

**Factors Affecting Moose Population Declines
in British Columbia
May 2022 Progress Report**



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Wildlife Working Reports frequently contain preliminary data, so conclusions based on these may be subject to change. Working Reports receive little review.

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Cover Photo: Collared cow during captures to assess body condition in the Prince George South study area (Morgan Anderson).

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EXECUTIVE SUMMARY

In 2013, the British Columbia Ministry of Forests initiated a 5-year moose research project to determine the factors affecting moose population change in central British Columbia (BC) and to evaluate a landscape change hypothesis proposed by Kuzyk and Heard (2014). This report provides preliminary results and interpretation of data collected from February 2012 to May 2022 from five study areas in central British Columbia: Bonaparte, Big Creek, Entiako, Prince George South (PGS), and the John Prince Research Forest (JPRF). It is preceded by six annual reports (Kuzyk et al. 2015; Kuzyk et al. 2016; Kuzyk et al. 2017; Kuzyk et al. 2018b; Kuzyk et al. 2019b, Procter et al. 2020) and follows the recently revised research design for this project (Kuzyk et al. 2019a).

The provincial moose research project was initiated following substantial moose declines in several parts of interior BC in the early 2000s, causing concern among wildlife managers, First Nations, and stakeholders. Much of the decline happened concurrently with a mountain pine beetle (MPB) outbreak that caused widespread mortality of mature pine trees and resulted in extensive logging and road building to harvest beetle-killed timber. The primary research objective of the project is to evaluate a landscape change hypothesis, which states that moose declines coincided with a MPB outbreak where habitat changes and increased salvage logging and road building resulted in greater vulnerability for moose, primarily from hunters and predators. The landscape change hypothesis predicts that moose survival will increase when: a) forest cutblocks regenerate to the point where vegetation obstructs the view of predators and hunters; b) resource roads created for logging are rendered impassable; and c) moose become more uniformly dispersed on the landscape. We evaluated that hypothesis by identifying rates and causes of cow moose mortality and examining factors that contributed to their vulnerability and mortality. Following the first 5 years of the project assessing adult female survival, we also assessed the causes and rates of 8- to 12-month-old calf mortality in Bonaparte and PGS to address the role calf recruitment plays in population dynamics.

Since this project was initiated in 2012, we have captured, sampled, and fitted GPS radio collars on 548 cow moose and 180 8-month-old calves. We recaptured and sampled 31 cow moose to replace collars over time, deploying a total of 579 GPS radio collars on cow moose. Since 2016/17, we have captured, radio-collared, sampled and monitored 180 8-month-old calf moose in the Bonaparte ($n = 100$) and Prince George South (PGS; $n = 80$) study areas. We collected a standardized set of biological samples and undertook biological and morphological assessments and measurements at the time of capture to inform pregnancy and health status, winter tick burden, reproductive status, size, age, and body condition. Since 2018/19, we also measured rump fat by ultrasonography on a random sample of cow moose in the Bonaparte and PGS study areas to gain more precise data on the body condition of cow moose entering winter. We collected similar observations and samples on calf moose at the time of capture and included direct measurements of their weight and body morphometry. Pregnancy rates varied over time in some study areas, and average pregnancy rates were lower than the North America average for several years in the Bonaparte and PGS study areas. Estimates of winter tick numbers varied across years and study areas. Serological screening and ancillary testing did not demonstrate significant exposure to pathogens associated with morbidity and mortality in any study area. Rump fat measurements indicate relatively low body fat levels (~8–10%) in all years monitored, with variation among individuals, years, and study areas. The weight and measurements of 8-month-old moose calves varied among study areas and years but with little significant difference in body weight.

As of 30 April 2022, 175 GPS collars were active on cow moose, and we have recorded 176 mortalities of cow moose (of the 548 moose cows collared since project inception). We identified the probable proximate cause of death for 164 cow mortalities, while causes of death for 12 remain unknown.

Assessment of ultimate cause of death is ongoing. Most (58%) mortalities were due to predation, predominantly due to wolves, but with 7% of mortalities attributed to bear predation and 3% to cougar predation. Health-related mortality causes made up 17% of proximate cause of death, and 11% of mortalities were due to hunting. We investigated 50 mortality events for calf moose since 2016/17 and found the probable proximate cause of calf mortalities to be primarily predation (65% wolf, 9% bear, 7% cougar). Health-related causes of death varied by year and constituted 17% of all calf mortalities.

We used age, body condition, and health results from laboratory analysis of tissue samples at time of death to assist in the determination of the ultimate cause of death and to assess the relative importance of various mortality factors. Assessments of bone marrow fat at time of death ($n = 118$) found that 49% of moose cows had high marrow fat content ($>70\%$ marrow fat), 21% ($n = 22$) were considered to be in poor condition (20–70% marrow fat), and 30% ($n = 31$) were in a state of acute malnutrition ($<20\%$ marrow fat). The majority of cow mortalities in acute malnutrition and poor body condition occurred between April and June. Average age at death was 10.4 years (range 1–18 years old). There were no significant differences in age of moose that died due to different probable proximate causes, and deaths were more likely to occur at an older age, regardless of cause.

The landscape change hypothesis, originally presented by Kuzyk and Heard (2014), assumed that cow survival was the primary driver of moose population change based on how rapidly populations in some areas declined. Subsequent evaluation of adult cow moose survival, however, revealed survival rates consistent with those reported for other stable moose populations (i.e., generally above 85%). Our data showed variation in cow survival, and some study areas (Entiako, PGS) have had lower survival rates in years that could contribute to population decline. In 2020/21 and 2021/22, cow moose survival was above 85% in all study areas (except 83% in Bonaparte in 2021/22). The relatively high survival rates of cow moose and continued population declines in most study areas led to recent work evaluating the effect of landscape change on moose calf survival and recruitment in the Bonaparte and PGS study areas from 2016/17 to 2020/21. Moose calf survival through the late-winter period to age one varied annually (45–85%) and consistently resulted in lower recruitment rates than identified mid-winter. Late winter calf survival in 2020/21 was the highest recorded in both study areas in 2016/17.

Additional theses, reports, and peer-reviewed papers have been produced by the Provincial Moose Research Project, including habitat use and selection in relation to disturbance variables (Scheideman 2018, Francis 2020, Francis et al. 2020, Mumma et al. 2020), landscape factors influencing survival (Mumma and Gillingham 2019) and predation risk (Boucher et al. 2022), and drivers of migratory behavior (Chisholm et al. 2021). Additional work is ongoing, with three PhD students (University of Northern BC and University of Victoria) and a MSc student (University of Northern BC).

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1. INTRODUCTION

Moose are highly valued by the citizens of British Columbia (BC) for consumptive and non-consumptive purposes. Moose populations in some areas of BC have declined by 50–70% since the early 2000s, while others have remained stable or are increasing (Kuzyk 2016; Kuzyk et al. 2018a). Moose declines in central British Columbia coincided with a Mountain Pine Beetle (*Dendroctonus ponderosae*; MPB) outbreak, which resulted in widespread mortality of pine trees >30 years old, and extensive road building and salvage logging of beetle-killed timber (Alfaro et al. 2015). The resulting large-scale alterations to the landscape may have influenced the distribution and abundance of moose, hunters, and predators (Janz 2006; Ritchie 2008). In 2012-13, the BC Ministry of Forests and its partners initiated a research project to examine causes of moose declines (Kuzyk and Heard 2014).

A landscape change hypothesis was developed to evaluate the effect of landscape change on moose population trends (Kuzyk and Heard 2014). The landscape change hypothesis states that moose declines coincided with an MPB outbreak because habitat change, increased salvage logging, and associated road building resulted in greater vulnerability of moose, primarily from predators and hunters. The primary predictions of the landscape change hypothesis are that moose survival will increase when: a) forestry cutblocks regenerate to the point where vegetation obstructs the view of predators and hunters; b) resource roads created for logging are rendered impassable due to deactivation or forest ingrowth; and c) moose become more uniformly dispersed on the landscape (Kuzyk and Heard 2014). We assumed that cow moose survival had a greater effect on population growth rates than did calf survival (Gaillard et al. 1998). Accordingly, we assessed cow moose mortality by monitoring a minimum of 30 GPS radio-collared cow moose annually 2012-2022 in each of five study areas across central British Columbia (Kuzyk and Heard 2014). Since initiation of this research, we acknowledged that calf survival could be a substantial contributing factor to moose population declines, either in isolation or in conjunction with declining cow survival. Having established that cow survival was sufficiently high to maintain stable populations in most study areas, we added additional research objectives focussed on assessing moose calf survival and recruitment in two study areas in 2016/17.

