five depending on the pack. We also determined summer pack counts and pup counts for packs that had known den/rendezvous sites using remote cameras. We consider the remote camera counts as minimum counts because we only counted individual wolves that could be reliably differentiated from each other based on coloration and markings in the photographs.

Figure 8. Pack count during December 2020 moose surveys of the Pinchi Lake pack (left) and remote camera image from Blackwater River den of breeding female and pups, May 2019 (right).

Pack size may be as important to predation rates as wolf density in some systems, as 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 number of packs was similar in both study areas (6 monitored in PGS and 5 monitored in JPRF) for a pack density of 1.9 packs/1000 km^2 in PGS and 1.6 packs/1000 km^2 in JPRF based on MCP home ranges. The difference in wolf density between the two study areas is therefore driven by pack size (see below) rather than the number of packs.

Wolf packs were on average larger in PGS (7.4 wolves/pack) than in JPRF (4.2 wolves/pack). The difference in pack size had also been noted in the 2017 track surveys although survey conditions were not ideal (3-5 wolves per pack in JPRF, 5-7 wolves per pack in PGS, Anderson et al. 2017). There could be several explanations and implications of differences in pack size between the two study areas. 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 are not able to assess this as a driver for pack size between the two sites – anecdotally there are active, successful trappers in parts of both PGS and JPRF, but effort varies depending on the year and not all traplines in either study area consistently target wolves. Furthermore, the mortality data suggests that hunter activity may be as important as trapper activity to total recent wolf harvest at the study area scale. This may be partially due to economic and logistic concerns that also govern the species targeted by individual trappers; wolves require significant effort not only to trap but also in fur handling, and recent low prices for wolf pelts have not provided much incentive to target wolves. Resident hunters have a long season and no species license (tag) requirement, facilitating more opportunistic harvest.

Wolf pack size is also 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. Large packs are also more successful than small packs at killing prey (MacNulty et al. 2012). Higher prey densities support larger packs (Sells et al. 2022). In both study areas, moose are the primary prey and densities are similar, suggesting that prey availability may not be the primary driver of pack size differences between sites. Wolves in JPRF do consume a higher proportion of smaller prey (elk, deer, bear), but moose still make up the majority of their diet. 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, Cassidy 2013, 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/1000 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).

Changing pack dynamics could also influence the pack density among years. The Bobtail Mountain/Clear Lake packs represent an interesting case, where the Bobtail Mountain pack apparently dissolved in summer 2018 with the collared male, believed to be the breeder, dispersing and eventually joining or starting a pack in the Tatelkuz Lake area a year later. Meanwhile, the Clear Lake wolves (including both collared animals, suggesting pack movement not individual dispersal) started using the former Bobtail Mountain home range. At other times, the Bobtail Mountain wolves have predominantly used areas either north of Bobtail Mountain around Norman and Dahl lakes, or southwest of Bobtail Mountain around Bobtail Lake. Removal of packs or most wolves in a pack could also alter pack densities. In fall 2019, 6 wolves from a pack of 7 along the Mud River (very likely Clear Lake pack, although the collared wolf had dispersed) were trapped due to cattle depredations (R. Berreth, pers. comm.), but by summer 2020 another pack of 6 wolves was using the area. It is not clear whether that was a changing pack boundary, as Clear Lake had demonstrated in summer 2018, or a stable territory with turnover in individuals, as was generally the case for harvest wolf populations examined in Idaho (Bassing et al. 2018).

Table 2. Home range sizes based on 95% kernel density estimator (KDE) and 95% minimum convex polygon (MCP) and average maximum midwinter pack counts for wolf packs monitored in PGS and JPRF 2018-2022 with density calculated at the home range scale and over the study area.

		Pack Count	Summer Range (km^2)		Winter Range (km^2)		Overall Range (km^2)		Density (wolves/1000 km^2)	
			KDE	MCP	KDE	MCP	KDE	MCP	KDE	MCP
PGS	Blackwater	7.0	486	469	509	400	501	423	14.0	16.6
	Bobtail Mountain	10.5	1186	1247	625	445	812	712	12.9	14.7
	Clear Lake	9.0	461	408	1043	897	810	702	11.1	12.8
	Ghost Pack	5.0	387	315	434	195	411	255	12.2	19.6
	Grizzly Lake	7.5	695	424	1075	513	822	454	9.1	16.5
	Tagai Lake	5.5	973	880	659	556	793	695	6.9	7.9
	Study area (6 packs)	44.5						4595		9.7
JPRF	Hat Lake	5.0	1040	1006	628	512	805	723	6.9	6.2
	Kazchek Lake	3.7	1249	1292	964	827	1106	1059	3.3	3.5
	Pinchi Lake	4.7	209	183	279	410	244	296	19.2	15.9
	Tachie	3.0	644	832	554	574	584	660	5.1	4.5
	Tanizul Lake	4.5	520	441	418	340	469	390	9.6	11.5
	Study area (5 packs)	20.9						4119		5.1
Other	Tatelkuz Lake	2.0	924	1030	1305	1746	1114	1388	1.8	1.4

Wolf density

We took the average maximum winter pack count over the 5 years and applied it across the study area to estimate densities of 9.7 wolves/1000 km^2 in PGS and 5.1 wolves/1000 km^2 in JPRF, with much higher densities for some pack home ranges (Table 2). Based on either overall density (total number of wolves in the study area) or density within home ranges (number of wolves in a pack territory), wolf density in PGS was higher than in JPRF, at around 10 wolves/1000 km^2 compared to around 5 wolves/1000 km^2 (Table 2). The density estimate calculated for the entire study area is likely lower than those calculated from an average of home range densities because it includes low density areas within the study area and potentially parts of other neighboring pack territories at the edge. Wolf density is also expected to fluctuate widely between seasons, with large litters of pups observed in both study areas on this project. Changing survival and dispersal rates for pups and adults would also change density estimates among years. Density estimates increase only slightly if we account for lone wolves, which make up about 10-15% of other populations where proportion of lone wolves has been examined (MN DNR 2001).

The density estimated for PGS was within the range of wolf densities reported for northern BC (10-44 wolves/1000 km^2, FLNRO 2014), while JPRF was somewhat lower. Both densities were similar to the regional wolf density estimated from ungulate biomass (6.9-13.7 wolves/1000 km^2, Kuzyk and Hatter

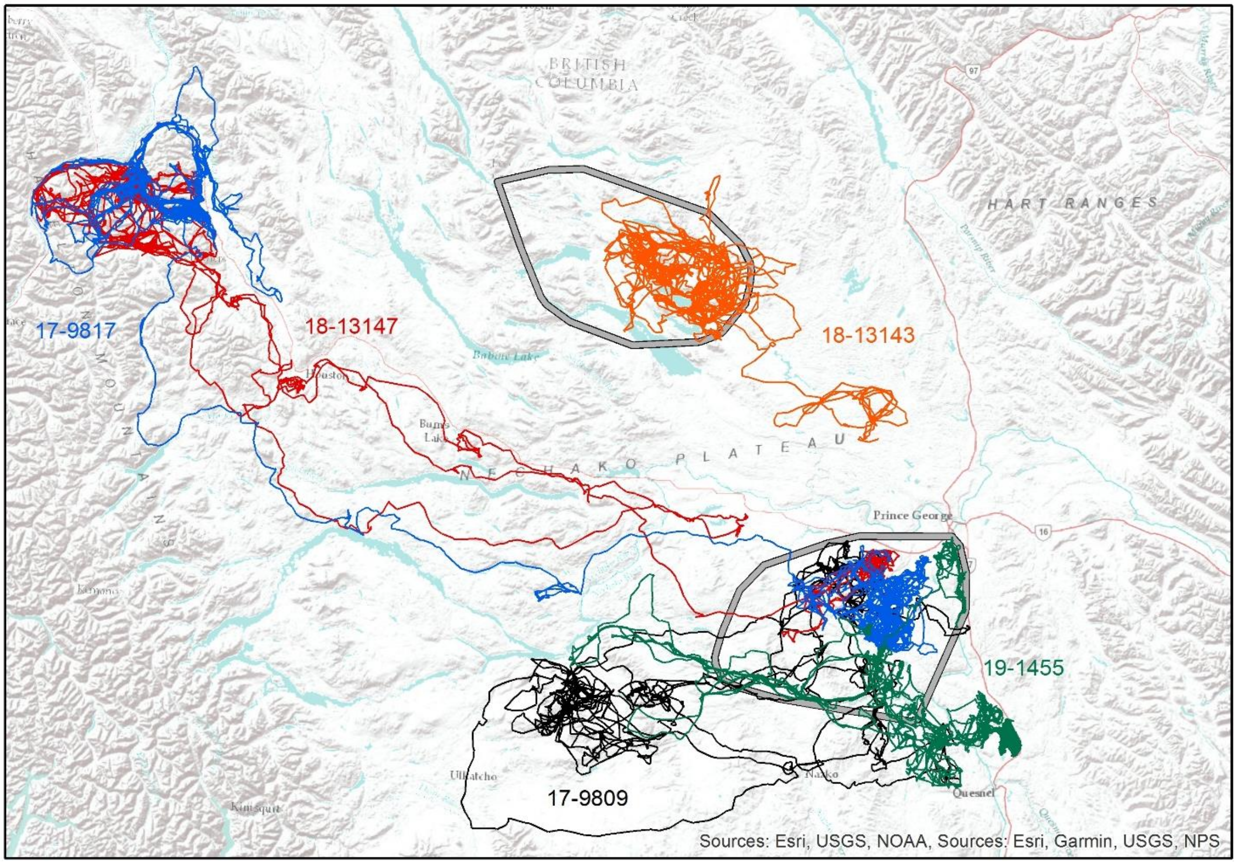
2014). The density determined here by monitoring collars over several years was notably different from the density estimates determined by snowtrack surveys in 2017 in PGS (20.5-23.3 wolves/1000 km^2) and JPRF (13.5-16.5 wolves/1000 km^2; Anderson et al. 2017). Conditions for the surveys were noted as suboptimal at the time, with low snowpack and melted areas making it difficult to follow wolf trails for their total length. This likely resulted in continuous trails being classified incorrectly as unique observations where observers were unable to follow them for their complete length, inflating the estimated number of packs and/or wolves in the survey area.

Dispersal

Assessing dispersal patterns was not a primary objective of this project. However, given the limited information available for central BC and the implications for management, including wolf removal for caribou recovery actions, it is worth summarizing the dispersal incidences from this project. In some cases, the dispersing wolves appeared to settle on a new territory – the former Bobtail Mountain male was seen with one other wolf in the Tatelkuz Lake area, and both Clear Lake dispersers appeared to settle between Smithers and Cedarvale, BC. The Hat Lake and Ghost Pack dispersers had not settled on new territories before monitoring ended due to wolf mortality or collar drop-off (Figure 9, Table 3).

Table 3. Summary of dispersal events for wolves collared 2018-2022 in PGS and JPRF study sites.

Wolf ID	Pack	Sex	Age at Dispersal	Dispersal Date	Fate
17-9809	Bobtail Mtn	M	Adult	30 Apr 2018	Hunter/conflict kill Apr 2019
17-9817	Clear Lake	M	3	2 Mar 2019	Collar dropped Mar 2020
18-13147	Clear Lake	M	4	3 May 2019	Collar offline Sep 2020
18-13143	Hat Lake	F	5	Unknown	Offline, hunter kill Dec 2019
19-1455	Ghost Pack	M	2	25 May 2020	Collar dropped Feb 2022



Sources: Esri, USGS, NOAA, Sources: Esri, Garmin, USGS, NPS

Figure 9. Movement trajectories of five collared wolves that dispersed from PGS and JPRF study areas (thick grey lines) between 2018-2022.

Wolf harvest

Wolves in Region 7A are managed as a Class 3 furbearer (i.e., not sensitive to harvest) and a big game species. There is no bag limit for hunters and the season is open from Aug 1-Jun 30. A species license (tag) is not required. The trapping season is open Oct 15-May 31. Harvest data is acquired through voluntary surveys for hunters and from royalty payments from fur sales by trappers. Region 7A has no compulsory reporting or inspection for harvested wolves, either by trapping or hunting, although this is employed in some other regions in the province.

Reported harvest through trapping reports and fur royalties (by trapline) and hunter sample surveys (at Wildlife Management Unit WMU scale) is not reliable for estimating true harvest or establishing relative abundance or population trend in our study areas (BC FLNRO 2014, Mowat et al. 2022). The hunter survey is less precise with smaller areas and the harvest reported for PGS (WMUs 7-10, 7-11, 7-12) and JPRF (WMUs 7-25, 7-26) probably underestimates the true harvest based on anecdotal reports (Figure 10, Figure 11, Figure 12, Figure 13). That said, the hunter survey generally overestimates wolf harvest across the province and trapping reports/ fur royalties tend to underestimate trapper harvest (Mowat et al. 2022).

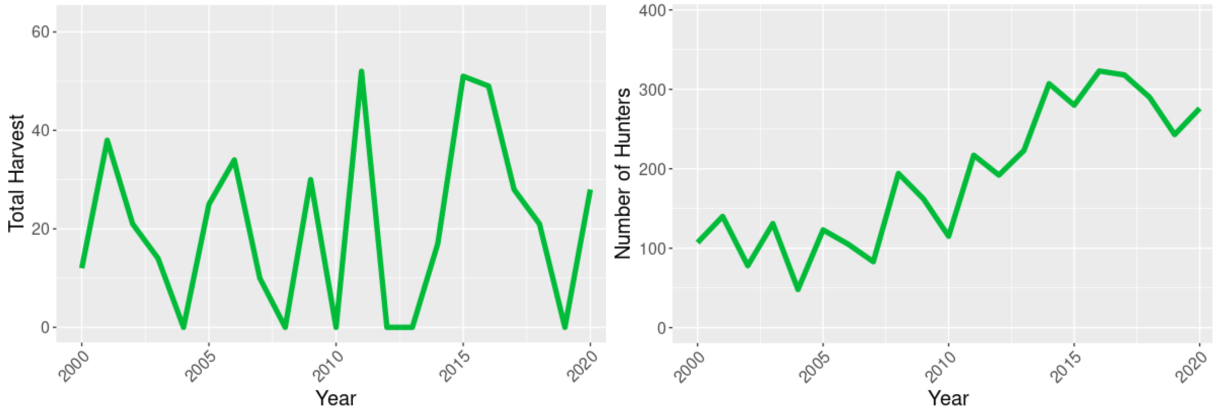


Figure 10. Total wolf harvest by licensed hunters in PGS (WMUs 7-10, 7-11, 7-12) and number of people hunting wolves based on BC Hunter Sample Survey and guide outfitter declarations. Actual number of wolves harvested by hunters is likely higher than that reported on the survey, given several years recording zero harvest.

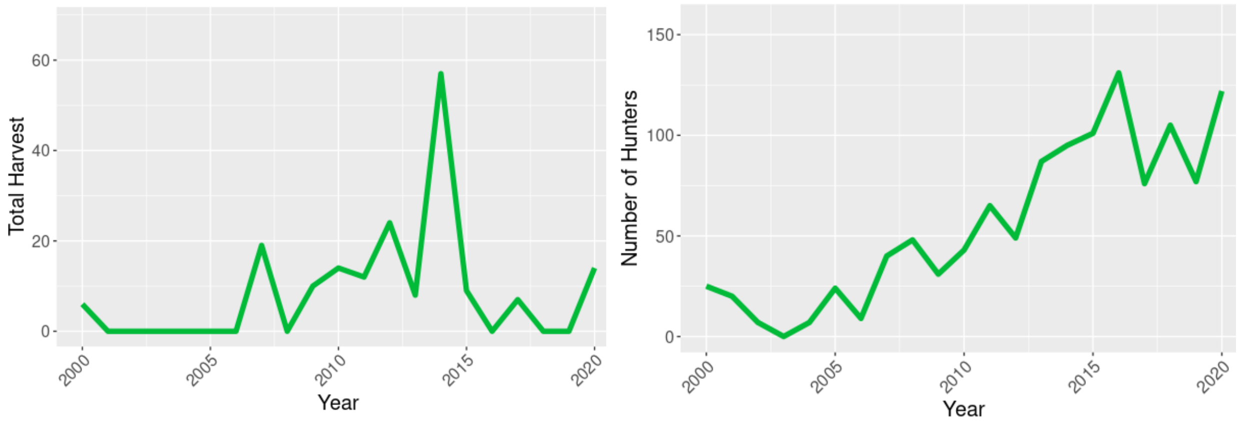


Figure 11. Total wolf harvest by licensed hunters in JPRF (WMUs 7-25, 7-26) and number of people hunting wolves based on BC Hunter Sample Survey and guide outfitter declarations. Actual number of wolves harvested by hunters is likely higher than that reported on the survey, given several years recording zero harvest.