The objective of this report is to provide an update on fieldwork and preliminary results from February 2012 to May 2022. Project results are also available in several publications, and the reader is referred to these for more information:

- Research design (Kuzyk and Heard 2014, Kuzyk et al. 2019a)
- Updated methodology and results in progress reports (Kuzyk et al. 2015, Kuzyk et al. 2016, Kuzyk et al. 2017, Kuzyk et al. 2018b, Kuzyk et al. 2019b, Procter et al. 2020).
- Analyses of moose habitat use and selection (Scheideman 2018; Francis 2020; Francis et al. 2020; Mumma et al. 2020)
- Cow survival relative to features of landscape change (Mumma and Gillingham 2019)
- Seasonal migratory movements of moose (Chisholm et al. 2021)
- Effect of landscape disturbance on moose diet (Koetke et al. 2023)
- Landscape features associated with wolf predation risk (Boucher et al. 2022, Anderson et al. 2023)

2. STUDY AREA

Research occurred in five study areas across the Interior Plateau of central British Columbia: Bonaparte, Big Creek, Entiako, PGS, and JPRF (Figure 1). Study areas were selected to encompass a range of MPB infestation and disturbance levels across rolling terrain with a mosaic of wetlands and mixed and coniferous forest at varied seral stages. Except for on-going timber harvesting in all study areas and notable wildfires that have occurred in Entiako (2013, 2018), Big Creek (2017), and Bonaparte (2017, 2021), there has been little variation in biotic or abiotic characteristics within study areas since the start of the study.

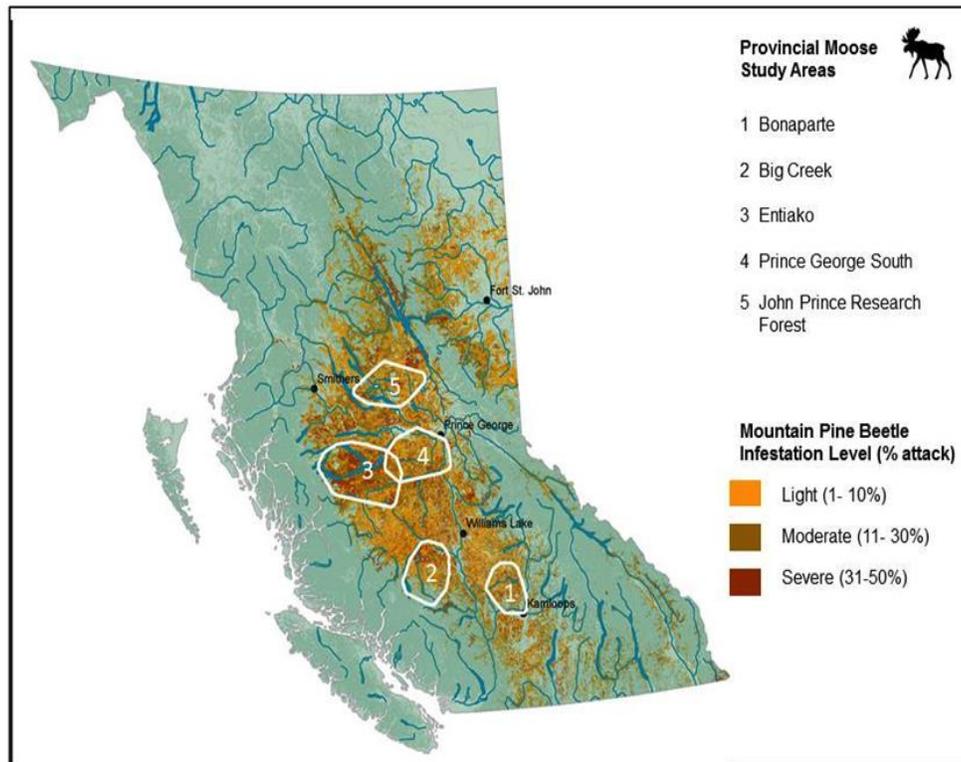


Figure 1. Moose research study areas in central British Columbia overlaid on severity of Mountain Pine Beetle infestation (2016).

3. METHODS

3.1 Moose Capture and Collar Deployment

Methodologies for capture, sampling, and monitoring were originally presented by Kuzyk and Heard (2014) and certain methodologies have since been updated and standardized (Procter et al. 2020). Cows have been captured annually since 2012 to maintain approximately 30 cows per study area with actively transmitting radio collars. Eight-month-old moose calves were captured from winter of 2016/17 to winter 2020/21 in the Bonaparte and PGS study areas. We captured cow and calf moose between December and March using chemical immobilization by aerial darting; however, aerial net-gunning was used to capture cow moose in earlier years of this research and moose calves more recently. We equipped calf collars with cotton spacers intended to rot off 1-2 years after deployment. Captures were conducted in accordance with the British Columbia *Wildlife Act* under permit CB17-277227.

3.2 Biological Assessments and Sampling

All moose were sampled according to a standardized protocol to collect samples and assess age class, body condition score, tick load, and calf presence. From 2018/19 to 2021/22 in PGS and Bonaparte, we also measured maximum rump fat (MAXFAT); when non-random cows were captured (i.e. targeted due to presence of a collared calf), their body fat measurements were excluded from analyses. To provide additional context to the MAXFAT measurements in PGS and Bonaparte, we also measured MAXFAT in 2021/22 on random cow moose in two other areas south of Kamloops (Pennask Plateau and Highland Valley Copper).

Biological samples – We collected fecal pellets for parasitology assessments, hair for cortisol analysis, biopsy punches for genetics, and 20–35 ml of blood. Serum was submitted for pregnancy testing using pregnancy-specific protein B levels (PSPB; Thacker et al. 2019). Initial serological analyses focussed on exposure to pathogens considered of high priority for impacts on survival and reproduction of wild ungulate populations: Johne’s disease, *Neospora caninum*, Bovine Viral Diarrhea virus, and Parainfluenza 3 virus, with a subset tested for exposure to *Erysipelothrix rhusiopathiae* and *Toxoplasma gondii*. Serum from blue-top vials was assessed for trace mineral levels (manganese, iron, cobalt, copper, zinc, selenium, and molybdenum). In most cases, plasma and buffy coat samples were archived at -80°C. Starting in 2018/19, whole blood in an RNA buffer was frozen to be analyzed for gene transcription levels. In some years, some moose were tested for *Mycoplasma ovipneumoniae* (M.ovi) by polymerase chain-reaction testing of nasal swabs.

Body condition and size – We scored body condition of cows and calves on a 5-point scale (emaciated, poor, fair, good, excellent). Cows with access to high quality nutrition are expected to raise larger calves with higher survival (Crête and Huot 1993, Schwartz et al. 1994, Cook et al. 2003, Holmes et al. 2021), so from 2016-2019 we weighed calves as well as taking morphometric measurements. We used these to develop a regression equation to estimate the weight of moose calves. When calves were not weighed, we estimated weights based on the best fit regression equation using data from 30 calves in the Bonaparte study area:

$$y = 1.7688x - 209.1920$$

Where y is body mass (kg) and x is total length (cm) (Kuzyk et al. 2019a).

3.3 Survival Rates

All cow moose were assumed to be random individuals and representative of the population with equal risk of mortality. Annual survival rates were calculated for cow moose from 28 February 2012 to 30 April 2022. The biological year was considered to begin on 1 May, immediately prior to the average timing of parturition for moose in BC (Poole et al. 2007, Gillingham and Parker 2008). Survival analysis and mortality results included only cow moose that lived >5 days post-capture to avoid the potential bias introduced by capture-related stresses and physiological changes (Neumann et al. 2011). Cow survival rates were calculated weekly and summarized by biological year using a Kaplan-Meier estimator (Pollock et al. 1989). We calculated survival rates both within and pooled across all study areas and we evaluated survival rates relative to a threshold of 85%, which indicates potential for stable moose populations (Bangs et al. 1989, Ballard et al. 1991, Bertram and Vivion 2002).

Although most collar deployments represent newly collared random cows, in some study areas cows have been recaptured to replace an old collar. In this case, there is a chance that we are monitoring a biased portion of the population (i.e., we continue to monitor cows that survive rather than a random segment of the population). To test whether our survival estimates may be biased toward these 'winners,' we examined whether survival rates changed over the course of monitoring for each cohort (i.e., cows originally captured and collared in the same year).

Calf survival rates were calculated from date of capture (at about 8 months of age) to the average birth date (calculated following Severud et al. 2015), using a Kaplan-Meier estimator (Pollock et al. 1989). Survival analysis and mortality results included only calves that lived >5 days post-capture (Neumann et al. 2011). We considered calves recruited into the population on their first birthday (Bender 2006), as we assume survival rates begin to align with adult survival rates at that time (Hickey 1955). To assess this assumption, we also calculated yearling survival rates for collared calves that retained their collars and survived to their second birthday (i.e., 21 May of their first year to 21 May of their second year).

3.4 Mortality Causes

We conducted mortality site investigations according to a standardized protocol (Procter et al. 2020) as soon as logistically feasible after receiving a mortality notification, typically within 24–48 hours. In some cases, collars were kept in motion post-mortem which prevented the mortality signal from being triggered. This was particularly true for predation events where the collar was frequently moved by predators or scavengers. In other cases, mortality signals were not immediately received when the collar was underwater or buried under debris. We determined the probable proximate (i.e., direct) cause of mortality following a standardized protocol (Kuzyk and Heard 2014). Samples collected during mortality site investigations informed proximate and ultimate cause of death, where ultimate cause of death is the sum of the underlying reasons an animal died or was susceptible to death from a proximate cause (Mumma and Gillingham 2019). We generally assessed age, health, and condition at time of death to inform ultimate cause of death. The information from tissue sample analyses was used to provide baseline moose health profiles and added to the determination of the ultimate cause of death.

3.5 Calf Production, Survival, and True Recruitment

Parturition rates and dates were calculated by assessing daily cow movement through the parturition period (DeMars et al. 2013, McGraw et al. 2014, Severud et al. 2015, Obermoller 2017). Calving movements are generally classified by a long-distance movement followed by very short movements

constrained by the low mobility of calves immediately post-birth. We used the first day where reduction in movement rates was observed as the estimated birth date (Severud et al. 2015). Mean parturition date was 21 May (± 0.6 days 95% CI), which was used to calculate calf survival rates to their first birthday. Aerial surveys were conducted 4–6 weeks post-parturition in Bonaparte and PGS to locate collared cows and determine presence of a calf at heel. Calf-at-heel status was also determined in early winter during cow captures and, when funding was available, in mid-late March.

To calculate true calf recruitment rates (survival to age 1), we corrected mid-winter calf ratios from aerial surveys in Bonaparte and PGS with survival rates of collared 8-month-old calves to their average first birthday. We assumed that cow deaths over the same period were too few to substantially alter the cow/calf ratios.

To understand the effect of true recruitment on moose population trends, we calculated the rates of population change λ using cow survival rates, the mid-winter recruitment index, and true recruitment at age 1, assuming that half the calves were female:

$$\lambda = \frac{S}{1 - R}$$

where S is survival from 8 months to age 1 as a proportion and R is the proportion of female calves in the female population; that is, (female calves)/(cows + female calves) (Hatter and Bergerud 1991).

3.6 Density Surveys

Moose abundance and density estimates are generated approximately every 5 years from stratified random block surveys in the study areas (Gasaway et al. 1986, Heard et al. 2008). These surveys follow established protocols and standards for accuracy and precision with a coefficient of variation of 15–25% (Resources Information Standards Committee 2002). Sightability correction factors were applied to correct sampling-based density estimates (Quayle et al. 2001). Stratification methods are generally consistent within study areas but vary among study areas. We assume that, despite differences in stratification methods, the surveys produce comparable density estimates.

4. RESULTS

4.1 Moose Capture and Collar Deployment

From February 2012 to March 2022, we captured, sampled, and radio-collared 579 cow moose and recaptured and sampled another 31 moose to replace collars with dead or low-voltage batteries and 113 moose for body condition measurements (no collar deployment, Table 1). We censored 224 cow collars when they ceased tracking moose movements due to low battery voltage, when the collar malfunctioned, or when the collar physically slipped from the moose.

Table 1. Number and status of all GPS radio collars deployed on cow moose in all study areas in central British Columbia, February 2012–March 2022. Active collars are as of March 31, 2022.

Study Year	Number of collars deployed ¹	Number of moose collared	Mortalities	Censored Collars	Active Collars
Bonaparte	172	165	40	92	34
Big Creek	104	102	32	42	30
Entiako	110	102	42	36	25
PGS	112	110	45	28	37
JPRF	81	69	17	26	26
Totals	579	548	176	224	152

¹ Includes recaptures where the original collar was replaced by a new collar; does not include recaptures to assess body condition.

Between 2016/17 and 2020/21, we captured and collared 180 moose calves in Bonaparte ($n = 100$) and PGS ($n = 80$, Table 2).

Table 2. Moose calves captured and collared in the Bonaparte and PGS study areas by sex and year from 2016 to 2021.

Study Year	Study Area					
	Bonaparte			PGS		
	Females	Males	Total Collars	Females	Males	Total Collars
2016/17	12	8	20	0	0	0
2017/18	6	14	20	11	9	20
2018/19	9	11	20	7	12	19
2019/20	10	10	20	12	9	21
2020/21	11	9	20	14	6	20
Totals	48	52	100	44	36	80

4.2 Biological Assessments and Sampling

Age at capture - Of the 544 captured moose assessed for age via tooth eruption, staining, and wear patterns, 85% were classified as adults (4.5–7.5 years old), 10% as aged (>8.5 years old), and 4% as young (1.5– 3.5 years old).

Cow body condition score - Of the 506 cow moose assessed for body condition, 16% were in excellent body condition, 68% were in good body condition, 12% were in fair body condition, 4% were in poor body condition, and 3 individuals were emaciated (Figure 2). Body condition assessments varied among years and study areas, with poorer overall condition scores in 2016/17 and in PGS (Figure 2, Figure 3).

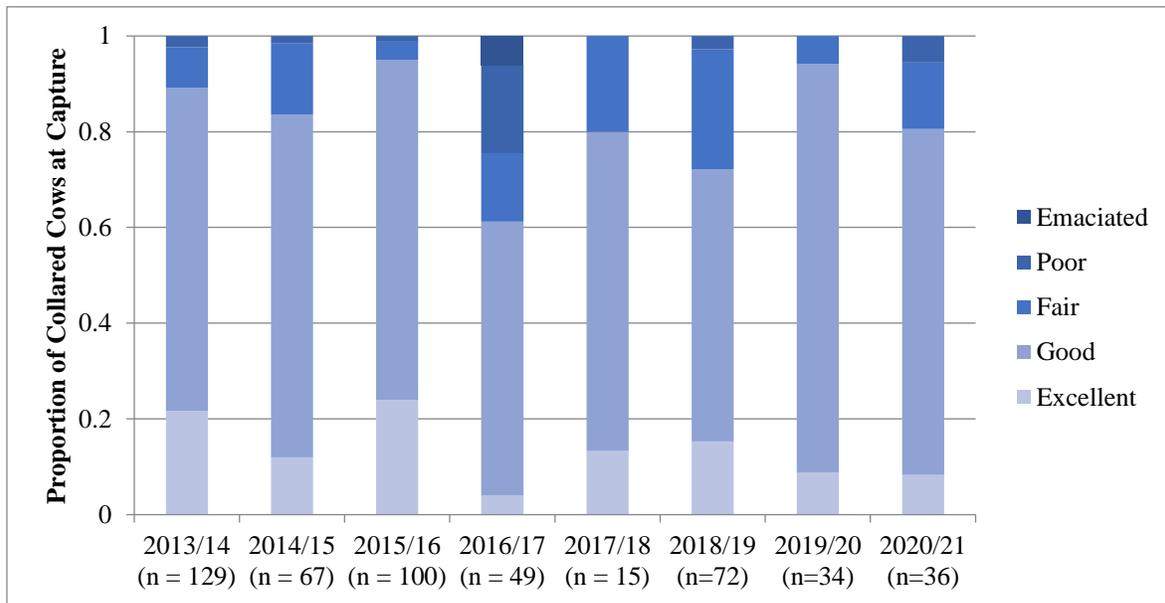


Figure 2. Annual body condition scores of 504 cow moose radio-collared in central British Columbia from February 2012–March 2021. Condition scores were assessed at capture using external physical traits modified from Franzmann (1977) and exclude non-random captured cows (i.e., targeted due to presence of a calf). Only two collars were deployed in 2021/22.

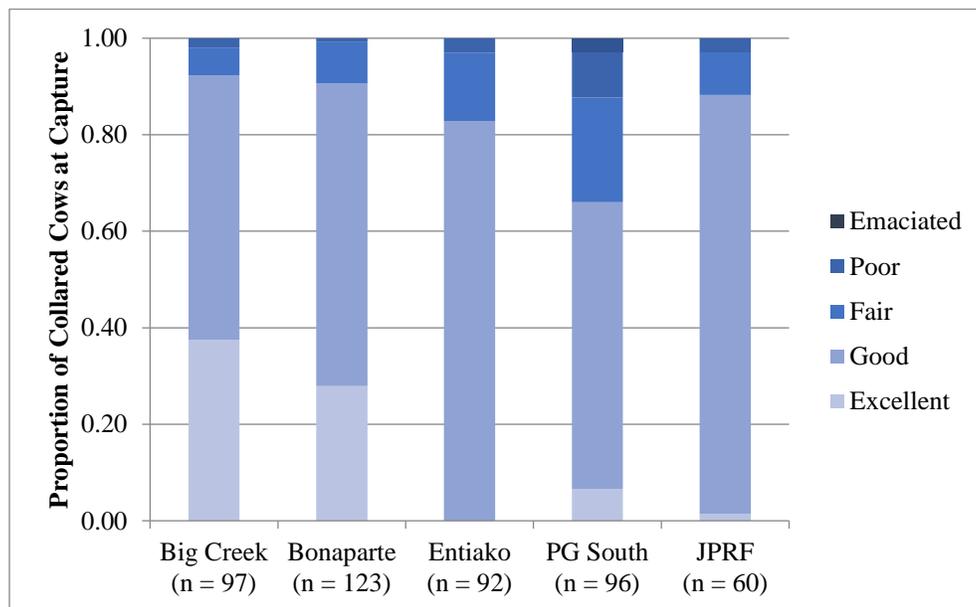


Figure 3. Annual body condition scores of 506 cow moose radio-collared in central British Columbia from February 2012–March 2022. Condition scores were assessed at capture using external physical traits modified from Franzmann (1977) and exclude non-random captured cows (i.e., targeted due to presence of a calf).