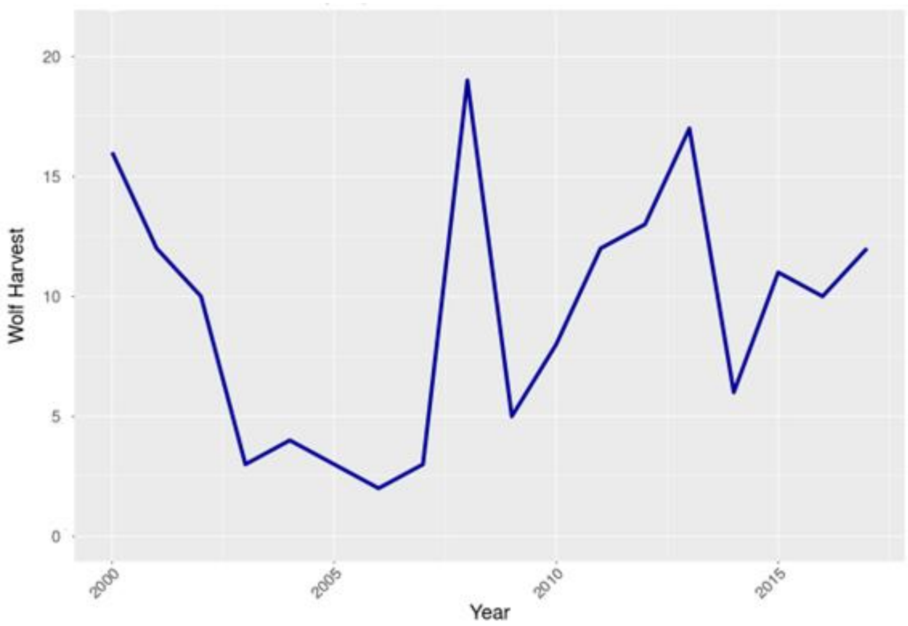


Figure 12. Total wolf harvest by trappers in PGS (WMUs 7-10, 7-11, 7-12). Actual number of wolves harvested is likely higher than that reported on the survey, given several years recording zero harvest. First Nations trapping for sustenance or cultural purposes is not included.

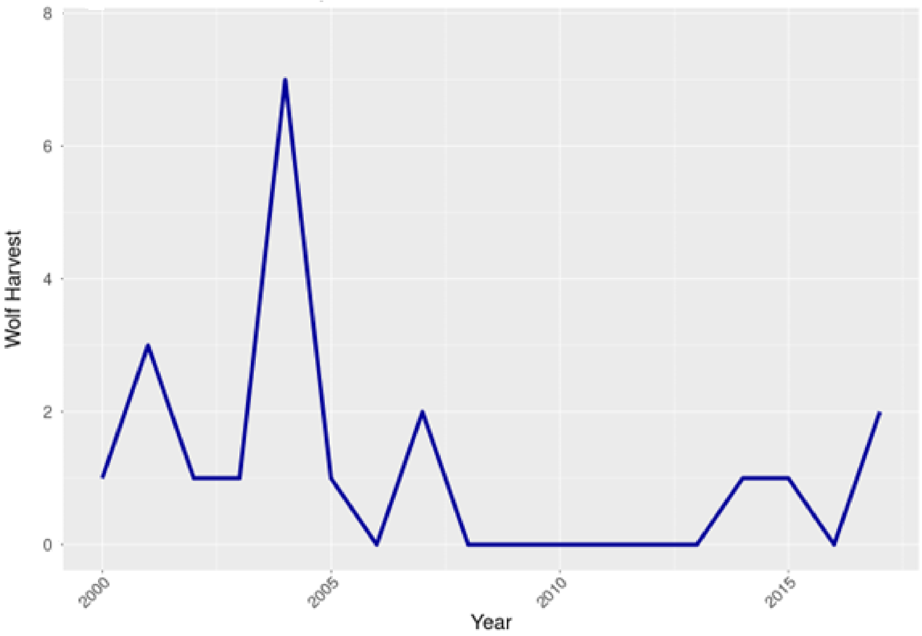


Figure 13. Total wolf harvest by trappers in JPRF (WMUs 7-25, 7-26). Actual number of wolves harvested is likely higher than reported, given several years recording zero harvest and anecdotal information that wolves were indeed harvested. First Nations trapping for sustenance or cultural purposes is not included.

The Chilako (Mud) River valley is comprised of private land, hobby farms, and cattle operations, and wolves are frequently removed by the BC Cattlemen's Association through their Livestock Protection Program to reduce livestock depredation. This may have a destabilizing effect in an area that represents prime wolf habitat based on high wintering moose densities and abundant beavers in the summer and may partly explain the range shift observed for the Clear Lake wolves. Fission-fusion of wolf packs does occur, and where mortality is high and pack structure regularly disrupted, this may become more common. 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 (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. Trapper reporting became mandatory (as of 2021-22 trapping season) and if hunter reporting is similarly improved, the Ministry of Forests may be able to build a useful wolf harvest dataset moving forward.

Characteristics of wolf prey

The identification of carnivore kill sites of large-bodied prey using GPS cluster analysis is a common and reliable method (Anderson and Lindzey 2003, Sand et al. 2005, Webb et al. 2008, Morehouse and Boyce 2011). We assumed that if a wolf killed a prey item, handling time of the carcass would be enough for the kill site to be detected as a cluster with hourly location fixes. Any prey consumed in less than an hour would not be detected, and we would be less likely to detect kills if wolves were quickly displaced from a kill or if the collared wolf was not there for the duration of handling time. We assumed that evidence of a kill would be present at each kill site, and for adult moose this was likely true. It is possible that false negatives occurred due to carcasses being fully consumed, minimal remains being undetected under cover, or carcass remains being moved by scavengers. These challenges are magnified for small-bodied prey like moose neonates, and a 1-hour fix schedule is also unlikely to detect these kills because they are rapidly consumed (Sand et al. 2005, Webb et al. 2008, Merrill et al. 2010, Gable et al. 2016). As such, we are not able to assess the landscape characteristics that are more likely to lead to wolf predation on neonates. Lastly, while we were able to identify some instances of scavenging (bear kills, hunter kills) and removed them from the kill site dataset, it is possible that some of the moose identified at kill sites were scavenged by wolves but died from another cause.

We used the Find Points Cluster Identification Program v.2 (Gillingham 2009) to identify potential kill sites for each GPS-collared wolf. Location clusters were determined using a 100 m search radius over 2 weeks (336 hours). The cluster algorithm was run monthly to allow clusters to accumulate and field visits were days to months following cluster occurrence. Kills made between November and March were often buried by snow almost immediately, so we visited winter kill sites as soon as snow melted in the spring and carcass remains could be seen. At each cluster, we searched the area for evidence of a carcass – usually hair, rumen, and bones at the kill site itself with other bones widely scattered in the vicinity (Figure 14). We determined prey species based on hair, size, and morphology of bones, used the presence of antlers or antler pedicels to determine sex, and tooth wear and eruption to determine age class. We took an incisor when available from adult ungulate kills for cementum annuli aging.

We investigated 1208 clusters between 2018 and 2022, 300 in JPRF and 908 in PGS (5% and 12% of all clusters respectively). We initially visited more small clusters (<10 location fixes) but consistently found no evidence of a carcass and instead prioritized larger clusters with >10 location points. Average number of points in visited clusters was 28 ± 2.1 (95%CI); average number of points in all clusters was 8 ± 0.2 (95%CI).

Figure 14. Kill site investigations for wolf packs monitored in PGS and JPRF: mule deer buck (top left), bull elk (top center), bull moose (top right), black bear (center left), cow moose (center right and center). Typical moose kill sites with hair and rumen and heavily chewed skeletal remains shown in bottom left and right.

Prey species

Of the 290 kill sites identified, most were moose in both PGS (n=200) and JPRF (n=52). We also found elk, deer, domestic cattle (PGS only), and black bear remains (Figure 15), as well as bait piles set by hunters and trappers, gut piles left by hunters, beaver activity, and snowshoe hare activity. We did not attempt to systematically quantify clusters associated with small prey activity. JPRF wolves had a higher proportion of their diet made up of non-moose prey. While we do not have precise estimates of elk, deer, and black bear density for either study area, elk are relatively rare in PGS and cattle are rare in JPRF. Deer densities are likely low to moderate and patchy in both study areas. Black bears are abundant in both areas, although field staff encountered them far more often in JPRF and hair snare work on grizzly bears in JPRF and southwest PGS also suggests higher relative abundance of black bears in JPRF (S. Marshall, pers. comm.). Other clusters were associated with dens, rendezvous sites, bed sites, old kill sites, illegal garbage dump sites, and shed antlers that had been chewed. The discrepancy in sample size of kill sites between PGS and JPRF is a function of how long collars were deployed, how often the collared wolves made kills, and how many cluster sites we were able to visit.

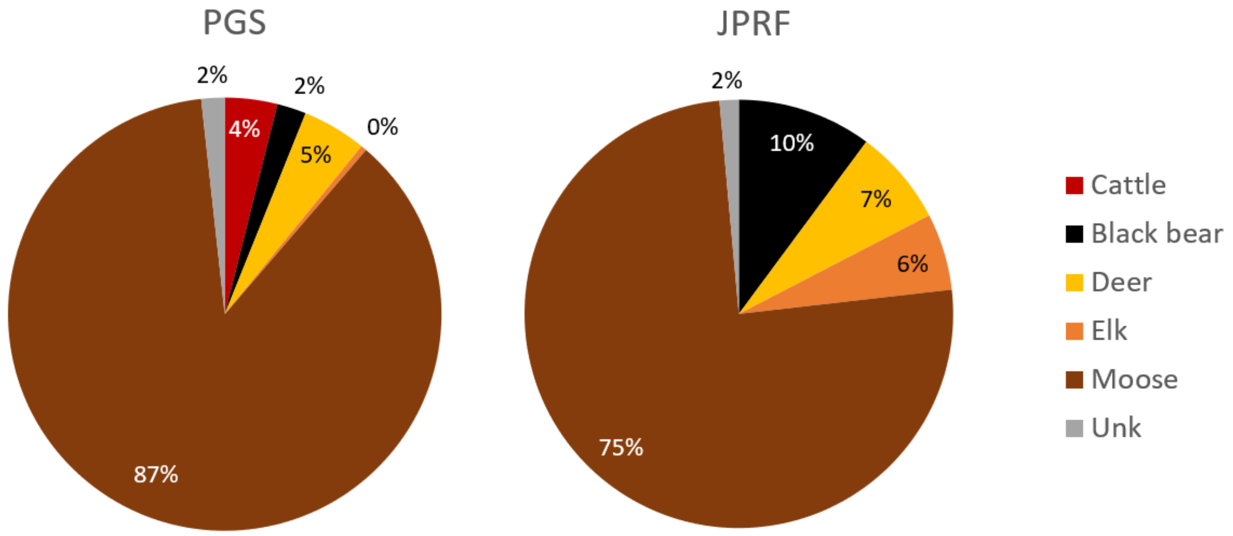


Figure 15. Proportion of species detected at wolf kill-sites in JPRF (n=65) and PGS (n=225), 2018-2022. One elk kill was detected in PGS (0% due to rounding).

Age of wolf-killed moose

Of the 252 moose kill sites detected, we found 69 calves, 175 adults (including 22 yearlings), and 8 moose of unknown age class (only indeterminate bone fragments and hair found). Besides calves and yearlings which were aged by tooth eruption, we determined ages for another 55 moose based on cementum annuli when incisor teeth could be collected. In some cases, especially where cementum ages were uncertain, tooth wear was also used to corroborate estimates.

In other systems where wolf predation patterns have been extensively investigated, wolves generally target young, old, or sick moose (Fuller and Keith 1980, Kunkel and Pletscher 1999, Hayes et al. 2000, Mech and Peterson 2003). We were unable to assess the importance of wolf predation on small moose calves over the summer because 1) we do not detect this small prey in the 1-hr fix intervals on our wolf collars and 2) we generally do not survey moose calves between the neonatal period in June and mid-winter. We can however examine selection of older calves in wolf diets. We have estimates of mid- and late-winter calf ratios (a time when calves are large enough for us to detect with cluster investigations), and if wolves select calves, we expect to see a higher percentage of calves at kill-sites than we see in the winter moose population. Calf ratios on the December 2016 moose survey in Prince George West (PGW; overlaps PGS) were 32 ± 4.6 SE calves per 100 cows or 20% of the population (accounting for 27 ± 4.4 SE bulls per 100 cows; Klaczek et al. 2016). The Fort St. James (FSJ; overlaps JPRF) survey area was also flown, with 35 ± 4.7 SE calves per 100 cows making up 22% of the population (25 ± 4.3 SE bulls per 100 cows; Klaczek et al. 2016). On the December 2020 moose survey, there were 35 ± 3.0 SE calves per 100 cows in PGW and 21 ± 3.0 SE calves per 100 cows in FSJ, or 21% and 13% of the populations respectively (31 ± 4.0 SE bulls per 100 cows PGW and 39 ± 6.0 SE bulls per 100 cows FSJ; Scheideman and Anderson 2021). Calf numbers would be expected to drop by close to 30% from mid-winter ratios up to recruitment at the mean birth date (May 21; Procter et al. 2020), suggesting about 15% of the moose population in our study areas would be calves by mid-May. Based on our kill sites, 27% of wolf-killed moose were calves, similar or somewhat higher than the proportion of calves in the population. This suggests that wolves in our study areas are selecting calves, based on three considerations: first, midwinter calf ratios overestimate the number of calves available to wolves throughout the entire winter because calf ratios decline over that period; second, most wolf kills are in late winter and spring, reflecting those lower calf ratios (Procter et al. 2020); and third, calves are more likely to be underrepresented or classified as unknown based on site investigations due to their smaller size and more complete consumption.

Without knowing the age structure of the moose population, we do not have a baseline dataset to compare with the ages of wolf-killed moose, so we cannot determine whether older moose were selected. This kind of data could be obtained from moose that die from non-age-dependent causes (generally human-caused mortality expected to affect all age and condition moose equally), but we currently lack the sample size to do so. Kuzyk et al. (2020) analyzed the age of more than 2000 hunter-killed moose from 1982-2003 when moose teeth were collected for aging and found the average age of harvested cows to be 4 years old. Moose cows monitored on the Provincial Moose Research Project dying from all causes were much older, averaging 11 years (n=47, Procter et al. 2020). The difference between average age of death identified by Kuzyk et al. (2020) and Procter et al. (2020) is likely due to the inclusion of natural mortality that would differentially affect older individuals, but moose populations may also have shifted to an older age structure following large-scale declines. The ages of 98 wolf-killed, non-collared adult cow moose from this project (7 ± 1.1 yrs 95% CI, range 1–17 yrs) were similar or slightly younger than the wolf-killed cow moose on the provincial moose project in the same study areas (10 ± 1.6 yrs 95% CI, range 1–16 yrs). This may be due in part to the large number of yearlings we were able to identify based on tooth eruption, whereas cow moose on the provincial project were rarely collared as yearlings. Considering only the moose older than 1 year old, ages on this project (10 ± 0.9 yrs 95% CI) were similar to ages on the provincial moose project. This suggests that the ages of collared moose dying from wolf predation are similar to the moose population in general, which is useful information for a study tracking survival of a representative sample of the moose population but does not tell us whether the wolves are selecting older moose. The average age of the 23 wolf-killed bull moose was not different from the average age of wolf-killed cow moose (5 ± 2.0 yrs 95% CI, range 1–14 yrs).