Calf body condition and size – The body condition of calves was scored for 175 moose calves and 58% were in good condition, 38% were in fair condition, and 1% were in poor condition. The average estimated weight of 177 calves 8 months of age in Bonaparte and PGS for all years was 172 kg (± 3 kg 95% CI). Except for 2019/20 (calves born in May 2019), there was no significant difference in calf weights between PGS and Bonaparte, and relatively little variation among years (Figure 4).

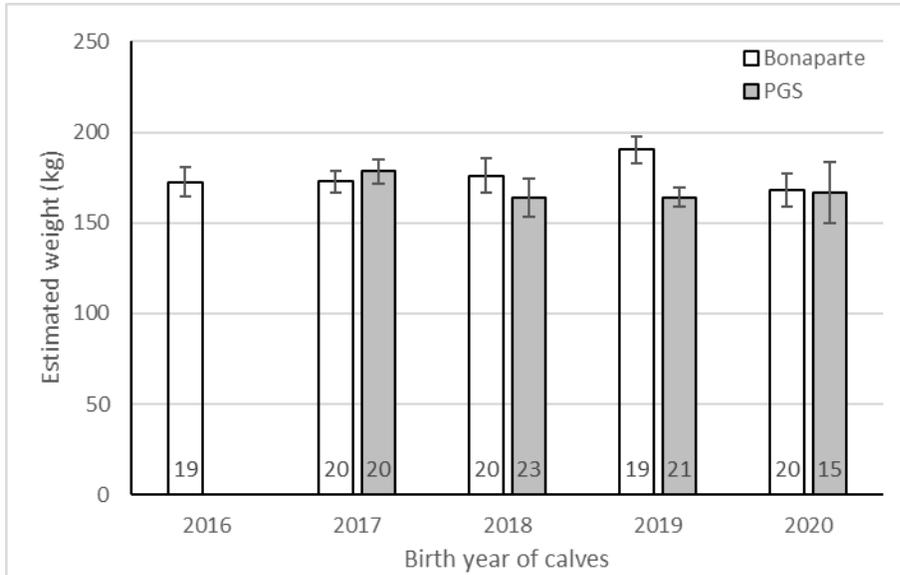


Figure 4. Estimated weight of 8-month-old moose calves based on body length in PGS and Bonaparte. Numbers at the base of the bars represent sample size.

Winter tick load – The number of winter ticks on cow moose at capture has been assessed systematically with transects on shoulder and rump since 2018/19. Tick load has varied significantly by year and study area, although in some years and study areas sample size has been small (Figure 5). Tick loading in 2020/21 was greatest in Big Creek (4.0 ± 4.7 ticks) and lowest in Entiako (0.7 ± 1.1 ticks). In 2021/22, PGS and Bonaparte cows had similar tick loads at 5.0 ± 6.9 ticks and 4.3 ± 4.6 ticks respectively.

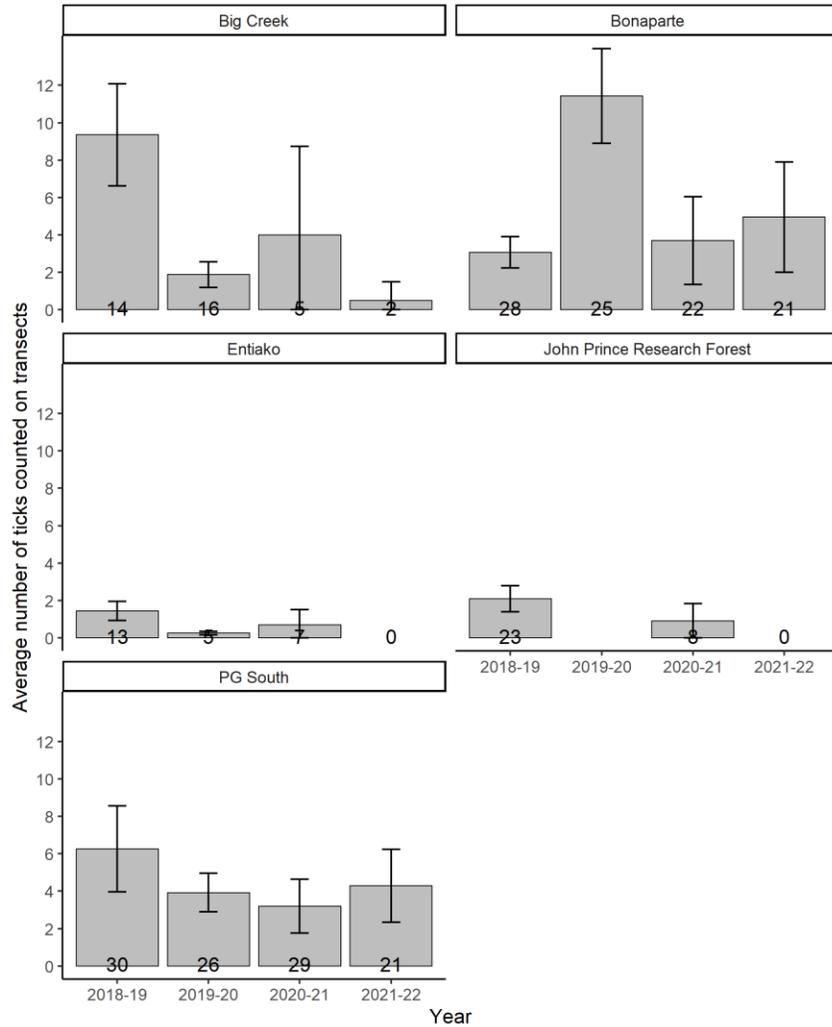


Figure 5. Average tick abundance from shoulder and rump transects on cow moose from 2018 - 2022. Numbers at the base of the bars represent sample size.

We also conducted tick transects on captured calves in Bonaparte and PGS. We have generally detected fewer ticks on moose calves since 2018-19. Tick abundance was only slightly higher in PGS (5.4 ± 3.1 ticks) than in Bonaparte (3.4 ± 2.4 ticks) and does not suggest a biological difference (Figure 6).

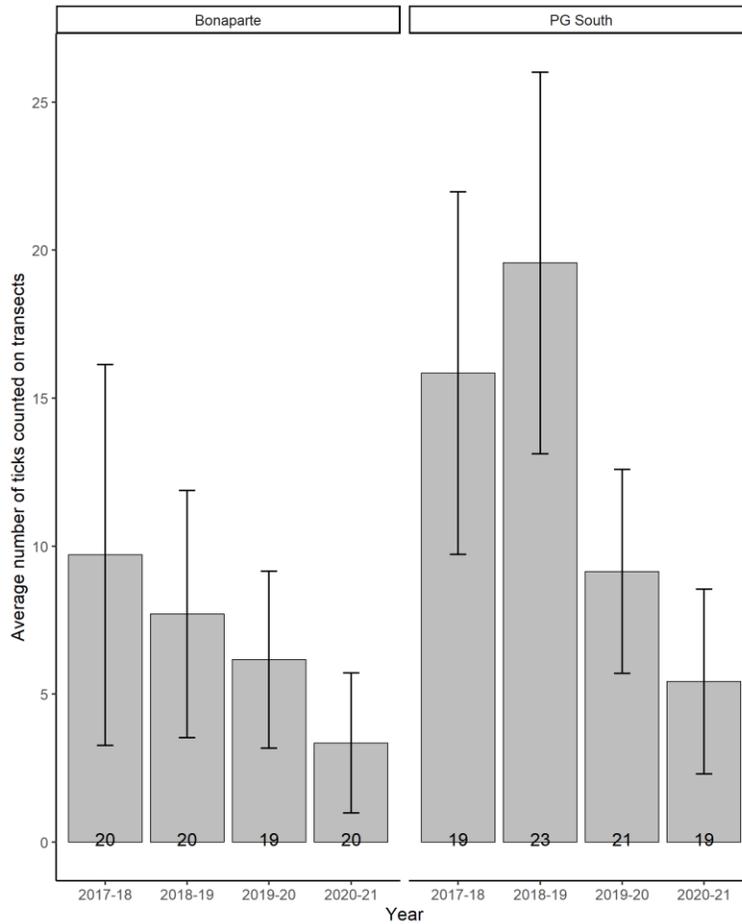


Figure 6. Average tick abundance from shoulder and rump transects on calf moose from 2017 - 2021. Numbers at the base of the bars represent sample size.