We did not see a clear increase in the number of wolf-killed moose at increasingly advanced ages, but there would be lower numbers of moose older than 12 yrs old on the landscape. The relatively constant number of moose killed by wolves at increasingly older ages, despite fewer of these moose being available, therefore suggests that wolves are selecting older individuals (Figure 16).

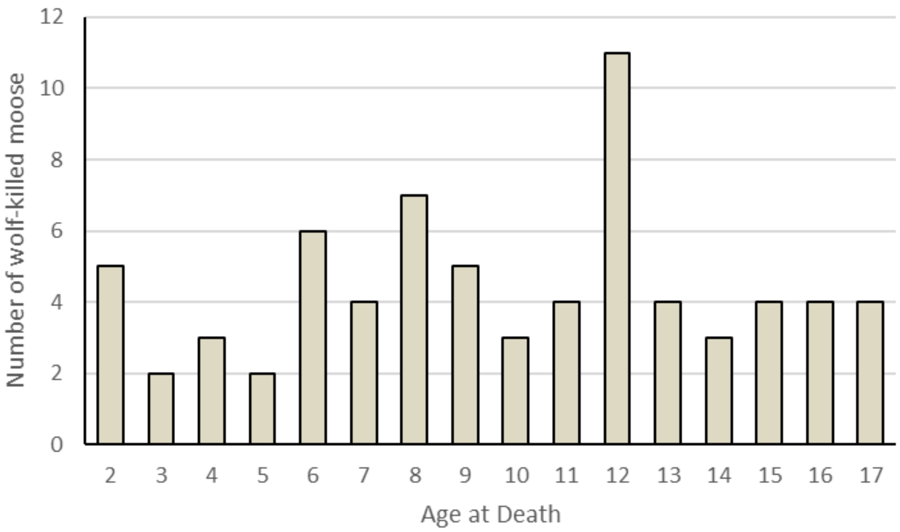


Figure 16. Cementum annuli ages from incisor teeth collected from 73 moose older than 1 year killed by wolves in PGS and JPRF 2018-2022. Calves and yearlings are not included as sample sizes for those age classes were much higher (incisors did not need to be recovered to estimate the age based on tooth eruption).

Sex of wolf-killed moose

Of the 252 moose kill sites detected, we determined sex for 108, including 7 female calves and 6 male calves. Although the sample size for sex of wolf-killed calves is small, it suggests that initial findings for collared moose calves in PGS that noted significantly more males than females dying from predation (Procter et al. 2020) may not be reflective of the overall trend. Bonaparte, the other study area where cause-specific calf mortality was monitored, also had no significant difference between the number of male and female calves dying from predation (Procter et al. 2020).

Of 95 adult moose with sex confirmed, we found 76 cows and 19 bulls, or 20% bulls. Bull ratios from the 2016 and 2020 PGW moose surveys were 27 ± 4.4 SE and 31 ± 4.0 SE bulls per 100 cows respectively (21% and 24% of the adult moose population; Klaczek et al. 2016, Scheideman and Anderson 2021). Bull ratios from the 2016 and 2020 FSJ moose surveys were 25 ± 4.3 SE and 39 ± 6.0 SE bulls per 100 cows respectively (20% and 28% of the adult moose population; Klaczek et al. 2016, Scheideman and Anderson 2021). Based on the proportion of bulls at the kill-sites and the observed bull ratios, wolves did not appear to select moose based on sex in our study areas, although other studies have noted selection for yearling or adult bulls (Fuller and Keith 1980).

Body condition of wolf-killed moose

We were often not able to collect long bones that would provide reliable estimates of marrow fat, and thus body condition, because of the delay between kill date and site visit. Long bones that are broken or exposed for long periods will dry out, biasing the marrow fat estimate high because the water content is lower than at death. In those cases, we qualitatively assessed marrow condition as waxy and white or pinkish, red and runny, or hollow. We analysed marrow fat content from 31 long bones from adult moose and 4 from calves. The calf samples averaged 91 ± 6.9% marrow fat (95% CI) which does not align with calves being expected to have lower marrow fat on average as their energy and resources are devoted to body growth rather than fat deposition; however, the sample size was very small (n=4) so unlikely to represent overall body condition of wolf-killed calves. Adult marrow averaged 87 ± 5.2% marrow fat (95% CI). We followed the Provincial Moose Research Project definitions of body condition based on marrow fat levels, with <20% as acute malnutrition, 20-70% as poor body condition, and >70% as considered good body condition (Procter et al. 2020). Only one of the wolf-killed moose was considered in acute malnutrition (8.5% marrow fat) and two were 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%). Work on white-tailed deer suggests that a qualitative assessment of marrow fat as red and runny equates to <46% marrow fat, while white waxy appearance equates to >56% marrow fat (Mech 2008). Although sample sizes were small and marrow fat percentage likely biased high even for samples collected and frozen relatively quickly, average marrow fat content overall was high. There appears to be a relatively low proportion of moose in acute starvation at wolf kill sites, which was also the case for wolf-killed collared moose in the Provincial Moose Research Project (Procter et al. 2020). This suggests that wolf predation is not primarily compensatory mortality in the moose population based on body condition. However, as always with assessing health status at time of death, we are limited by the lack of samples available after the wolves have consumed the carcass to determine any other predisposing health conditions.

Inferring body condition from marrow fat is not infallible, as bone marrow is one of the last sites of fat storage to be mobilized under nutritional stress, and as such, individuals with high marrow fat may not be in good condition (Mech and DelGiudice 1985). Marrow fat levels also vary with the specific bones selected for analysis (Spears et al. 2003), and while we attempted to sample a femur or humerus, these were not always available (the ball joint on femurs was frequently chewed by the wolves, making the bones unsuitable for analysis). Marrow fat is also only one parameter that attempts to quantify moose health in this situation, and we are unable to make any conclusions about other aspects of health that could have predisposed an animal to predation. 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. Ongoing work with the Provincial Moose Research Project should better inform our understanding of moose herd health and the population implications (MacBeth 2017, Thacker et al. 2019).

Kill rates and predation rates

Estimating missed kill sites

Although we attempted to visit all large prey kills (see Appendix 2), we missed several of these sites either because they were inaccessible (e.g., on a lake with remains sinking after ice-out), uncertain after investigation (e.g., extremely thick vegetation likely to obscure small remains), or not prioritized (smaller clusters that nonetheless have some chance of representing a kill site). Furthermore, even if we were able to visit every wolf location point, not all wolves are at all kills made by a pack and the probability of attendance varies based on several factors for which we do not always have accurate information. Before estimating kill rates and predation rates, we therefore must address uncertainty in the number of kills.

Predicting kill sites from cluster characteristics

We considered attributes of the location clusters that were likely to differentiate kills (and specifically moose kills) from other cluster types: 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). We considered wolf ID as a random variable in our models and grouped clusters by summer, winter, and both seasons, as well as by PGS, JPRF, and both study areas. Number of points in the cluster was consistently a significant variable in seasonal study area models, many of which were equivalent based on AICc scores (Figure 17, Figure 18, Figure 19, Figure 20, Appendix 3).

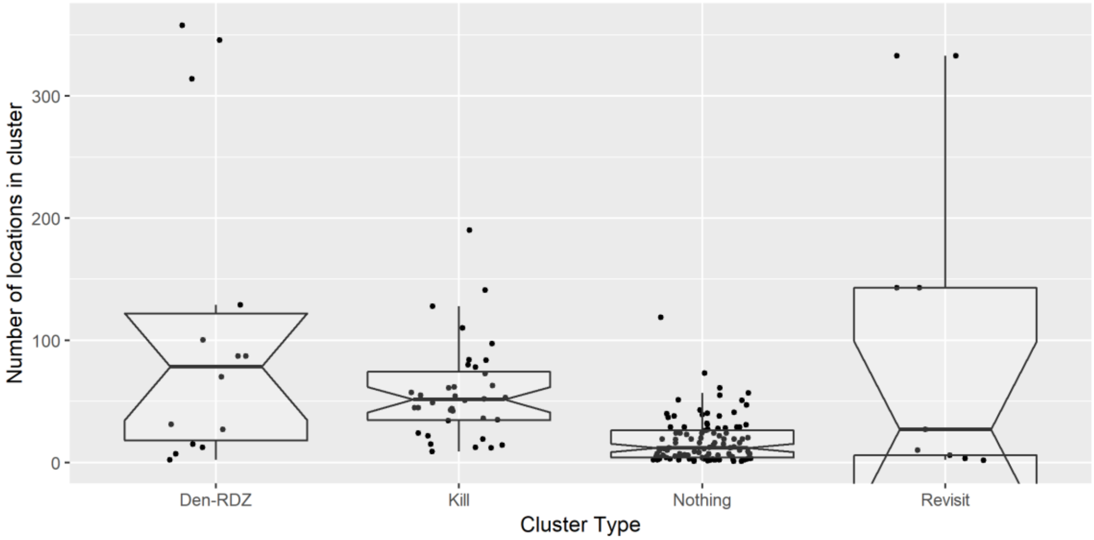


Figure 17. Boxplot showing number of locations in summer (Apr 1-Oct 31) clusters in PGS field-verified to be a den or rendezvous (RDZ) site, large prey kill, a site where no evidence was found, or a revisit to a previous kill site (or scavenge or bait site). Beaver activity was not consistently recorded and was included with ‘no evidence found’ category.

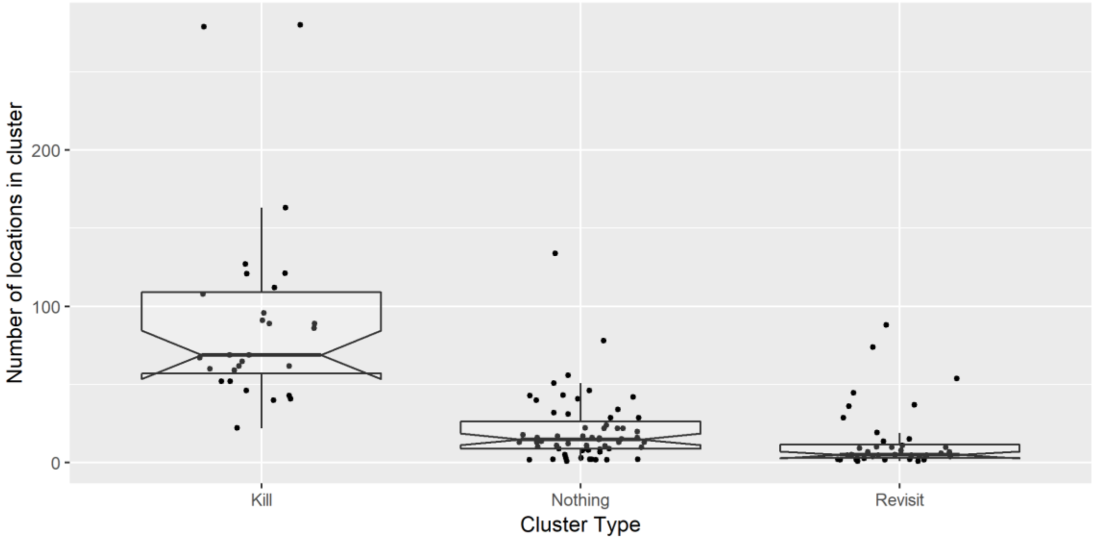


Figure 18. Boxplot showing number of locations in winter (Nov 1-Mar 31) clusters in JPRF field-verified to be a large prey kill, a site where no evidence was found, or a revisit to a previous kill site (or scavenge or bait site). Beaver activity was not consistently recorded and was included with ‘no evidence found’ category.

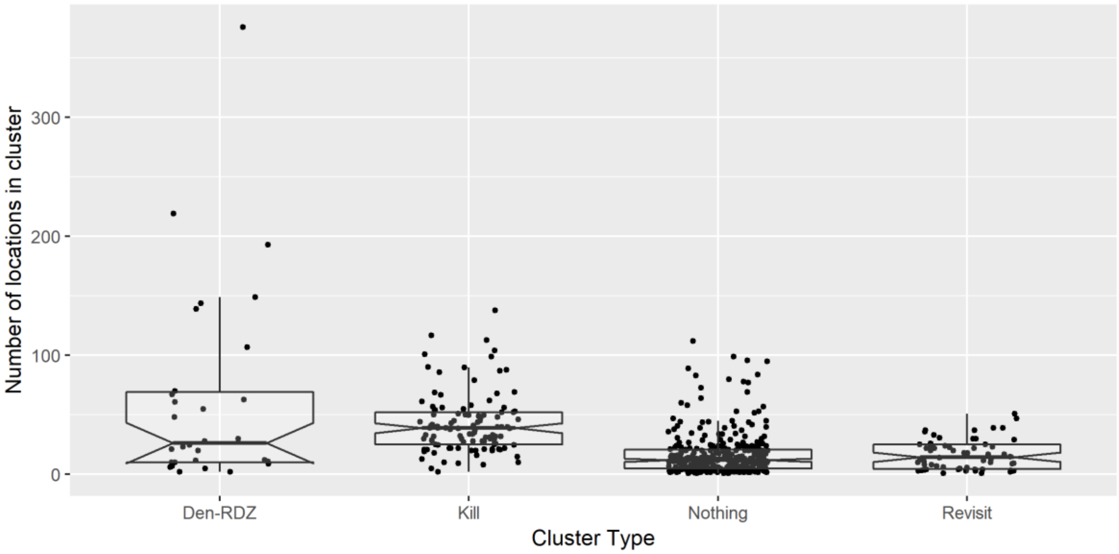


Figure 19. Boxplot showing number of locations in summer (Apr 1-Oct 31) clusters in PGS field-verified to be a den or rendezvous (RDZ) site, large prey kill, a site where no evidence was found, or a revisit to a previous kill site (or scavenge or bait site). Beaver activity was not consistently recorded and was included with 'no evidence found' category.

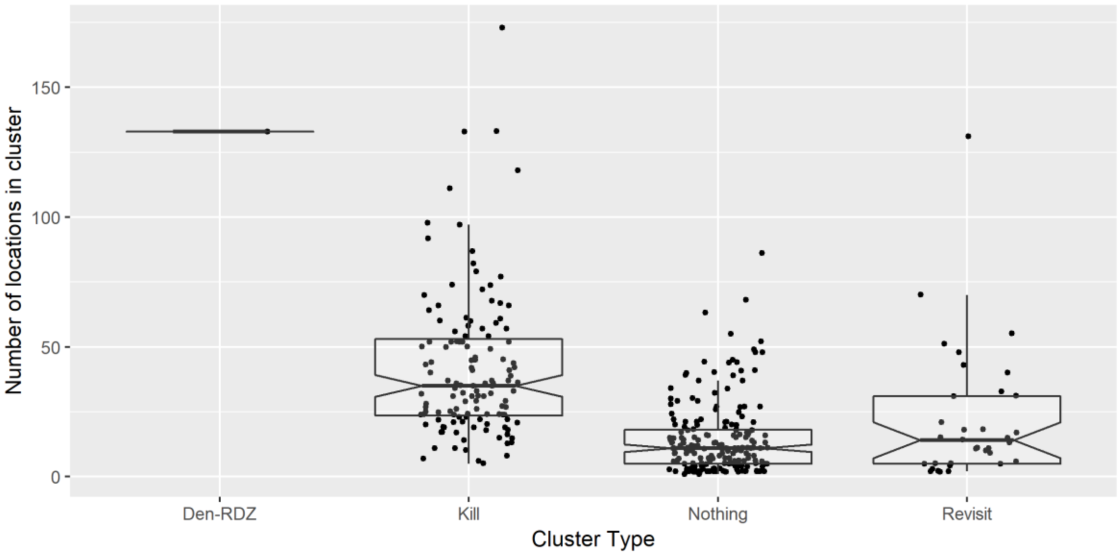


Figure 20. Boxplot showing number of locations in winter (Nov 1-Mar 31) clusters in PGS field-verified to be a den or rendezvous (RDZ) site, large prey kill, a site where no evidence was found, or a revisit to a previous kill site (or scavenge or bait site). Beaver activity was not consistently recorded and was included with 'no evidence found' category.

Clusters with many location points were more likely to represent kills, but this relationship was not as clear in summer, especially in JPRF (Figure 21, Figure 22, Figure 23). Large clusters in summer are often associated with rendezvous sites and dens, which obscures the relationship between persistence time at a site and likelihood of kill. Summer kill rates can differ from winter kill rates (Sand et al. 2008), and cluster analysis is not as effective for small prey with shorter handling times, which can make up significant portions of the summer diet when beaver and ungulate neonates are available (White and Garrott 2005, Barber-Meyer et al. 2010, Metz et al. 2012, Gable et al. 2016, Gable and Windels 2018).

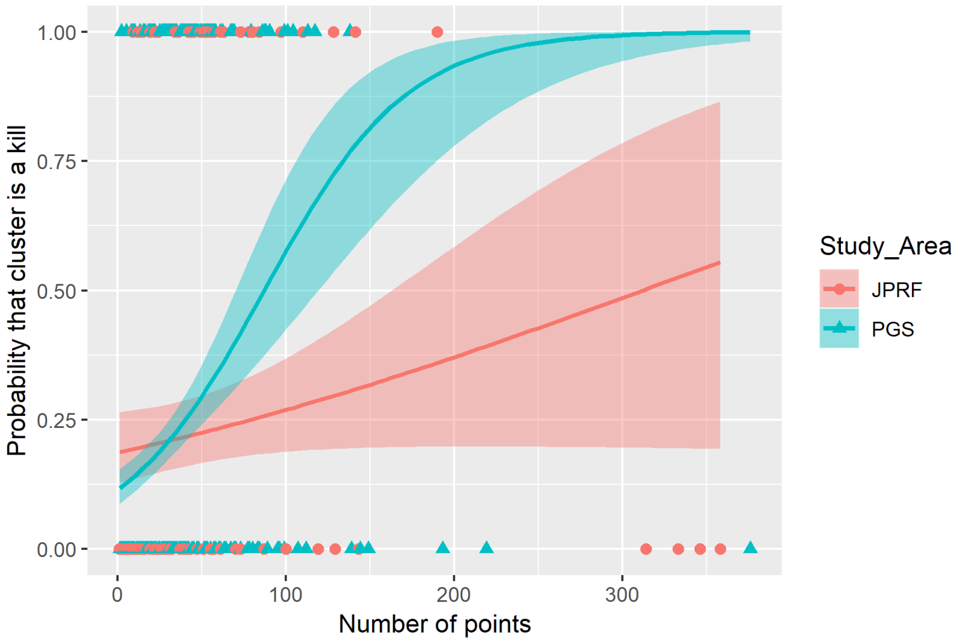


Figure 21. Probability that a summer cluster site is a large prey kill based on number of location points in the cluster for PGS and JPRF. Shaded area is 95% confidence limits.

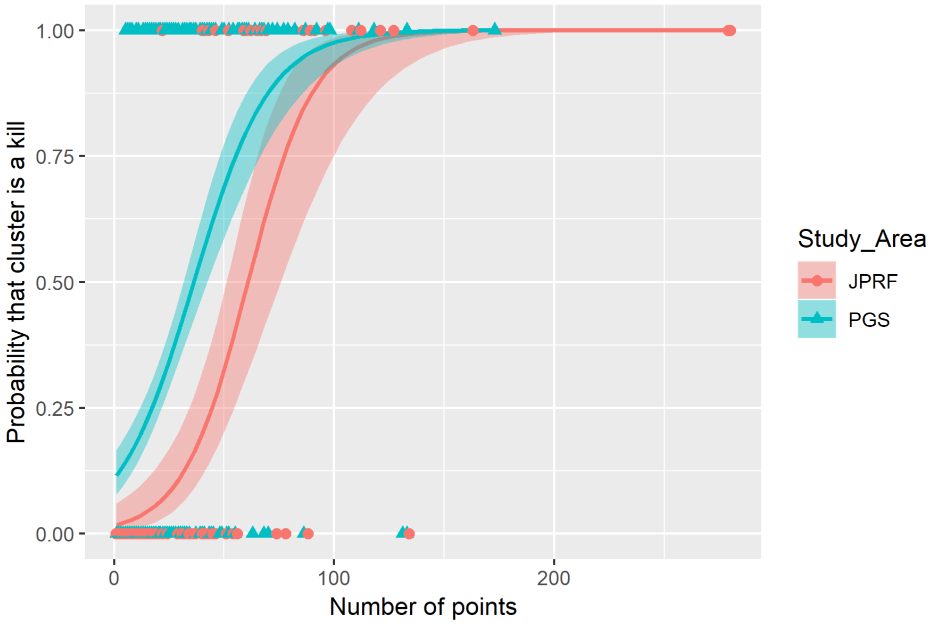


Figure 22. Probability that a winter cluster site is a large prey kill based on number of location points in the cluster for PGS and JPRF. Shaded area is 95% confidence limits.

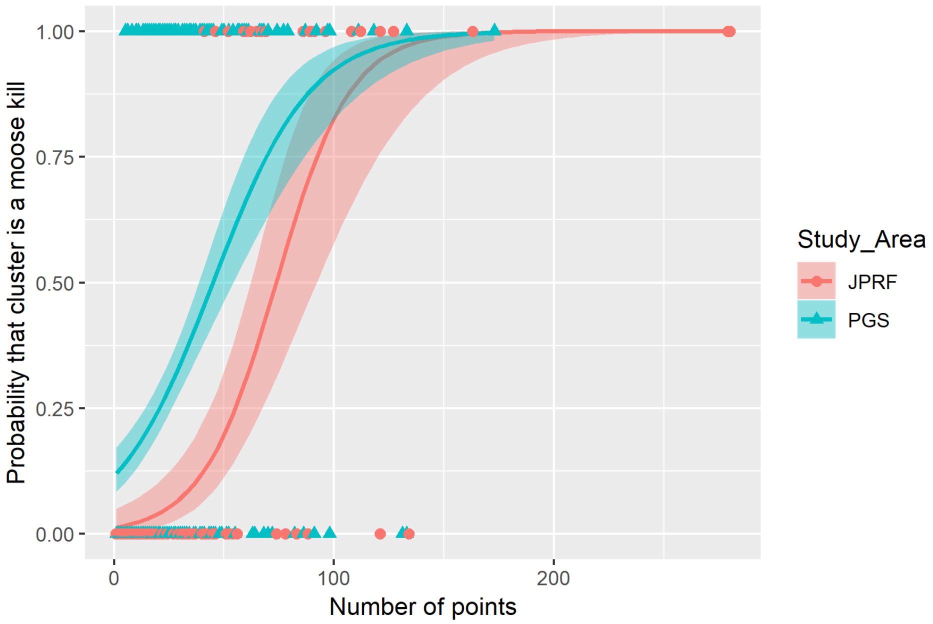


Figure 23. Probability that a winter cluster site is a moose kill based on the number of location points in the cluster for PGS and JPRF. Shaded area is 95% confidence limits.

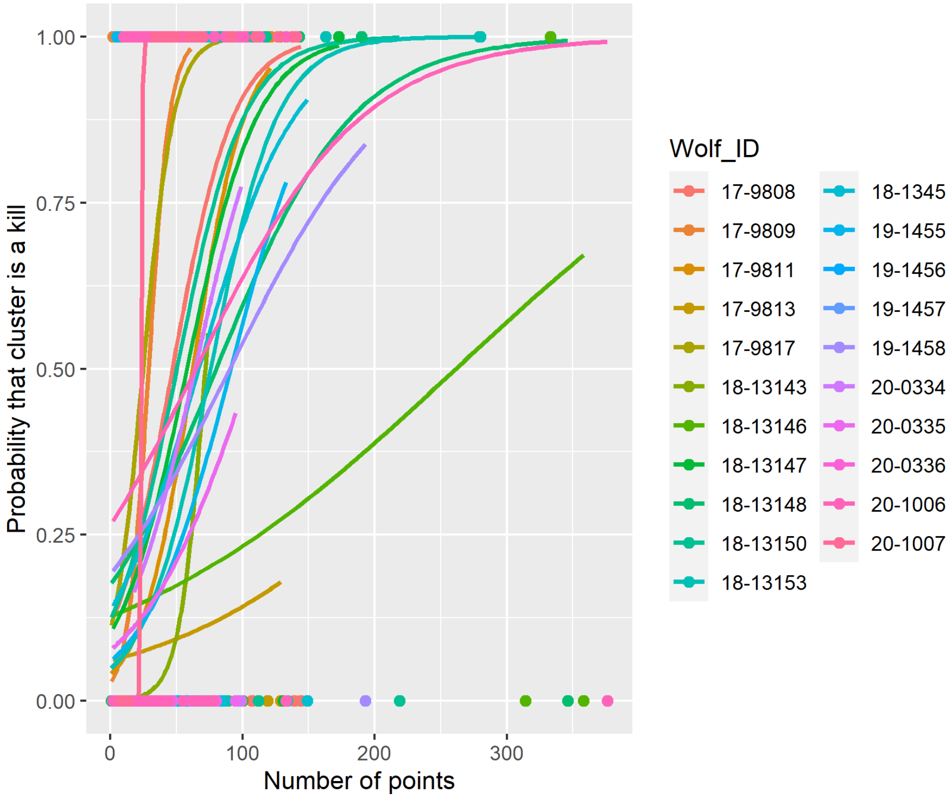


Figure 24. Probability that winter cluster sites are associated with a large prey kill site, with each curve representing a different individual wolf. Number of clusters investigated per individual varied.

In general, there was high variation in the coefficient estimates and prediction of whether a cluster represented a kill site, even for large kill sites. Considering the 95% confidence intervals around the coefficient estimates led to wide variation in predicted probability that a cluster site represented a kill, or a moose kill specifically. Individual variation among wolves was high (Figure 24).

Other investigators have used fewer categories of cluster types and slightly different approaches to defining clusters for investigation (Web et al. 2008, Knopff et al. 2009, Metz et al. 2011), or worked in systems and seasons where wolves may have had fewer options for prey acquisition (Neilson and Boutin 2017). Neilson and Boutin (2017) visited 59 clusters over 2 winters and used the 12 moose, 7 deer, and one unknown large prey as the basis for estimating the locations of 988 potential kills (199 potential moose kills) for further analysis. While the researchers found this approach adequate for inferring landscape characteristics influencing moose predation risk in their study area, such an approach likely would not work in our study areas given the variation observed, the multiple prey and other food resources available, and our interest in differentiating kills from scavenging. Wolves may spend as much time at a bait site as at a moose kill, but predicting moose kills from bait sites would be problematic for defining landscape characteristics at putative kill sites or calculating kill rates.

Assessing complete kill time series

If we based our kill rate only on the number of kills detected over the monitoring period of each collar, we would not have accounted for the clusters we were unable to investigate that could have been kills. Estimating missed kills based on the models presented above would result in an overestimation of kills (most models assigned about a 10% probability that a cluster of 2 location points would be a kill site). Instead, we considered short time periods of intensive observation (Fuller and Keith 1980, Fuller 1989, Palm 2001), specifically time periods for which we were able to visit all clusters that were likely to be kill sites based on the behaviour of individual wolves. Generally, this was larger clusters (>15 points) with additional investigation on smaller clusters for long durations between confirmed kills, and more investigation of small clusters for wolves that did not have consistent movement patterns of many small non-kill clusters and much larger kill clusters. This resulted in 50 complete kill chronologies for PGS and 22 for JPRF, averaging about 5 weeks long and including all collared packs (Appendix 4). Several of these time series extended from our defined winter (Nov 1-Mar 31) to summer (Apr 1- Oct 31) or summer to winter, so we assigned them to the season they predominantly represented. We did not include time series less than 2 weeks in duration and considered only one wolf if two wolves in the pack were comprehensively monitored at the same time. 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 in JPRF (a moose every 21 days). Assigning the monitoring periods to winter (approximately Nov 1-Mar 31) or summer (approximately Apr 1-Oct 31) provided seasonal kill rates of a moose every 15 days in the summer for a pack in PGS and every 37-38 days for a pack in JPRF, and every 8-9 days in the winter for a pack in PGS and every 13 days for a pack in JPRF. This provides an initial estimate of moose killed, but still needs to be adjusted for the probability of collared wolves not being at a kill that the other members of the pack have made.

Estimating probability of attendance

Estimating kill rates of social carnivores requires consideration of how often members of the social group are foraging together. We calculate kill rates and assess clusters for wolf packs, but we do so based on individuals. In most cases, we only monitored one individual at a time in each pack, and their roles in their respective packs encompassed breeders, non-breeders, and dispersers. We stopped investigating kill sites for collared wolves once they had dispersed, as their activities no longer reflected the pack. Metz et al. (2011) examined the probability of a wolf attending a kill site in Yellowstone National Park, one of the few study systems for which this data is available. They found that accounting for the probability of attendance increased estimated kill rates for summer by 32% (Metz et al. 2011). Probability of attendance varied by season, wolf age, pack size, and prey size (Metz et al. 2011).

We had 3 packs in PGS with more than one GPS-collared wolf simultaneously, but we did not have simultaneous collar deployments in JPRF. The Tagai Lake pack had both the breeding male and a subordinate male collared between Mar 25-Dec 13, 2019. The Clear Lake pack had two subordinate males collared between Jan 21-Mar 7, 2019. The Grizzly Lake pack had collars on a yearling female, subordinate male, and subordinate female, but collar failures meant that overlap between any two collared Grizzly Lake wolves was only a week between Jun 23-Jul 1, 2021. This short time coincided with one moose kill, attended by the collared adult female but not the other two collared wolves.

Metz et al. (2011) used a 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 ‘detection.’ The probability of detection (PD) for each individual A and B is calculated as:

$$PD_A = \frac{N_{AB}}{N_B} \qquad \text{and} \qquad PD_B = \frac{N_{AB}}{N_A}$$

Where N refers to the number of detections by both individuals (N_{AB}), by individual A (N_A), or individual B (N_B). The estimated PD and number of detections by that individual can be used to estimate total detections? by:

$$N_{total} = \frac{N_{detected}}{PD}$$

For packs with only a single wolf, PD can be estimated and applied to the number of detections for the collared individual.

For Clear Lake, wolf 18-13142 was present at 7 kills, wolf 17-9817 was present at 9 kills, and 13 individual kills (all moose) were detected between the two wolves for the 56 days when both were collared (Appendix 4). This equates to PD of 0.33 for 18-13142 and 0.43 for 17-9817. The estimated number of kills for the pack during that time would be 21 moose, versus 13 moose detected (2.6 moose/week).

For Tagai Lake, wolf 18-13150 (breeder) was present at 17 moose kills and a black bear kill, wolf 18-13145 (subordinate) was present at 13 moose kills, and there were 22 kills detected for the pack over 257 days when both were collared (Appendix 4). This equates to PD of 0.50 for 18-13145 and 0.69 for 18-13150. The estimated number of kills for the pack during that time would be 26 kills, versus 22 kills detected (0.7 kills/week). Considering only the summer kills (183 days and 16 individual kills detected, 10 by 18-13145 and 13 by 18-13150), PD was 0.54 for 18-13145 and 0.70 for 18-13150. Only 6 kills were recorded for 46 days of monitoring in winter for Tagai when both collars were active (3 by 18-13145 and 5 by 18-13150), and PD was 0.40 for 18-13145 and 0.67 for 18-13150.