MAXFAT and ingesta-free body fat (IFBF) – In 2020/21, we measured MAXFAT on 23 cows in Bonaparte and 29 cows in PGS. Mean MAXFAT was 16.2 ± 3.5 mm (95% CI) in Bonaparte and 23.9 ± 3.5 mm (95% CI) in PGS, corresponding to an estimated average percent IFBF of $8.9 \pm 0.7\%$ (95% CI) for Bonaparte and 10.5% ($\pm 0.7\%$ 95% CI) for PGS. We measured rump fat on 42 cow moose in 2021/22 (21 each in Bonaparte and PGS) and mean MAXFAT was 11.2 ± 3.6 mm (95% CI) in PGS and 20.9 ± 5.1 mm (95% CI) in Bonaparte. This corresponded to an estimated average percent IFBF of $7.9 \pm 0.7\%$ (95% CI) and $9.9 \pm 1.0\%$ (95% CI) for Bonaparte and PGS, respectively (Figure 7).

Differences between study areas and year did not appear significant. Cows with calves at capture consistently had lower MAXFAT than those without calves, although the difference does not appear to be significant. The range of IFBF observed in PGS was 7.2–15.2% in 2020/21 and 7.0–15.9% in 2021/22 (Figure 7). The range of IFBF observed in Bonaparte was 6.3–12.5% in 2020/21 and 5.6–10.9% in 2021/22 (Figure 7).

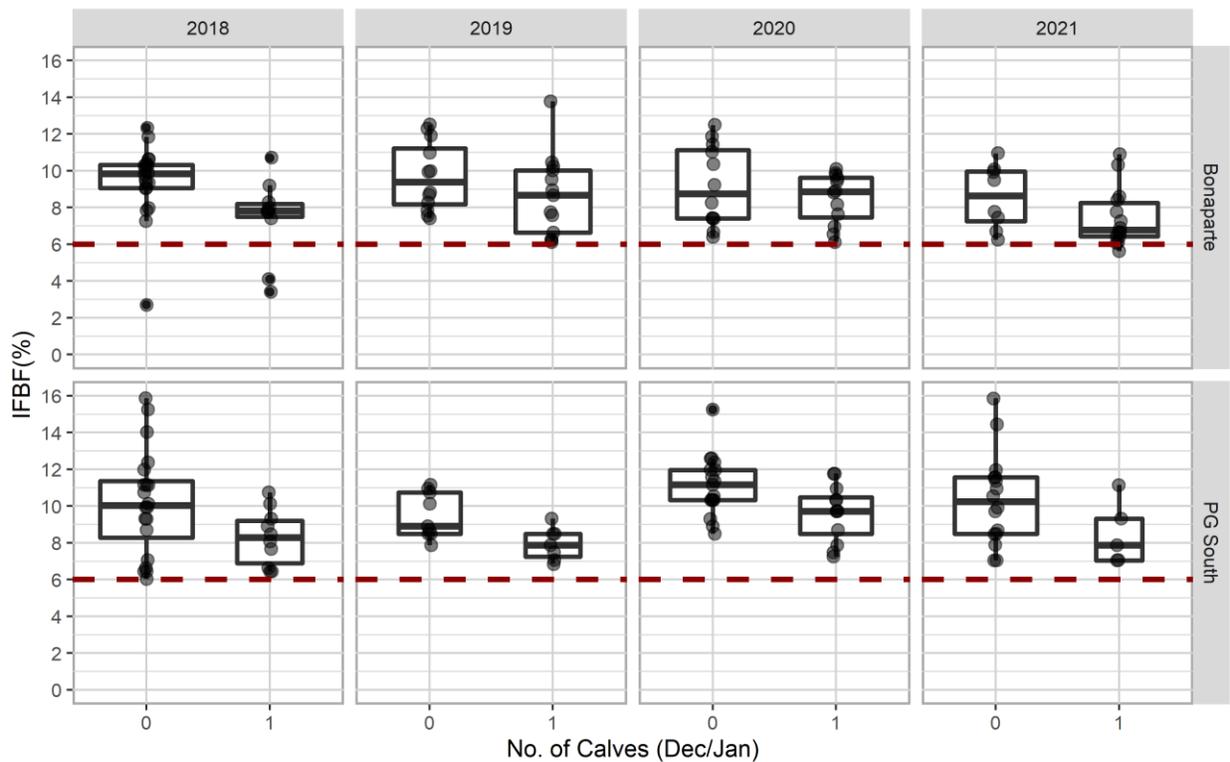


Figure 7. Boxplots of ingesta free body fat (IFBF) of adult cow moose estimated from ultrasound rump fat measurements (MAXFAT, Stephenson et al. 1998) at time of capture in the Bonaparte and PGS study areas, December–January 2018/19 to 2021/22. The red line is the threshold suggested by Ruprecht et al. (2016) above which increasing body fat does not increase likelihood of pregnancy.

In addition to the Bonaparte and PGS MAXFAT measurements, we also measured MAXFAT on 21 and 12 cows in the Pennask Plateau and Highland Valley Copper (HVC) area, respectively. Estimated body fat did not appear to differ between Bonaparte, Pennask Plateau and Highland Valley Copper entering winter of 2021/22 (Figure 8).

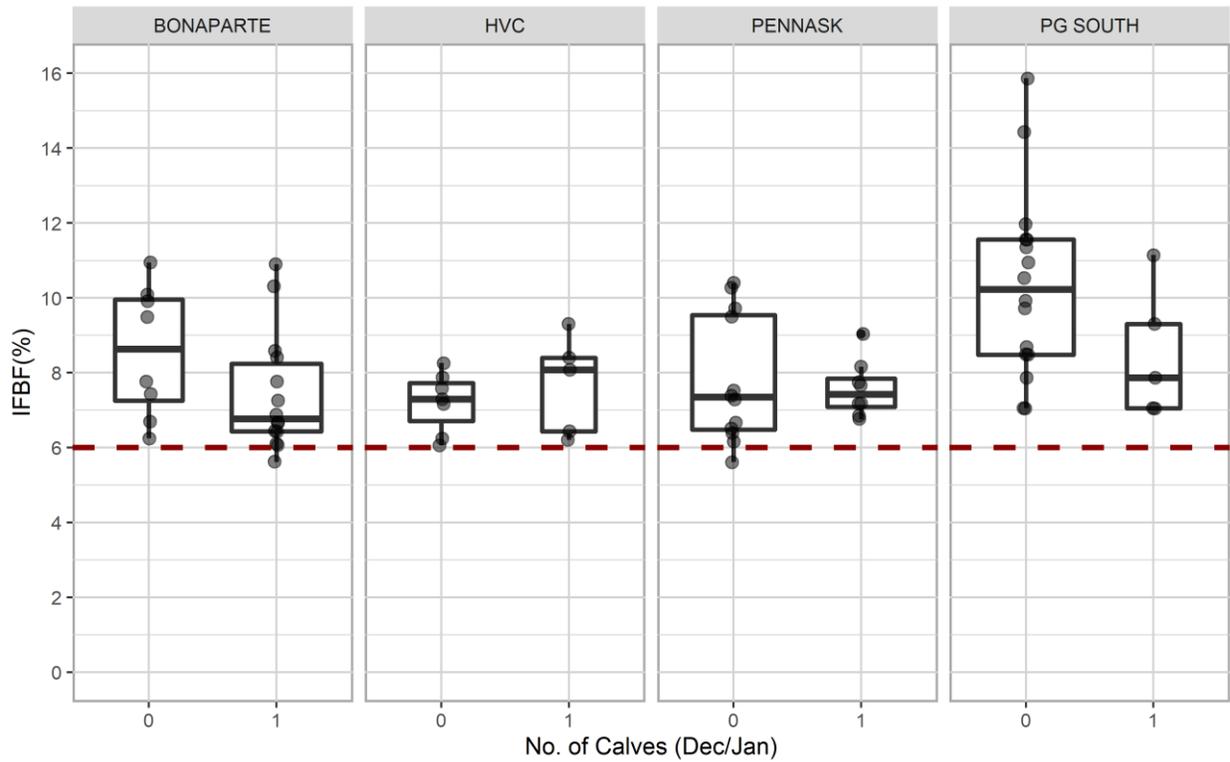


Figure 8. Boxplots of ingesta free body fat (IFBF) of adult cow moose estimated from ultrasound rump fat measurements (MAXFAT, Stephenson et al. 1998) at time of capture in December-January 2021/22 in Bonaparte, PGS, HVC, and Pennask Plateau. The red line is the threshold suggested by Ruprecht et al. (2016) above which increasing body fat does not increase likelihood of pregnancy.

We also considered whether maternal condition (measured as % IFBF) influenced calf survival through the neonate period to approximately 30 days of age. The 2021 calf-at-heel survey could not be completed in Bonaparte due to the Sparks Lake wildfire, but we had 94 measurements of early winter condition where we also knew calf survival to approximately 30 days in the next year. There does not appear to be a significant relationship between maternal condition and neonate survival across the range of IFBF we measured (Figure 9).

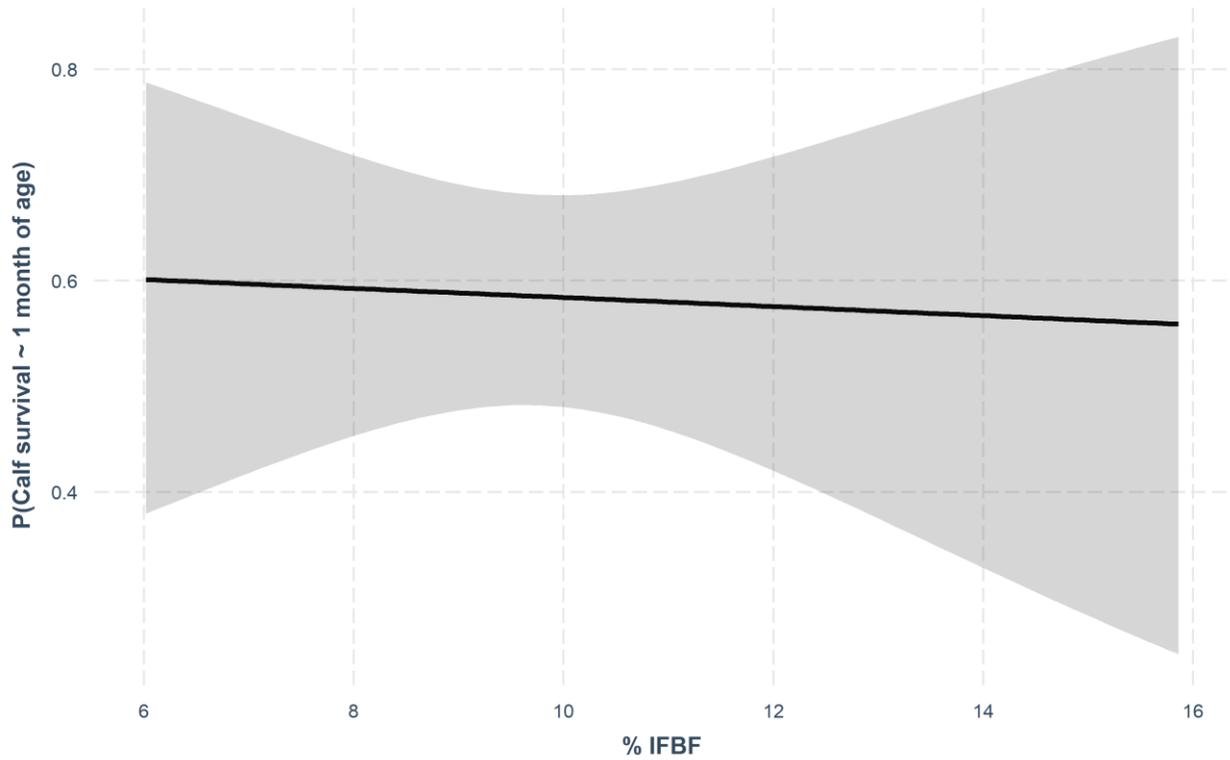


Figure 9. Relationship between maternal condition in early winter (%IFBF) and calf survival to approximately one month of age the following year for PGS and Bonaparte, 2018/19 to 2020/21.

Pregnancy rates – Pregnancy rates were variable among study areas and years, with the lowest pregnancy rate observed in Bonaparte in 2015/16 ($47 \pm 16\%$ of 36 cows sampled). JPRF has had consistently high pregnancy rates, although sampling has been more sporadic. All other study areas have had years with unexpectedly low pregnancy rates occasionally below 70%, but generally pregnancy rates are fairly high, at or near 85% (Figure 10).

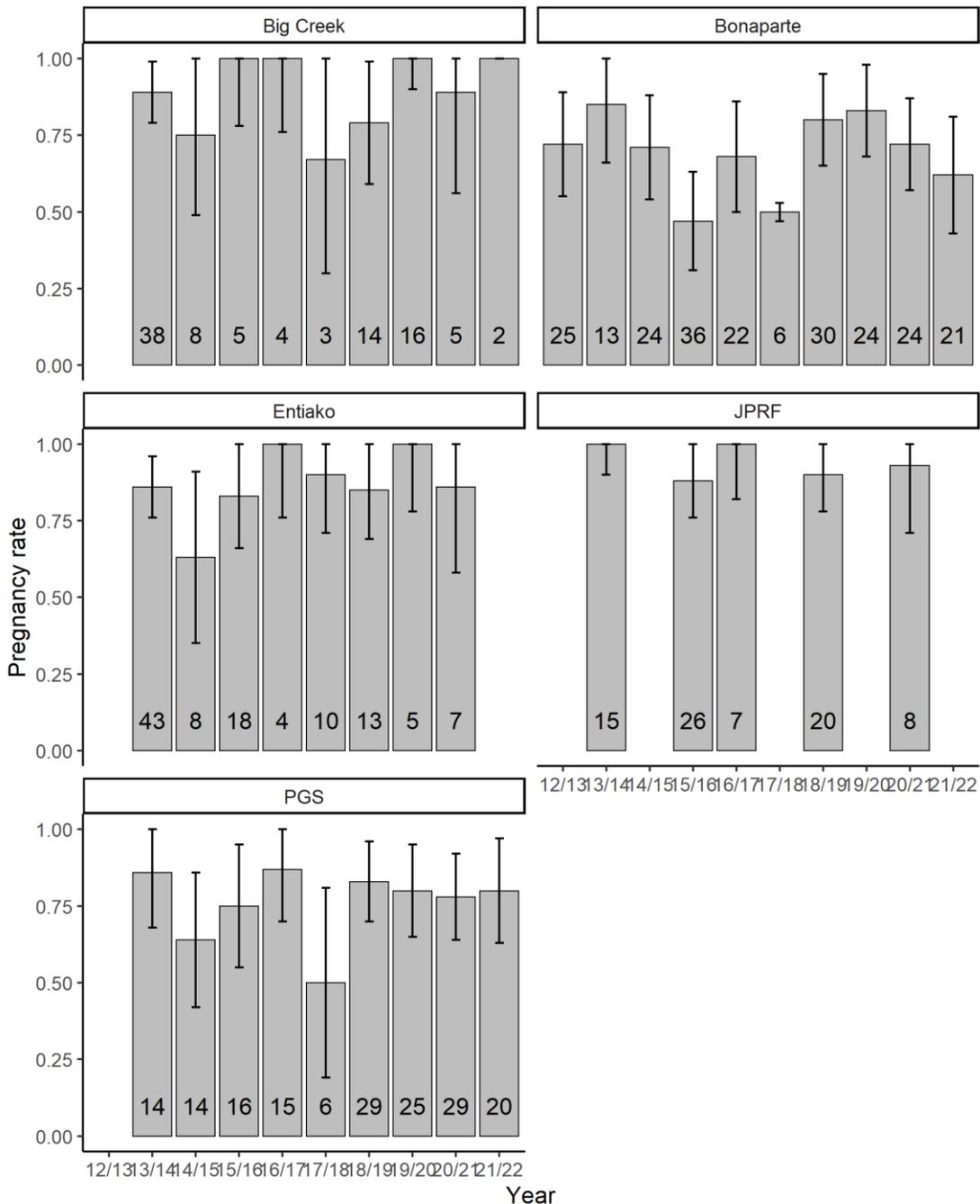


Figure 10. Pregnancy rates for cow moose sampled 2012-2022 by study area. Numbers at the base of bars indicate sample size; note that some years and study areas had small sample size that may make extrapolation of pregnancy rates unreliable.

Serological screening – Serological screening of cow moose to date has indicated minimal exposure to a suite of pathogens selected for assessment at the early stages of the project. Additional assessments have been added and some removed. Trace mineral requirements and other metabolic parameters are not well characterized for moose; however, some mineral levels (e.g., copper, selenium) appear to be sub-optimal in some moose, with variation observed between study areas. Thacker et al. (2019) present a detailed assessment of moose health results from this project current to October 2019, providing the first comprehensive baseline herd health assessment of moose populations in British Columbia. The health data from cow and calf moose captures and some mortality investigations in 2019 and 2020 are incomplete due to covid- and natural disaster-related laboratory closures, including BVD/IBR serology, fecal parasitology, gene transcription, hair cortisol, and M.ovii status. Lab analyses are on-going.