Under conditions when packs are not as cohesive, including for larger packs (Jedrzejewski et al. 2002), we would expect lower probabilities of attendance at kill sites. The PDs calculated for Clear Lake and Tagai Lake were lower than those determined for the Yellowstone wolves, but packs in our study were smaller than the average 13 wolves/pack in Yellowstone. Larger pack size is therefore unlikely to be the main reason for lower PD in Clear Lake and Tagai Lake than Yellowstone, and other factors in our study areas may lead to lower pack cohesion. Wolves are actively hunted and trapped in our study areas, which also have a high density of roads and cutblocks, and wolves may use that landscape more efficiently by splitting up. We also did not find the same clear seasonal difference in pack cohesion as Metz et al. (2011; summer PD 0.58 and winter PD 0.95). Higher PD in winter would be expected because packs are more cohesive in winter with individuals travelling together more often and therefore more likely to be at the same kills (Peterson et al. 1984). Prey size and abundance can also influence cohesion in social carnivores (Smith et al. 2008); our study sites' primary prey is moose while Yellowstone wolves primarily hunt elk. Collaring subordinates rather that breeders could lead to lower calculated PD, although Metz et al. (2011) did not identify breeding status as an important variable in predicting attendance (age was, however, and many of the examined variables were correlated, making it difficult to interpret ecological implications). The variables influencing pack cohesion in disturbed landscapes for hunted wolf populations could be an important consideration in assessing kill rates.

Estimating kill rates

If we consider the kill rates estimated above from the kill time series and assign a probability of attendance of 0.4 to subordinate wolves and 0.7 to breeders based on the Tagai and Clear Lake wolves in 2019, the estimated kill rate increases markedly. In PGS, the annual estimate of a moose every 12 days increases to a moose every 6 days and in JPRF, the annual estimate of a moose every 21 days increases to a moose every 10 days (Table 4). If we used the higher probability of attendance calculated for Yellowstone, we would expect packs in PGS to kill a moose every 7-8 days in the winter and every 10-11 days in the summer. We would expect a pack in JPRF to kill a moose every 12 days in the winter and every 25 days in the summer (Table 4).

Table 4. Kill rates adjusted for probability of attendance based on averages 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 based on periods of continuous monitoring 2018-2022 (JPRF n=10 winter, 12 summer; PGS n=17 winter, 22 summer).

		Unadjusted kill rate ± SE		PGS-adjusted kill rate		YNP-adjusted kill rate	
		Moose/ pack/ wk	Days/ moose/ pack	Moose/ pack/ wk	Days/ moose/ pack	Moose/ pack/ wk	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

Per capita kill rates

Kill rates are calculated as the number or biomass (kg) of prey killed by a predator (or biomass of 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/metabolic demands of pups over the summer. Seasonality is also important due to the presence of neonate prey (also growing rapidly) over the summer (Sand et al., Metz et al. 2011). Kill rates refer to prey killed and do not include all prey or biomass acquired by the wolves – notably many of our cluster sites included gut piles left by hunters, bait sites set by hunters and trappers, dumped livestock carcasses, and scavenged carcasses that would have provided significant biomass intake for the wolves. Winter per capita kill rate was similar between PGS (average pack size 7.4 wolves) and JPRF (average pack size 4.2 wolves), contrary to results from work elsewhere with similar pack sizes indicating higher per capita kill rates by smaller packs (Ballard et al. 1987, Hayes et al. 2000). This may be due to different prey availability or minimal loss to scavengers even for small packs. Differences in winter moose kill rates between the two study areas are therefore largely due to differences in pack size, rather than differences in the behaviour of the wolves in the two areas. Per capita kill rates in PGS for summer were also similar, but may have been slightly higher, possibly due to more non-moose prey in JPRF (both large prey in the diet and small prey that were not quantified; Table 5). Estimated kilograms of moose per wolf per day was within the broad range reported for wolf-moose systems (1.8-24.8 kg/wolf/day; reviewed in Mech and Peterson 2003).

Table 5. Per capita kill rates adjusted for probability of attendance based on averages 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 based on periods of continuous monitoring 2018-2022 (JPRF n=10 winter, 12 summer; PGS n=17 winter, 22 summer). Average midwinter pack sizes were 4.2 wolves in JPRF and 7.4 wolves in PGS. Biomass assumes 297 kg/moose based on kills in the Yukon (Kaczensky et al. 2005, Hayes et al. 2000).

		Unadjusted kill rate (moose/ wolf/wk) ± SE	PGS-adjusted kill rate		YNP-adjusted kill rate (moose/wolf/wk)	
			Moose/wolf/wk	Kg/wolf/day	Moose/wolf/wk	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

Estimating predation rates

The predation rate is the proportion of a prey population killed by a predator over a specified period. In addition to the per capita kill rate (or per pack kill rate), estimation of predation rates requires information on the abundance of the prey population. Moose population boundaries have not been defined, and moose have relatively high dispersal capability and flexible habitat requirements, enabling mixing of individuals across wide areas and therefore making it difficult to define population boundaries. Although not as large as a population management unit, moose survey areas are sufficiently large to characterize moose population parameters across a large area encompassing several wolf pack territories. Moose abundance is estimated every 5 years with stratified random block (SRB) surveys in the Fort St James and Prince George West survey areas, which closely correspond to the JPRF and PGS study areas respectively. Moose SRBs were flown over JPRF and PGS in December 2020, with 0.62 ± SE 0.051 moose/km^2 in Prince

George West and 0.84 ± SE 0.115 moose/km^2 in Fort St. James (Scheideman and Anderson 2021). This equates to 2849 moose (2390-3308 95% CI) in the PGS wolf study area and 3460 moose (2531-4388 95% CI) in the JPRF study area and would include 8-month-old calves. 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 6). 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 report for PGS and higher than for JPRF. Kill rates tend to be higher when wolves are more highly selective for smaller calves due to the shorter handling time (Fuller and Keith 1980, Palm 2001).

Table 6. Estimated predation rates on moose (proportion of moose killed) in PGS (6 packs, average pack size 7.4 wolves) and JPRF (5 packs, average pack size 4.2 wolves) using moose densities from winter 2020-21 (Scheideman and Anderson 2021). 95% CI refers to the moose population estimate; average kill rates were applied after adjusting for probability of attendance based on PGS wolves and by values reported from Yellowstone wolves (YNP).

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%

Implications of predation rates

Annual predation rates in both study areas appear to be within the ranges reported for stable to increasing moose populations, although the interaction between variable predation rates, calf recruitment, and adult survival would result in variable effects on moose population trend in any given year. This is consistent with the survey results of stable to increasing moose populations in PGS and JPRF (Scheideman and Anderson 2020).

A simple way to assess the immediate impact of predation rates involves comparing the number of moose killed by wolves and the number of moose recruited into the population (Fuller and Keith 1980, Ballard et al. 1987). Fuller and Keith (1980) determined predation rates in a wolf-moose-caribou system in northeastern Alberta were 11-12% of the adult moose population but high calf production suggested that the moose population could sustain the predation rate. However, calf recruitment (and predation rate) can be highly variable. Comparing overall adult mortality of moose to stable or increasing populations can also provide insight on population trajectory with predation rates – moose populations in Alaska and Yukon with 5-9% adult mortality were stable to increasing (Ballard et al. 1987).

Other interacting factors are important to consider beyond just wolf predation rates. Predation rates of 13-34% of the winter moose population interacted with hunting pressure in Alaska following severe winters and resulted in moose declines (Gasaway et al. 1983, Gasaway et al. 1992). Predation rates of 10-15% in the Yukon were maintained on 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 act on populations that are both at high and low densities. 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. Messier (1994) estimated moose densities around 2 moose/km^2 in undisturbed habitat with no wolf predation, 1.3 moose/km^2 with wolf predation, and substantially lower (0.2-0.4 moose/km^2) with bear predation and habitat change, with no or a very shallow 'predator pit' detected at these lower densities. A predator pit occurs when predation is high enough on a low-density population to prevent that population 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). Messier (1994) examined deterministic models without inclusion of stochasticity, and predator pits have been recorded in moose-wolf systems in Alaska (Gasaway et al. 1983, Boertje et al. 1996, Regelin et al. 2001). 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). Habitat change may therefore be a more important factor than predation in changes to moose density in our study areas.

Wolf habitat selection and movement

We used several approaches to quantify wolf movement and habitat selection to inform risk layers for moose. First, we considered an integrated step selection analysis (iSSA) that compares used to available locations of steps (the connection between successive relocations) for wolves in PGS where we had higher sample sizes and higher proportions of landscape disturbance associated with salvage logging. This approach integrates habitat selection and movement within a conditional logistic regression model framework (Avgar et al. 2016); detailed methods and results are presented in Boucher et al. (2022). Work is ongoing using a used-available resource selection function (RSF) following Manley et al. (2002) for both PGS and JPRF wolves, but model predictability so far has been low (L. Koetke, pers. comm.).

Wolves in PGS selected for linear features, which increased their movement rates, as other investigators have found in similar systems (Latham et al. 2011, Whittington et al. 2011, Newton et al. 2017, Dickie et al. 2017, DeMars and Boutin 2018). There was no clear selection for areas based on linear feature density, however. Mumma and Gillingham (2019) also found that moose in areas of lower, not higher, road density in the previous year were more likely to die from wolf predation. This suggests that there is a functional response to roads, that is, selection for a resource is dependent on the availability of that resource.

Functional responses may indicate trade-offs between resource acquisition and risk and have consequences for predator acquisition of prey and prey avoidance of predation risk.

One hypothesis for why wolves may select linear features but not areas of high linear feature density could be that those areas represent higher risk of human-caused mortality. Several studies suggest that wolves avoid areas of high human activity due to perceived risk or realized mortality, generally in highly populated areas (Mladenoff and Sickley 1998, Oakleaf et al. 2006, Lovari et al. 2007, Benson et al. 2015). Muhley et al. (2011) noted that predators (including wolves) avoided high human use roads and trails in the Canadian Rockies, but the effect was most notable with >18 humans/day on trails, a substantially higher human visitation rate than most of PGS or JPRF. While work in southeastern Alaska showed higher mortality risk for wolves with increasing road density, this risk did not increase with road densities above 0.9 km/km^2 (Person and Russell 2008), and PGS road density is 3.6 km/km^2. Neither PGS nor JPRF has extensive urban, suburban, or agricultural areas. Wolf densities are what would be expected based on ungulate biomass indices, which suggests that the area would not support substantially more wolves with less human impact. All mortality recorded on this project was human-caused, but annual mortality rates were low enough that we would not expect to see a decline. It is not clear whether human-caused mortality is additive or compensatory in our study areas, but wolf densities do not appear to be maintained at an artificially low level by human-caused mortality (hunting, trapping, vehicle strikes). Selection for roads and cutblocks suggests that if wolves perceive these features as risky, they may consider the benefits of increased movement and prey acquisition to outweigh the risks. Alternatively, wolf avoidance of heavily roaded areas could be a strategy that reduces mortality risk and high road density areas are avoided to mitigate risk.

Another hypothesis could be the utility of roads to wolves that are hunting widely distributed or low-density prey. Kittle et al. (2017) suggested that wolves may use roads more when prey abundance is low, increasing movement rates among patches of prey habitat. Muhly et al. (2019) assessed the functional response of wolves to road density across boreal North America and found increased selection for roads with increasing road density; however, the range of road densities examined was 0.001-0.122 km/km^2 – at least an order of magnitude lower than in PGS. The shape of the functional response is likely different for these exponentially higher road densities. Wolves may be more likely to use the few roads that are present in largely unroaded areas, but when road density is high, there are many roads available, and wolves are less likely to use any one specific road over any other road (or may use roads with lower perceived risk or human activity). Any given road in the less roaded area would therefore be more dangerous for a moose than any given road in a highly roaded area, assuming the same wolf density. Given moose selection for heterogeneity in their home ranges including mature cover in PGS (Scheideman 2018), it is also possible that wolf selection for areas of lower road density is due to the persistence of mature timber patches in less roaded areas that are also better moose habitat. If moose are more predictably associated with these less roaded habitat patches, wolves would be more likely to hunt and kill moose in areas of low road density (Mumma and Gillingham 2019), while still using the roads to access the habitat patches, suggesting that selection (or use) of roads is scale dependent.

Wolves also selected forest edges and areas closer to water in both seasons but avoided deciduous-leading stands. Deciduous stands were, however, selected by moose in all study areas and seasons

(Scheideman 2018). New (0 – 8 years since harvest) cutblocks were selected by wolves in summer and winter, although selection for new cutblocks in summer decreased with increasing cutblock size. This age class of cutblocks is generally not selected by moose, except in early winter (Mumma et al. 2021). In early winter when moose do select new cutblocks, selection by wolves could make these areas ecological traps (seemingly attractive habitats with elevated mortality risk), but moose mortality is generally low in early winter (Procter et al. 2020). Wolves did not show clear selection for regenerating cutblocks (9-24 years old and selected by moose; Mumma et al. 2021), but did have slower more tortuous movement patterns there, possibly due to reduced visibility especially with summer leaf-out.

Landscape characteristics of moose kill sites

To relate landscape features to sites of mortality, we compared habitat features at sites of successful moose kills (n=158) to random sites selected in PGS (Boucher et al. 2022; work is on-going for JPRF). We applied a used-available RSF approach (Manley et al. 2002) to determine what landscape characteristics were associated with wolf-killed moose, including: proportion of deciduous-leading stands, coniferous-leading stands, mixed forest stands, pine-leading stands, new (0-8 yr old) cutblocks, regenerating (9-24 yr old) cutblocks, distance to linear feature, linear feature density, distance to edge (both inside and outside of the forest), NDVI and distance to water (Table 7).

Moose kill sites had a higher probability of occurring in areas with higher proportions of new (selected by wolves, not by moose) and regenerating (selected by moose, not by wolves) cutblocks. This appears to represent an intersection of differing selection patterns that allows overlap between predator and prey. Moose kill sites were also more likely in areas of higher vegetative productivity (based on NDVI value) and closer to water. Moose kill sites were less likely to occur in deciduous stands, which were not selected by wolves but consistently selected by moose. This suggests that deciduous stands may be important to moose for more than the forage resources they provide – these areas may also provide refuge from wolf predation. Possible mechanisms could be the dense shrub and herbaceous layers associated with some deciduous stands in our study areas that would impede wolf sightlines, or higher snow depths in winter due to lack of canopy cover. Moose kill sites were not located closer than expected to linear features, so while wolves use roads to travel throughout their territory, they are not necessarily killing moose along the roads. Using roads likely allows wolves to increase encounter rates with moose and travel rapidly between habitat patches where prey are encountered.

Table 7. Coefficients of top model predicting moose kill sites, from Boucher et al. 2022 Table 3.

Covariate	Coefficient estimate	Standard error
Intercept	− 13.06	1.42
Pine	− 0.28	0.92
Deciduous	− 2.20	1.28
Mixed forest	− 0.46	0.67
Coniferous	− 4.69	4.77
ln(Water)	− 0.16	0.14
ln(Edge in)	0.065	0.096
ln(Edge out)	− 0.031	0.067
NDVI	12.17	1.86
New cut	2.25	0.85
Regenerating cut	2.60	0.58

Management Recommendations

Management recommendations will depend on species- or area-specific objectives. These recommendations would be to reduce wolf predation risk to moose to enhance moose populations (GOABC 2016, Gorley 2016), while maintaining wolves on the landscape consistent with the provincial wolf management plan (BC FLNRO 2014).

Maintain deciduous stands on the landscape

Previous work showed that moose select deciduous stands year-round, and our work suggests that wolves make fewer moose kills in these stands and do not select them as habitat or to facilitate movement. This suggests that not only do deciduous stands provide year-round forage and security for moose, but they can also act as refuge habitat from wolf predation.

Reduce sightlines in cutblocks

Wolves are primarily visual predators, and our work shows that new cutblocks are selected by wolves, despite not being selected by moose in most seasons. Maintaining visual screening cover, making smaller blocks, and making more irregular block boundaries would reduce sightlines and potentially make these areas less attractive to wolves while also making them more attractive to moose by decreasing dash distances to mature forest cover.

Minimize roads

Wolves selected for areas near roads and increased travel speed along them but did not select for areas of high road density. Moose were also at lower risk of dying from wolf predation in areas of higher road density, suggesting that wolves likely have a more complicated functional response to roads. Rehabilitating roads to the extent necessary for wolves to no longer use them as efficient travel corridors is difficult and expensive but would reduce their search efficiency and travel between otherwise separated habitat patches. Roads that provide access to isolated habitat patches or that have intensive wolf use should be prioritized for rehabilitation.

Maintain liberal wolf harvest opportunities

Although not an objective of the study, this work confirmed that the study areas have relatively high wolf densities with survival rates expected of a stable population. Given their high dispersal and reproductive capacity, the wolf population can sustain relatively high hunting and trapping pressure, as well as removals for livestock protection. Licensed wolf harvest opportunities are already liberal in the study areas, but current, or even somewhat elevated, harvest levels are unlikely to have a long-term effect on wolf abundance in the study areas.

Improve harvest reporting

Wolf harvest as currently reported is insufficient to infer any relative abundance or population trend. The shift to online licensing and reporting provides an opportunity to implement more accurate harvest reporting for all licensed hunting in BC and may provide an opportunity to track wolf population trends in the study areas, especially if the new data stream includes an independent measure of hunter effort.

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Appendix 1. Wolves and packs monitored 2018-2022 in PGS and JPRF

Table 8. Details of collared wolves in PGS and JPRF including age, sex, condition, and breeding status. WHID refers to the Wildlife Health Identification Number, which is a unique identifier assigned by the Wildlife Health Team.

Study Area	Pack	WHID	Sex	Status	Color	Age	Body condition	Weight (kg)
PGS	Blackwater River	17-9808	M	Breeder	White	Adult	Good	52.3
PGS	Blackwater River	17-9819	F	Non-breeder	Brown	1	Fair	35.9
PGS	Bobtail Mountain	17-9809	M	Breeder	Grey-brown	Adult	Fair	51
PGS	Bobtail Mountain	17-9812	F	Non-breeder	Grey-brown	2	Fair	35
PGS	Bobtail Mountain	19-1456	F	Non-breeder	Black	1	Fair	31
PGS	Bobtail Mountain	20-0335	F	Non-breeder	Grey	3	Fair	
PGS	Bobtail Mountain	20-1006	M	Non-breeder	Black	4	Good	
PGS	Clear Lake	17-9817	M	Non-breeder	Black	2	Fair	40.5
PGS	Clear Lake	17-9818	M	Breeder	Black	Adult	Good	61
PGS	Clear Lake	17-9821	F	Breeder	White	Adult	Good	56.8
PGS	Clear Lake	18-13147	M	Non-breeder	Black	3	Good	64
PGS	Ghost Pack	19-1455	M	Non-breeder	Grey-brown	1	Fair	est 30
PGS	Ghost Pack	19-1459	M	Unknown	Grey-brown	3	Good	est 50
PGS	Grizzly Lake	19-1458	M	Unknown	Grey-brown	5-6	Good	53
PGS	Grizzly Lake	19-3377	F	Non-breeder	Grey-brown	3-4	Good	44
PGS	Grizzly Lake	20-0334	F	Non-breeder	Grey-brown	4	Fair	
PGS	Grizzly Lake	20-0336	M	Non-breeder	Grey-brown	2	Fair	
PGS	Grizzly Lake	20-0337	F	Non-breeder	Grey	1	Fair	24
JPRF	Hat Lake	17-9813	F	Non-breeder	Black	Adult	Fair	30.5
JPRF	Hat Lake	18-13143	F	Non-breeder	Grey	4-5	Fair	
JPRF	Hat Lake	19-1457	M	Non-breeder	Grey	2	Good	est 35
JPRF	Kazchek Lake	18-13153	M	Breeder	Grey	4	Good	
JPRF	Kazchek Lake	19-1460	F	Breeder	Grey	3	Good	
JPRF	Kazchek Lake	20-1007	M	Unknown	Grey	3	Good	
JPRF	Pinchi Lake	17-9811	F	Breeder	Black	Adult	Fair	37.7
JPRF	Tachie	18-13146	M	Breeder	Black	6-7	Good/ fair	
PGS	Tagai Lake	18-13141	F	Non-breeder	Grey	3-4	Good	41
PGS	Tagai Lake	18-13145	M	Non-breeder	Grey	2	Good	est 40
PGS	Tagai Lake	18-13150	M	Breeder	Grey	4-5	Good	est 55
PGS	Tagai Lake	18-13151	F	Non-breeder	Grey	1	Fair	31
PGS	Tagai Lake	18-13151	F	Non-breeder	Grey-brown	2	Good	41
PGS	Tagai Lake	19-3378	F	Non-breeder	Grey-brown	6-7	Good	35
JPRF	Tanizul Lake	18-13148	M	Non-breeder	White-grey	5-6	Good	47

Table 9. Duration of monitoring and fate of wolves captured and monitored in PGS and JPRF, 2018-2022.

Study Area	Pack	WHID	Collar Number	Monitoring Start	Monitoring End	Days collared	Location Fixes	Fix success (%)	Fate
PGS	Blackwater River	17-9808	26820	06-Mar-18	25-Feb-19	356	8201	96.3	Offline
PGS	Blackwater River	17-9819	VHF only	06-Mar-18	11-Nov-18	250			Mortality - resident hunter
PGS	Bobtail Mountain	17-9809	26813	22-Feb-18	30-Apr-18	67	10310	99.7	Dispersed; to Tatelkuz Lake
PGS	Bobtail Mountain	20-0335	26815	19-Jun-21	14-Oct-21	117	2745	99.9	Offline
PGS	Bobtail Mountain	17-9812	VHF only	26-Feb-18	Jan-19				Not located; likely dispersed or dead
PGS	Bobtail Mountain	20-1006	46224	14-Jan-21	11-Mar-22	424	9892	98.6	Deactivated at end of project
PGS	Clear Lake	17-9817	26815	06-Mar-18	02-Mar-19	361	8534	98.8	Dispersed
PGS	Clear Lake	18-13147	26814	21-Jan-19	03-May-19	102	2420	99.8	Dispersed, offline May 2019
PGS	Clear Lake	19-1456	32106	06-Feb-20	13-Feb-20	7	123	100.0	Mortality - resident hunter
PGS	Clear Lake	17-9818	VHF only	26-Feb-18	Jan-19				Not located; likely dispersed or dead
PGS	Clear Lake	17-9821	VHF only	19-Mar-18	Jan-19				Not located; likely dispersed or dead
PGS	Ghost Pack	19-1455	26818	27-Feb-20	25-May-20	88	2061	99.9	Dispersed, then dropped Feb 2022
PGS	Ghost Pack	19-1459	VHF only	27-Feb-20	Jan-21				Not located; likely dispersed or dead
PGS	Grizzly Lake	19-1458	26813	28-Feb-20	05-Jun-20	98	1838	79.8	Offline
PGS	Grizzly Lake	20-0337	32106	23-Jun-20	01-Jul-20	8	148	94.9	Offline, then dropped Aug 2021
PGS	Grizzly Lake	20-0336	26812	10-Jun-21	20-Jul-21	40	594	66.9	Offline
PGS	Grizzly Lake	20-0334	26817	10-Jun-21	19-Dec-21	192	4320	95.0	Offline Nov 2021, mortality (trapped) so downloaded
PGS	Grizzly Lake	19-3377	VHF only	18-Mar-20					
PGS	Kazchek Lake	19-1460	VHF only	19-Feb-20			3668	99.9	
PGS	Tagai Lake	18-13145	26819	05-Jan-19	13-Dec-19	342	7600	99.9	Offline
PGS	Tagai Lake	18-13150	32120	25-Mar-19	22-Mar-21	728	6587	99.8	Dropped
PGS	Tagai Lake	18-13141	VHF only	10-Jun-19					
PGS	Tagai Lake	18-13151	VHF only	10-Jun-19			10770	99.7	
PGS	Tagai Lake	19-3378	VHF only	18-Mar-20			8695	99.0	
PGS	Tagai Lake	18-13151	VHF only	18-Mar-20			6483	96.1	
PGS	Tatelkuz Lake	17-9809	26813	20-Jan-19	27-Apr-19	97	5996	98.4	Mortality - resident hunter
JPRF	Hat Lake	17-9813	26811	09-Jun-18	11-Nov-18	155	7754	95.0	Mortality - trapped

Study Area	**Pack**	**WHID**	**Collar Number**	**Monitoring Start**	**Monitoring End**	**Days collared**	**Location Fixes**	**Fix success (%)**	**Fate**
JPRF	Hat Lake	18-13143	26817	06-Feb-19	21-Dec-19	318	17287	99.4	Offline, then mortality (resident hunter)
JPRF	Hat Lake	19-1457	32119	19-Feb-20	23-Nov-20	278			Offline
JPRF	Kazchek Lake	18-13153	26812	12-Jul-19	07-Oct-20	453			Mortality - resident hunter
JPRF	Kazchek Lake	20-1007	46223	03-Feb-21	07-Feb-22	369			Offline
JPRF	Pinchi Lake	17-9811	26821	16-Jun-18	25-Mar-19	282			Offline
JPRF	Tachie	18-13146	26811	06-Feb-19	19-Oct-19	255	8984	99.0	Offline, then mortality (trapped, Feb 2022)
JPRF	Tanizul Lake	18-13148	32105	08-Feb-19	24-Feb-20	381	2328	100.0	Offline

Appendix 2. Wolf cluster time series and investigation results

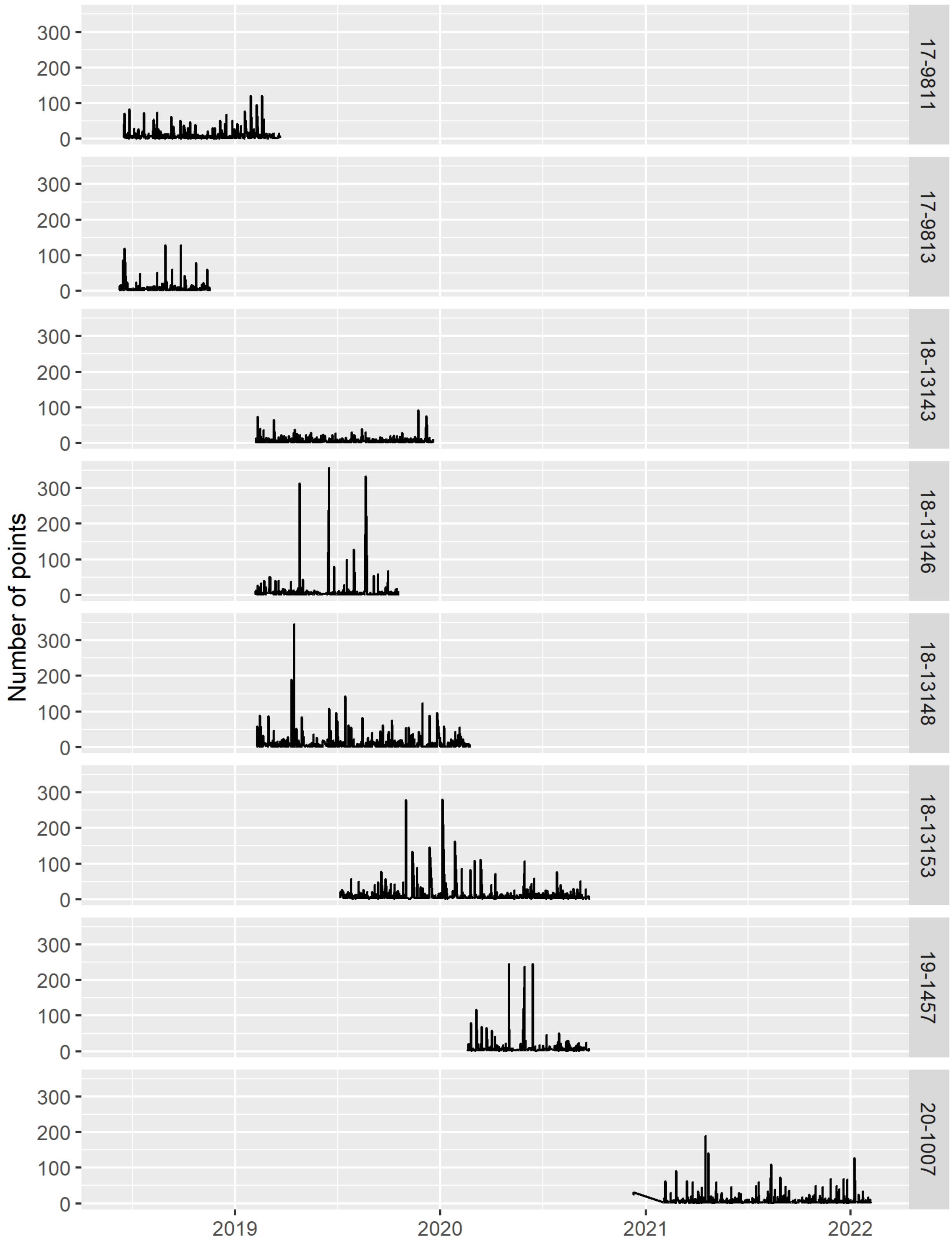

Figure 25. Time series of clusters for wolves collared in JPRF from collaring to mortality or collar malfunction with taller peaks representing clusters with more location points.

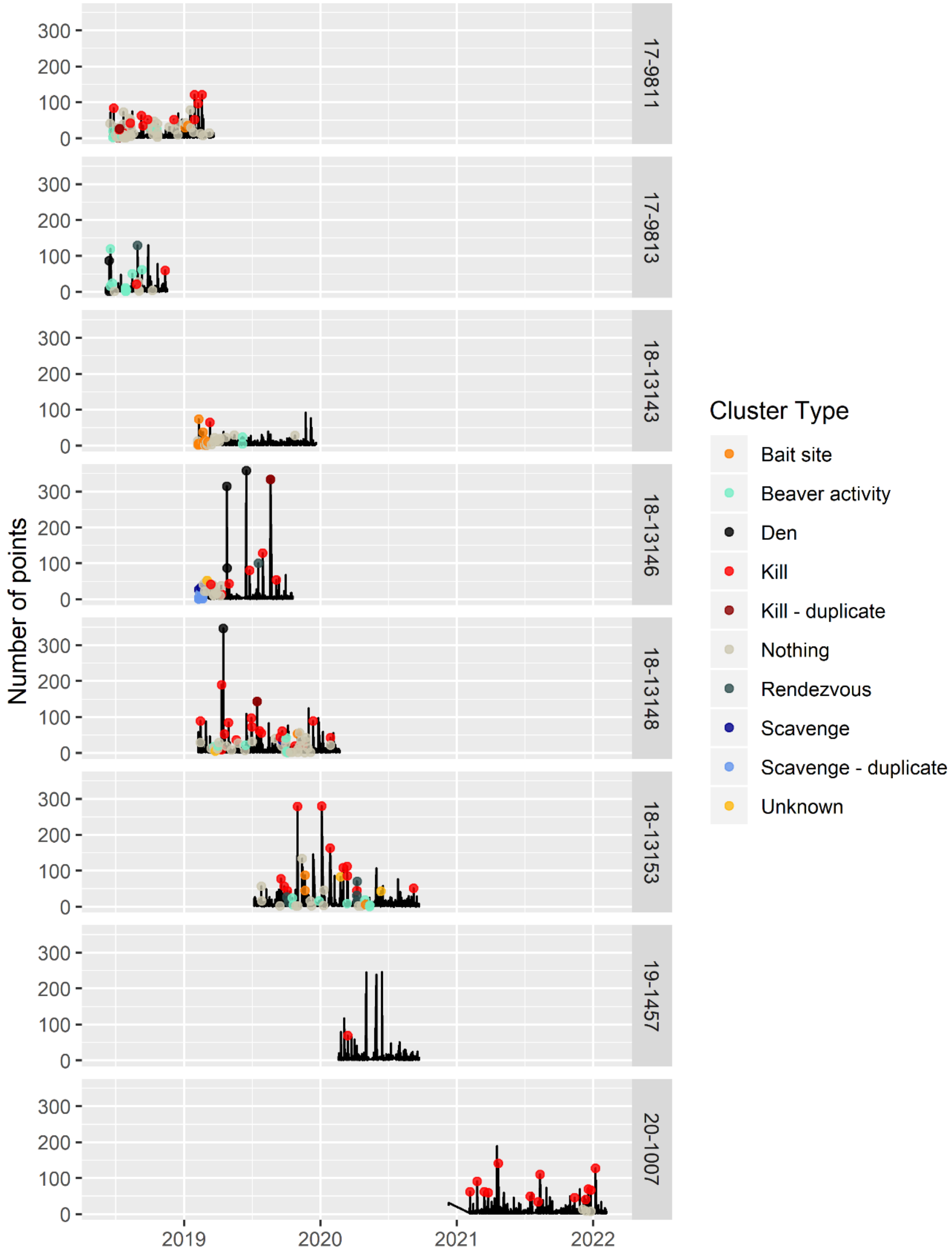

Figure 26. Time series of clusters for wolves collared in JPRF from collaring to mortality or collar malfunction results of all investigated clusters indicated by colored circles Duplicate kills and scavenges indicate an independent visit by a collared wolf to an already identified carcass, generally when multiple wolves were collared in the same pack.