4.3 Survival Rates

Adult female survival rate – Survival rates were generally consistent over the course of monitoring, and we did not see steep declines in survival over the first year of monitoring for any of the cohorts (

Figure 11). From 2012 to 2022, the annual survival rate of all cows in all study areas varied from 85 to 100% (Figure 12), although only 9 cows were monitored for survival in 2012. Cow survival rates varied by study area and were generally lowest in Entiako and PGS, where mean survival rates below the 85% threshold occurred in some years. The lower 95% confidence interval was often below the 85% survival threshold in many years and study areas. In 2020/21 and 2021/22, cow survival was above the 85% threshold in all study areas (except Bonaparte in 2021/22).

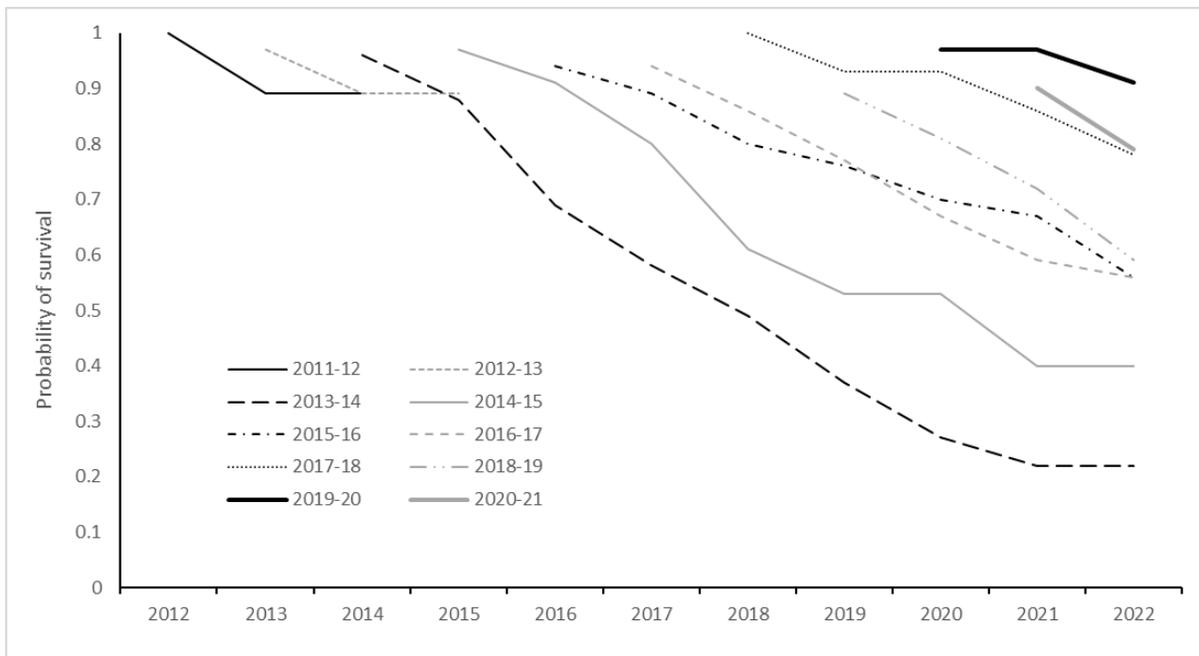


Figure 11. Survival over time for collared cow moose monitored in all study areas, 2012-2022, based on cohorts captured in each year.

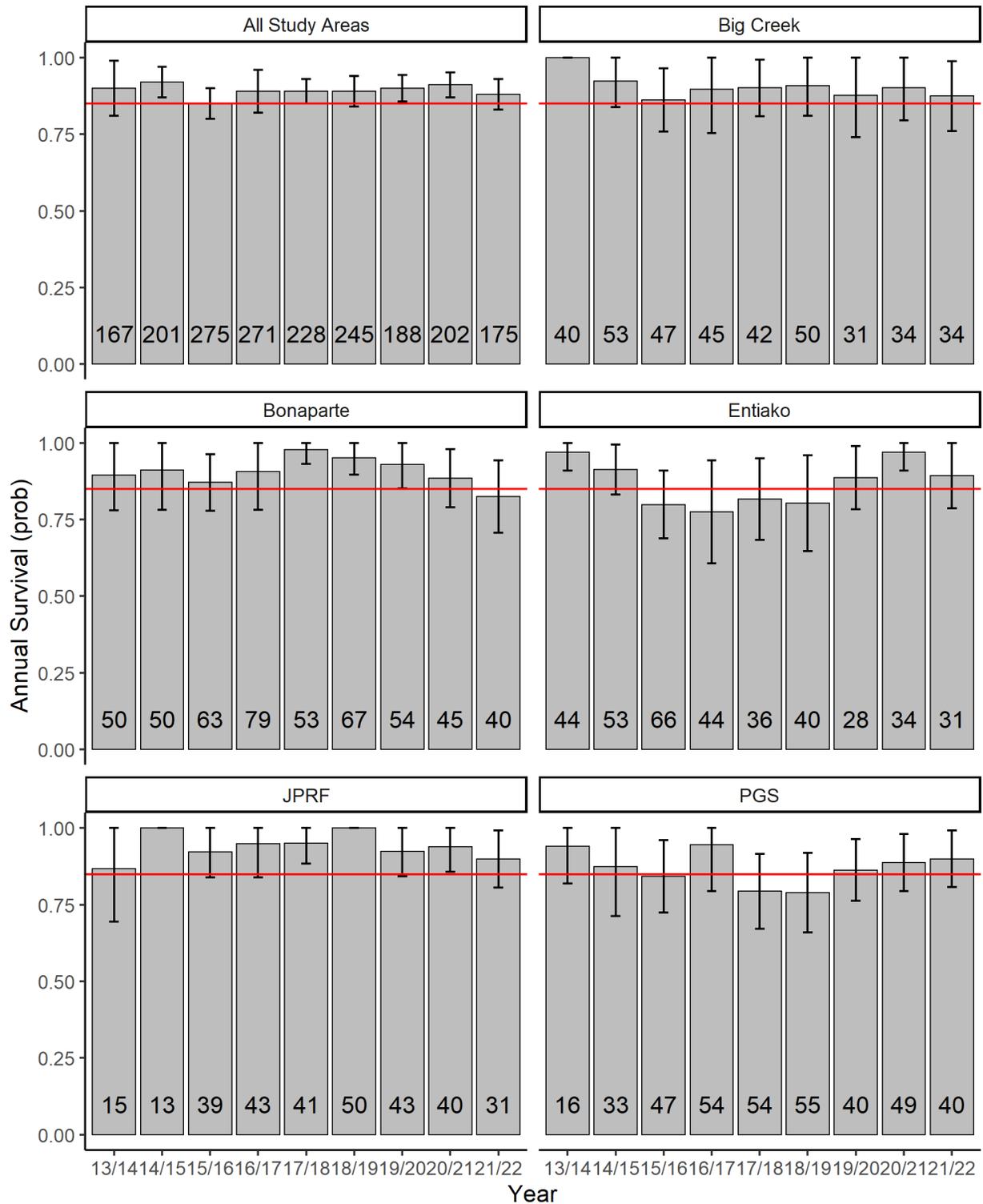


Figure 12. Survival rates of radio-collared cow moose by study area and combined, 1 May 2012–30 April 2022. Red line indicates a survival rate of 85%, the threshold indicating stable moose populations and used to evaluate and interpret estimated survival rates in this study. Sample size is indicated at the base of the bars.

Calf survival rates – Moose calf survival from capture to age 1 varied from 45 to 85% (Figure 13). Following poor calf survival in 2016/17 in Bonaparte, that study area has consistently had higher calf survival to age 1 than PGS, although differences are not significant. Winter calf survival was higher in 2020-21 than the three previous years of calf monitoring. Caution is warranted when interpreting survival rate estimates for calves due to sample size ($n = 20$ in each study area).