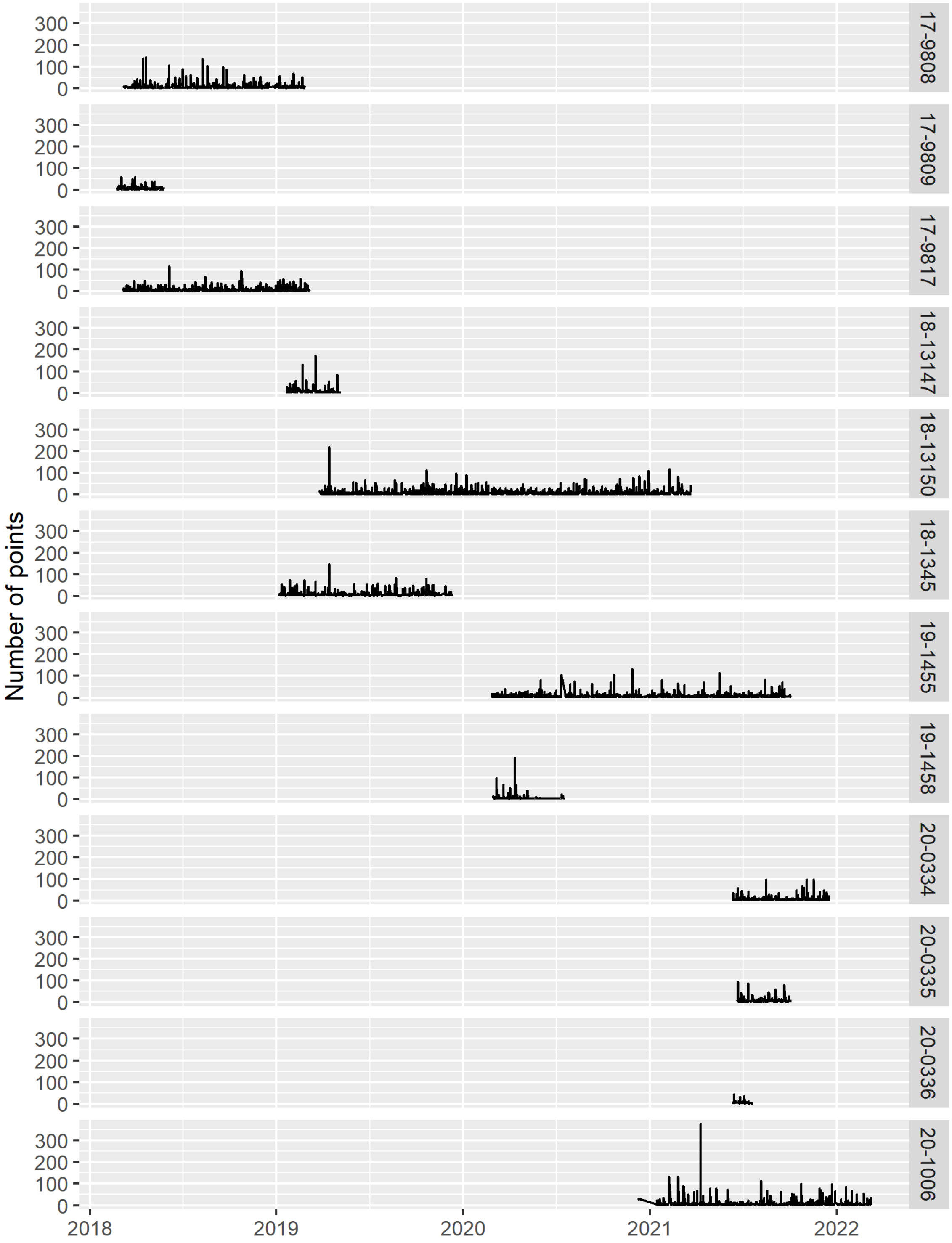

Figure 27. Time series of clusters for wolves collared in PGS from collaring to mortality or collar malfunction with taller peaks representing clusters with more location points.

Figure 28. Time series of clusters for wolves collared in PGS from collaring to mortality or collar malfunction results of all investigated clusters indicated by colored circles Duplicate kills and scavenges indicate an independent visit by a collared wolf to an already identified carcass, generally when multiple wolves were collared in the same pack. Revisits indicate subsequent visits by the same wolf to a previously identified carcass.

Appendix 3. Candidate models for predicting kill sites

Table 10. Candidate models for seasons and study areas predicting kill sites. Coefficients in italics were not significant in the regression; top or equivalent models are denoted in bold. 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).

Study Area and season	**Candidate model (Wolf ID as random effect in all)**	**Intercept**	**Number of Points Coefficient**	±SE	**Mean Distance Coefficient**	±SE	**Days Coefficient**	±SE	**AICc**
PGS+JPRF; all seasons	Num_Pts + Av_Dist	-2.1330	0.0303	0.0030	0.0000	0.0039			1198.3
	Num_Pts	-2.1274	0.0303	0.0029					1199.9
	Av_Dist	-1.4336			0.0100	0.0035			1351.3
	Days	-1.1087					0.0010	0.0030	1358.0
	Num_Pts + Days	-2.0595	0.0326	0.0031			-0.0106	0.0040	1182.4
	Num_Pts + Days + Av_Dist	-2.1196	0.0323	0.0031	0.0024	0.0040	-0.0111	0.0041	1180.5
PGS all seasons	Num_Pts + Av_Dist	-2.0620	0.0352	0.0039	*0.0015*	0.0043			938.3
	Num_Pts	-2.0169	0.0355	0.0038					940.0
	Av_Dist	-1.4441			0.0132	0.0038			1048.2
	Days	-1.0122					*0.0004*	0.0035	1056.7
	Num_Pts + Days	-1.9662	0.0383	0.0040			-0.0102	0.0045	924.0
	Num_Pts + Days + Av_Dist	-2.0557	0.0376	0.0041	*0.0036*	0.0044	-0.0110	0.0046	921.9
JPRF all seasons	**Num_Pts + Av_Dist**	-1.7599	0.0223	0.0046	*-0.0123*	0.0094			254.6
	Num_Pts	-2.0930	0.0212	0.0044					254.4
	Av_Dist	-0.8859			-0.0080	0.0084			297.1
	Days	-1.1632					*0.0024*	0.0057	300.1
	Num_Pts + Days	-1.9576	0.0231	0.0047			*-0.0130*	0.0091	254.0
	Num_Pts + Days + Av_Dist	-1.7267	0.0236	0.0048	*-0.0093*	0.0097	*-0.0109*	0.0093	255.1
PGS+JPRF; winter	**Num_Pts + Av_Dist**	-2.9327	0.0658	0.0073	*-0.0020*	0.0067			431.2
	Num_Pts	-2.8562	0.0658	0.0071					433.2
	Av_Dist	-1.3407			0.0205	0.0056			574.1
	Days	-0.7038					*0.0043*	0.0047	595.4
	Num_Pts + Days	-2.8037	0.0684	0.0074			*-0.0102*	0.0063	432.5
	Num_Pts + Days + Av_Dist	-2.9379	0.0680	0.0076	*0.0047*	0.0069	*-0.0112*	0.0065	430.1
PGS winter	**Num_Pts + Av_Dist**	-2.3710	0.0657	0.0083	*0.0060*	0.0068			359.6
	Num_Pts	-2.1861	0.0664	0.0082					362.0
	Av_Dist	-1.0477			0.0181	0.0058			457.7
	Days	-0.5230					*0.0043*	0.0050	472.0
	Num_Pts + Days	-2.1387	0.0683	0.0084			*-0.0079*	0.0067	362.6
	Num_Pts + Days + Av_Dist	-2.3638	0.0674	0.0085	*0.0081*	0.0070	*-0.0094*	0.0069	359.7
JPRF winter	**Num_Pts + Av_Dist**	-3.7450	0.0887	0.0287	*-0.0433*	0.0287			66.8
	Num_Pts	-4.3957	0.0720	0.0152					67.4
	Av_Dist	-2.0467			0.0312	0.0151			117.3
	Days	-1.0032					*0.0044*	0.0117	124.5
	Num_Pts + Days	-4.3857	0.0832	0.0191			*-0.0335*	0.0246	66.9

Study Area and season	Candidate model (Wolf ID as random effect in all)	Intercept	Number of Points Coefficient	±SE	Mean Distance Coefficient	±SE	Days Coefficient	±SE	AICc
	Num_Pts + Days + Av_Dist	-3.8539	0.0962	0.0238	*-0.0366*	0.0294	*-0.0292*	0.0264	67.3
PGS+JPRF; summer	Num_Pts + Av_Dist	-1.9459	0.0163	0.0032	*0.0028*	0.0055			698.5
	Num_Pts	-1.8662	0.0168	0.0031					696.7
	Av_Dist	-1.6748			0.0109	0.0053			731.8
	Days	-1.3138					-0.0009	0.0044	726.2
	Num_Pts + Days	-1.7884	0.0191	0.0034			-0.0109	0.0057	684.0
	Num_Pts + Days + Av_Dist	-1.9290	0.0184	0.0034	*0.0053*	0.0057	-0.0120	0.0059	685.1
PGS summer	Num_Pts + Av_Dist	-2.1652	0.0215	0.0044	0.0056	0.0065			529.3
	Num_Pts	-2.0036	0.0229	0.0042					528.0
	Av_Dist	-2.0081			0.0177	0.0061			556.5
	Days	-1.3794					*-0.0019*	0.0053	555.5
	Num_Pts + Days	-1.9271	0.0259	0.0044			-0.0134	0.0071	514.8
	Num_Pts + Days + Av_Dist	-2.1494	0.0242	0.0046	*0.0082*	0.0067	-0.0151	0.0073	515.3
JPRF summer	**Num_Pts + Av_Dist**	-1.1377	0.0089	0.0040	*-0.0147*	0.0117			169.2
	Num_Pts	-1.5213	0.0086	0.0039					168.7
	Av_Dist	-0.6975			*-0.0145*	0.0121			173.2
	Days	-1.0588					*-0.0011*	0.0077	174.6
	Num_Pts + Days	-1.4018	0.0097	0.0042			*-0.0082*	0.0097	170.0
	Num_Pts + Days + Av_Dist	-1.1104	0.0095	0.0042	*-0.0128*	0.0122	*-0.0051*	0.0098	171.0

Table 11. Candidate models for seasons and study areas predicting moose kill sites. Coefficients in italics were not significant in the regression; top or equivalent models are denoted in bold. 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).

Study Area and season	Candidate model (Wolf ID as random effect in all)	Intercept	Number of Points Coefficient	±SE	Mean Distance Coefficient	±SE	Days Coefficient	±SE	AICc
PGS+JPRF; all seasons	Num_Pts + Av_Dist	-2.1645	0.0287	0.0029	*-0.0051*	0.0042			1115.2
	Num_Pts	-2.2844	0.0277	0.0028					1118.3
	Av_Dist	-1.4960			*0.0055*	0.0037			1255.0
	Days	-1.3041					*0.0003*	0.0032	1255.0
	Num_Pts + Days	-2.2016	0.0303	0.0030			-0.0126	0.0044	1099.6
	Num_Pts + Days + Av_Dist	-2.1427	0.0307	0.0031	*-0.0028*	0.0043	-0.0120	0.0045	1097.6
PGS all seasons	Num_Pts + Av_Dist	-1.9688	0.0342	0.0038	*-0.0050*	0.0045			891.1
	Num_Pts	-2.0699	0.0328	0.0036					893.9
	Av_Dist	-1.3854			0.0076	0.0038			997.6
	Days	-1.1314					*-0.0005*	0.0037	998.2
	Num_Pts + Days	-2.0098	0.0359	0.0038			-0.0122	0.0049	876.8
	Num_Pts + Days + Av_Dist	-1.9562	0.0367	0.0040	*-0.0029*	0.0046	-0.0117	0.0050	874.9
JPRF all seasons	**Num_Pts + Av_Dist**	-1.9991	0.0195	0.0043	*-0.0132*	0.0107			215.2
	Num_Pts	-2.3682	0.0189	0.0041					214.8
	Av_Dist	-1.1436			*-0.0108*	0.0097			250.8

Study Area and season	**Candidate model (Wolf ID as random effect in all)**	**Intercept**	**Number of Points Coefficient**	±SE	**Mean Distance Coefficient**	±SE	**Days Coefficient**	±SE	**AICc**
	Days	-1.5245					*0.0030*	0.0060	252.3
	Num_Pts + Days	-2.2197	0.0208	0.0045			*-0.0142*	0.0104	214.5
	Num_Pts + Days + Av_Dist	-1.9483	0.0211	0.0046	*-0.0104*	0.0110	*-0.0124*	0.0105	215.6
PGS+JPRF; winter	**Num_Pts + Av_Dist**	-2.2146	0.0608	0.0079	*-0.0013*	0.0070			355.5
	Num_Pts	-2.2220	0.0601	0.0077					357.1
	Av_Dist	-1.0072			0.0122	0.0058			446.6
	Days	-0.6418					*0.0030*	0.0052	455.9
	Num_Pts + Days	-2.1701	0.0626	0.0080			*-0.0096*	0.0069	357.1
	Num_Pts + Days + Av_Dist	-2.1766	0.0629	0.0081	*0.0009*	0.0071	*-0.0098*	0.0070	355.5
PGS winter	**Num_Pts + Av_Dist**	-2.2146	0.0608	0.0079	*-0.0013*	0.0070			355.5
	Num_Pts	-2.2220	0.0601	0.0077					357.1
	Av_Dist	-1.0072			0.0122	0.0058			446.6
	Days	-0.6418					*0.0030*	0.0052	455.9
	Num_Pts + Days	-2.1701	0.0626	0.0080			*-0.0096*	0.0069	357.1
	Num_Pts + Days + Av_Dist	-2.1766	0.0629	0.0081	*0.0009*	0.0071	*-0.0098*	0.0070	355.5
JPRF winter	**Num_Pts + Av_Dist**	-4.0574	0.0818	0.0195	*-0.0429*	0.0317			60.9
	Num_Pts	-4.7912	0.0683	0.0150					61.0
	Av_Dist	-2.3757			0.0319	0.0161			106.5
	Days	-1.5408					*0.0151*	0.0131	109.3
	Num_Pts + Days	-4.6619	0.0718	0.0161			*-0.0186*	0.0250	62.4
	Num_Pts + Days + Av_Dist	-4.0384	0.0830	0.0200	*-0.0397*	0.0323	*-0.0119*	0.0267	62.8
PGS+JPRF; summer	Num_Pts + Av_Dist	-2.1161	0.0148	0.0032	*0.0006*	0.0060			620.6
	Num_Pts	-2.0990	0.0149	0.0030					618.6
	Av_Dist	-1.8620			*0.0082*	0.0059			647.7
	Days	-1.5620					*-0.0026*	0.0048	639.6
	Num_Pts + Days	-1.9971	0.0175	0.0034			-0.0137	0.0066	604.9
	Num_Pts + Days + Av_Dist	-2.0902	0.0171	0.0034	*0.0036*	0.0067	-0.0145	0.0067	606.6
PGS summer	Num_Pts + Av_Dist	-2.1019	0.0223	0.0045	*-0.0015*	0.0066			483.1
	Num_Pts	-2.1466	0.0219	0.0041					481.1
	Av_Dist	-2.0166			0.0131	0.0064			511.2
	Days	-1.5388					*-0.0026*	0.0058	505.5
	Num_Pts + Days	-2.0486	0.0256	0.0045			-0.0165	0.0081	467.2
	Num_Pts + Days + Av_Dist	-2.0798	0.0254	0.0047	*0.0011*	0.0069	-0.0168	0.0083	469.2
JPRF summer	**Num_Pts + Av_Dist**	-1.3848	*0.0062*	0.0036	*-0.0205*	0.0157			132.9
	Num_Pts	-1.9217	*0.0063*	0.0036					132.5
	Av_Dist	-1.0709			*-0.0216*	0.0159			134.0
	Days	-1.5160					*-0.0055*	0.0087	135.4
	Num_Pts + Days	-1.7503	0.0081	0.0040			*-0.0134*	0.0115	133.0
	Num_Pts + Days + Av_Dist	-1.3701	*0.0075*	0.0040	*-0.0159*	0.0162	*-0.0103*	0.0115	134.2

Appendix 4. Kill site chronologies for monitored wolves

Table 12. Time periods for which observers were able to visit all likely kill sites (>15 locations per cluster and additional sites based on movements) for wolves in PGS. Bold font indicates overlap with another collared wolf in the same pack.

Collar	WHID	Pack	Start	End	Days	Moose kills	Kills/week
26820	17-9808	Blackwater	07-Mar-18	11-Sep-18	188	24	0.9
26820	17-9808	Blackwater	11-Sep-18	29-Sep-18	18	2	0.8
26820	17-9808	Blackwater	11-Oct-18	23-Nov-18	43	3	0.5
26820	17-9808	Blackwater	23-Nov-18	10-Dec-18	17	2	0.8
26820	17-9808	Blackwater	06-Jan-18	08-Feb-18	33	5	1.1
26820	17-9808	Blackwater	09-Feb-18	25-Feb-18	16	2	0.9
26813	17-9809	Bobtail Mtn	23-Feb-18	15-Mar-18	20	3	1.1
26813	17-9809	Bobtail Mtn	21-Mar-18	10-Apr-18	20	5	1.8
26813	17-9809	Bobtail Mtn	18-Apr-18	26-May-18	38	3	0.6
26815	17-9817	Clear Lake	06-Mar-18	10-Apr-18	35	3	0.6
26815	17-9817	Clear Lake	30-Apr-18	28-May-18	28	2	0.5
26815	17-9817	Clear Lake	05-Jun-18	23-Jun-18	18	1	0.4
26815	17-9817	Clear Lake	09-Jul-18	01-Sep-18	54	1	0.1
26815	17-9817	Clear Lake	05-Sep-18	25-Sep-18	20	2	0.7
26815	17-9817	Clear Lake	26-Sep-18	18-Dec-18	83	10	0.8
26815	17-9817	Clear Lake	21-Dec-18	30-Jun-19	191	11	0.4
26815	17-9817	Clear Lake	01-Feb-19	08-Mar-19	35	7	1.4
26814	18-13142	Clear Lake	21-Jan-19	05-May-19	104	9	0.6
32120	18-13150	Tagai Lake	01-Apr-19	04-May-19	33	5	**1.1**
32120	18-13150	Tagai Lake	05-May-19	14-May-19	9	1	**0.8**
32120	18-13150	Tagai Lake	14-May-19	12-Jun-19	29	1	**0.2**
32120	18-13150	Tagai Lake	13-Jun-19	28-Jun-19	15	1	**0.5**
32120	18-13150	Tagai Lake	01-Jul-19	31-Jul-19	30	2	**0.5**
32120	18-13150	Tagai Lake	31-Jul-19	25-Sep-19	56	2	**0.3**
32120	18-13150	Tagai Lake	29-Oct-19	09-Nov-19	11	2	**1.3**
32120	18-13150	Tagai Lake	24-Jan-20	31-Jan-20	7	2	2.0
32120	18-13150	Tagai Lake	31-Jan-20	04-Mar-20	33	5	1.1
32120	18-13150	Tagai Lake	03-Nov-20	12-Nov-20	9	0	0.0
32120	18-13150	Tagai Lake	17-Jan-21	03-Mar-21	45	2	0.3
26819	18-13145	Tagai Lake	24-Jan-19	03-Mar-19	38	6	1.1
26819	18-13145	Tagai Lake	01-Apr-19	05-May-19	34	4	**0.8**
26819	18-13145	Tagai Lake	06-May-19	16-Jun-19	41	0	**0.0**
26819	18-13145	Tagai Lake	07-Jul-19	21-Sep-19	76	3	**0.3**
26819	18-13145	Tagai Lake	29-Oct-19	27-Nov-19	29	1	**0.2**
26818	19-1455	Ghost Pack	22-Nov-20	03-Dec-20	11	1	0.6
26813	19-1458	Grizzly Lake	29-Feb-20	30-Mar-20	30	1	0.2
26813	19-1458	Grizzly Lake	31-Mar-20	16-Apr-20	16	2	0.9
26813	19-1458	Grizzly Lake	30-Apr-20	04-Jun-20	35	2	0.4
26817	20-0334	Grizzly Lake	11-Jun-21	26-Jun-21	15	1	**0.5**
26815	20-0335	Clear Lake	21-Jun-21	08-Aug-21	48	2	0.3
26815	20-0335	Clear Lake	21-Aug-21	10-Sep-21	20	1	0.4
26815	20-0335	Clear Lake	11-Sep-21	04-Oct-21	23	0	0.0
26812	20-0336	Grizzly Lake	12-Jun-21	19-Jul-21	37	0	**0.0**
46224	20-1006	Bobtail Mtn	14-Jan-21	09-Apr-21	85	8	0.7
46224	20-1006	Bobtail Mtn	10-Apr-21	09-Aug-21	121	5	0.3
46224	20-1006	Bobtail Mtn	09-Aug-21	28-Aug-21	19	2	0.7
46224	20-1006	Bobtail Mtn	02-Sep-21	02-Oct-21	30	0	0.0
46224	20-1006	Bobtail Mtn	07-Oct-21	06-Nov-21	30	3	0.7
46224	20-1006	Bobtail Mtn	06-Nov-21	13-Nov-21	7	1	1.0
46224	20-1006	Bobtail Mtn	14-Nov-21	10-Mar-22	116	16	1.0

Table 13. Time periods for which observers were able to visit all likely kill sites (>15 locations per cluster and additional sites based on movements) for wolves in JPRF.

Collar	WHID	Pack	Start	End	Days	Moose kills	Kills/week
26821	17-9811	Pinchi Lake	25-Jun-18	12-Aug-18	48	3	0.4
26821	17-9811	Pinchi Lake	22-Aug-18	03-Oct-18	42	1	0.2
26821	17-9811	Pinchi Lake	08-Feb-19	22-Feb-19	14	1	0.5
26811	17-9813	Hat Lake	01-Nov-18	17-Nov-18	16	1	0.4
26817	18-13143	Hat Lake	20-Feb-19	20-Mar-19	28	1	0.3
26811	18-13143	Tachie	06-Feb-19	12-Feb-19	6	0	0.0
26811	18-13143	Tachie	13-Feb-19	23-Apr-19	69	2	0.2
26811	18-13143	Tachie	02-May-19	12-Jul-19	71	1	0.1
26811	18-13143	Tachie	31-Jul-19	12-Sep-19	43	0	0.0
32105	18-13148	Tanizul Lake	11-Mar-19	24-Mar-19	13	0	0.0
32105	18-13148	Tanizul Lake	05-Apr-19	02-May-19	27	4	1.0
32105	18-13148	Tanizul Lake	08-May-19	06-Jun-19	29	1	0.2
32105	18-13148	Tanizul Lake	25-Jun-19	08-Jul-19	13	1	0.5
32105	18-13148	Tanizul Lake	16-Jul-19	31-Jul-19	15	1	0.5
32105	18-13148	Tanizul Lake	16-Sep-19	06-Oct-19	20	0	0.0
32105	18-13148	Tanizul Lake	25-Oct-19	11-Nov-19	17	1	0.4
32105	18-13148	Tanizul Lake	16-Nov-19	01-Dec-19	15	0	0.0
26812	18-13153	Kazchek Lake	28-Oct-19	27-Nov-19	30	1	0.2
26812	18-13153	Kazchek Lake	05-Jan-20	23-Jan-20	18	1	0.4
26812	18-13153	Kazchek Lake	27-Feb-20	17-Mar-20	19	3	1.1
26812	18-13153	Kazchek Lake	12-Apr-20	28-May-20	46	0	0.0
46223	20-1007	Kazchek Lake	14-Feb-21	15-Mar-21	29	2	0.5

Appendix 5. Probability of attendance at kill sites

Table 14. Packs with more than one active collar used to assess probability of attendance at a kill site in PGS.

Pack	Date	Prey	In attendance
Tagai Lake (Mar 25-Dec 13, 2019)	23-Mar-19	Moose ad unk	Both
	05-Apr-19	Moose ad unk	Both
	08-Apr-19	Moose ad unk	32120 only
	12-Apr-19	Moose ad unk	Both
	25-Apr-19	Moose ad unk	Both
	01-May-19	Moose ad fem	Both
	10-May-19	Moose ad fem	32120 only
	06-Jun-19	Moose ad unk	32120 only
	16-Jun-19	Moose calf unk	32120 only
	07-Jul-19	Moose ad fem	Both
	12-Jul-19	Moose ad fem	26819 only
	12-Jul-19	Yearling fem	26819 only
	12-Jul-19	Moose ad fem	32120 only
	16-Jul-19	Moose ad unk	Both
	20-Aug-19	Moose calf unk	Both
	23-Aug-19	Moose ad fem	26819 only
	23-Aug-19	Moose calf unk	32120 only
	02-Nov-19	Moose ad fem	26819 only
	02-Nov-19	Moose ad male	32120 only
	05-Nov-19	Moose ad unk	32120 only
	05-Dec-19	Moose calf unk	Both
	09-Dec-19	Black bear ad unk	32120 only
	Totals:		
	257 days	9 kills	Both
		13 kills	26819 only
		18 kills	32120 only
Clear Lake (Jan 21-Mar 7, 2019)	22-Jan-19	Moose ad fem	26815 only
	22-Jan-19	Moose calf male	Both
	27-Jan-19	Moose ad unk	Both
	08-Feb-19	Moose ad fem	Both
	13-Feb-19	Moose ad unk	26814 only
	15-Feb-19	Moose ad fem	26815 only
	17-Feb-19	Moose ad fem	26815 only
	26-Feb-19	Moose calf unk	26815 only
	28-Feb-19	Moose ad fem	26815 only
	28-Feb-19	Moose ad fem	26814 only
	04-Mar-19	Moose ad unk	26815 only
	13-Mar-19	Moose calf unk	26814 only
	19-Mar-19	Moose ad fem	26814 only
	Totals:		
	56 days	3 kills	Both
		7 kills	26814 only
		9 kills	26815 only

Appendix 6. Health Sampling

Wolf health sampling was not a primary objective of this project, but samples collected at capture provided an opportunity to work with collaborators to investigate previous outbreaks and baseline seroprevalence of several diseases with population consequences for wolves. Wolves captured in 2018-19 (12 in PGS, 6 in JPRF, as well as 7 in the Hart Ranges east of our study areas during caribou recovery activities) were included in a continent-wide assessment of disease prevalence (Brandell et al. 2021). The region-specific results are summarized here, as Brandell et al. (2021) focused on a larger scale, and Ellen Brandell (Pennsylvania State University) and Helen Schwantje (Provincial Wildlife Veterinarian, ret.) provided additional information and regional interpretation.

Table 15. Seroprevalence of five common wolf pathogens in 3 study areas in south-central Region 7A: Infectious canine hepatitis/ canine adenovirus-1 (CAV), canine alpha herpesvirus-1 (CHV), canine distemper virus (CDV), canine parvovirus-2 (CPV), and *Neospora caninum*.

Pathogen	Standard positive titer threshold	Conservative positive titer threshold	PGS seroprevalence	JPRF seroprevalence	Hart Ranges seroprevalence
CAV	≥1:20	≥1:40	12 (100%)	6 (100%)	4 (57%)
CHV	≥1:20	≥1:40	10-11 (83-92%)	6 (100%)	6 (86%)
CDV	≥1:20	≥1:40	0 (0%)	0 (0%)	0 (0%)
CPV	≥1:20	≥1:40	10 (83%)	5 (83%)	3 (42%)
Neospora caninum	≥1:25	≥1:50	10 (83%)	2 (33%)	5-6 (71-86%)

Infectious canine hepatitis

Infectious canine hepatitis is caused by canine adenovirus-1 (CAV). It causes acute liver disease, although most infected individuals recover. There was very high prevalence in all populations examined in BC and across North America. CAV causes acute liver disease, although most individuals survive. Wolves captured in the Hart Ranges, northeast of our study areas, had about half the CAV prevalence of PGS and JPRF.

Canine alpha herpesvirus-1

Canine alpha herpesvirus-1 (CHV) is a sexually transmitted pathogen that can also be transmitted vertically from mother to offspring. It has a high mortality rate in domestic dog pups, but adult symptoms are less severe, and CHV may be latent for years. Seroprevalence was high across BC overall and in our study areas specifically.

Canine distemper

Canine distemper is caused by canine distemper virus (CDV), a morbillivirus that affects carnivores, pinnipeds, and some primates. It is highly contagious through fecal-oral transmission, bodily fluids, and fomites (persisting on inanimate objects and surfaces). Symptoms progress from fever, respiratory and gastrointestinal problems, anorexia, and lethargy to inflammation of the spinal cord and brain. This leads to seizures, circling, convulsions, and paralysis. Distemper is fatal to most pups and some adults. CDV was not detected in serum samples in BC prior to 2019, but then showed elevated titers in some areas, suggesting a recent outbreak. None of our study areas had seropositive wolves, suggesting that the outbreak elsewhere in the province did not occur here.

Canine parvovirus

CPV was high across BC, including both study areas – although as with CAV, about half as prevalent in the Hart Ranges. CPV is highly contagious, mostly through fecal-oral transmission or nasal fluids, and remains viable in the environment for several months. Symptoms progress from fever, lethargy, anorexia, vomiting, and bloody diarrhea to dehydration and shock. CPV has a high mortality rate for domestic dogs <4 months old. While the impacts of CPV on wild wolves are unknown, it is likely that pups are exposed early and may die prior to emerging from the den.

Neospora caninum

Symptoms of *Neospora caninum* vary from minor to ulcers, pneumonia, hepatitis, neuromuscular degeneration, and paralysis. Canids are the definitive host for *Neospora*, with ungulates as an intermediate host. *Neospora* prevalence is often of interest to livestock producers, as *Neospora* can cross the placenta and cause spontaneous abortion in cattle. Exposure in BC was moderate to high, including in PGS, although JPRF had lower seroprevalence.

Mange

Mange refers to symptoms of hair loss caused by mites. We did not specifically assess mange in wolves in PGS or JPRF but did note observations of hair loss on several wolves, including small patches of hair loss on a male Bobtail Mountain wolf in 2021 and a male Blackwater wolf in 2018. We did not collect any mites or skin/hair samples to determine the type of mange. An uncollared pack of 5 seen on the Fraser River on Feb 27, 2020, near Hixon and apparently occupying a territory east of the river all had moderate to severe hair loss, including one large male missing almost all the hair on his body and tail. Trappers have observed mangy wolves in both study areas.