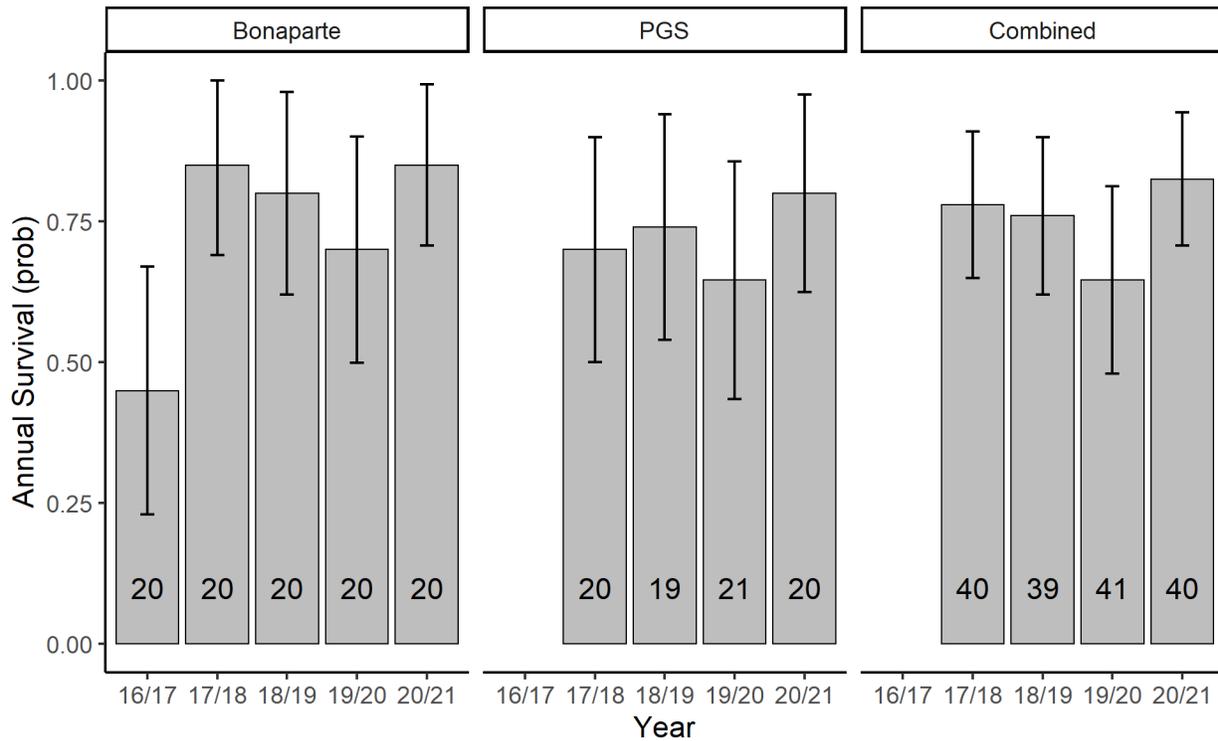


Figure 13. Late-winter survival rates (i.e., time of capture to age 1) of radio-collared calf moose in central British Columbia from time of capture (variable dates), January 2017–22 May 2021. Error bars are 95% CIs, sample size is noted for each year and study area on the grey bar.

4.4 Mortality Causes

Cow moose proximate cause of death – We recorded 176 mortalities of the 553 radio-collared cow moose between 1 February 2012 and 30 April 2022. Probable proximate causes of death were 58% from predation, 17% from health-related causes, 11% from hunting, 6% from natural accidents, 1% from vehicle strikes, and 7% unknown (Figure 14). We classified mortalities as unknown when there was insufficient evidence available at the mortality site to determine cause of death, generally when there was an extended delay between the mortality and the site investigation due to delayed signal transmission or logistics. Health-related mortalities were most evident in Bonaparte and PGS, and Entiako was the only study area where we did not record hunting-related mortality. Health-related mortalities have decreased over time over all study areas, although more sophisticated analyses of cause-specific mortality over time is under way (Figure 15).

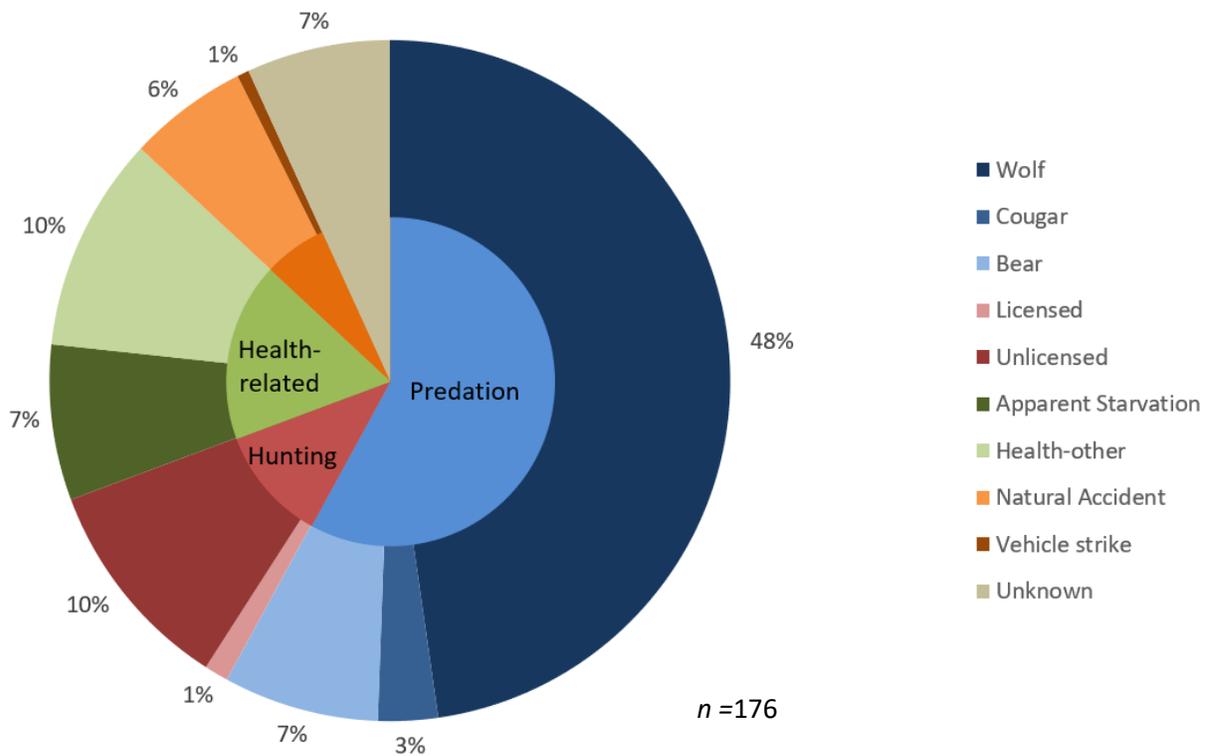


Figure 14. Probable proximate cause of death of radio-collared cow moose (*n* = 176) in central British Columbia, February 2012–30 April 2022.

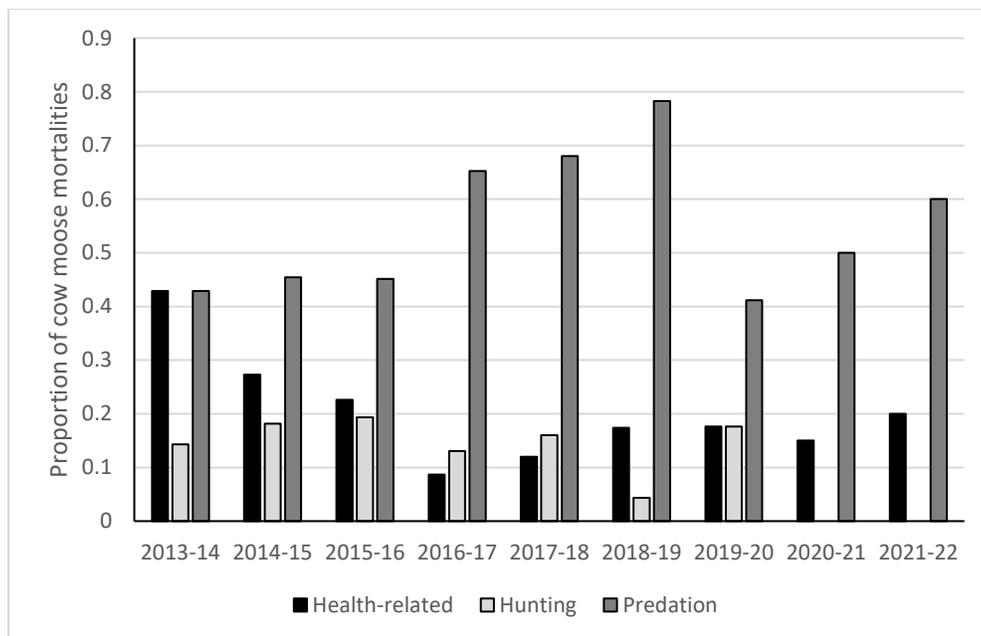


Figure 15. Proportion of cow moose mortalities attributed to predation, hunting, or health-related proximate causes (*n* = 149) by biological year (May 1 – Apr 30, 2014-2022).

Seasonality of cow moose mortalities – Most of the cow moose mortalities occurred between March and May (Figure 16). Predation mortalities also followed seasonal patterns: cougar predation events occurred between February and April ($n = 5$), peak wolf predation occurred between March and May although wolf predation was also high in December and January ($n = 84$), and peak bear predation occurred between May and July ($n = 13$, Figure 16). Apparent starvation also peaked in April (Figure 16).

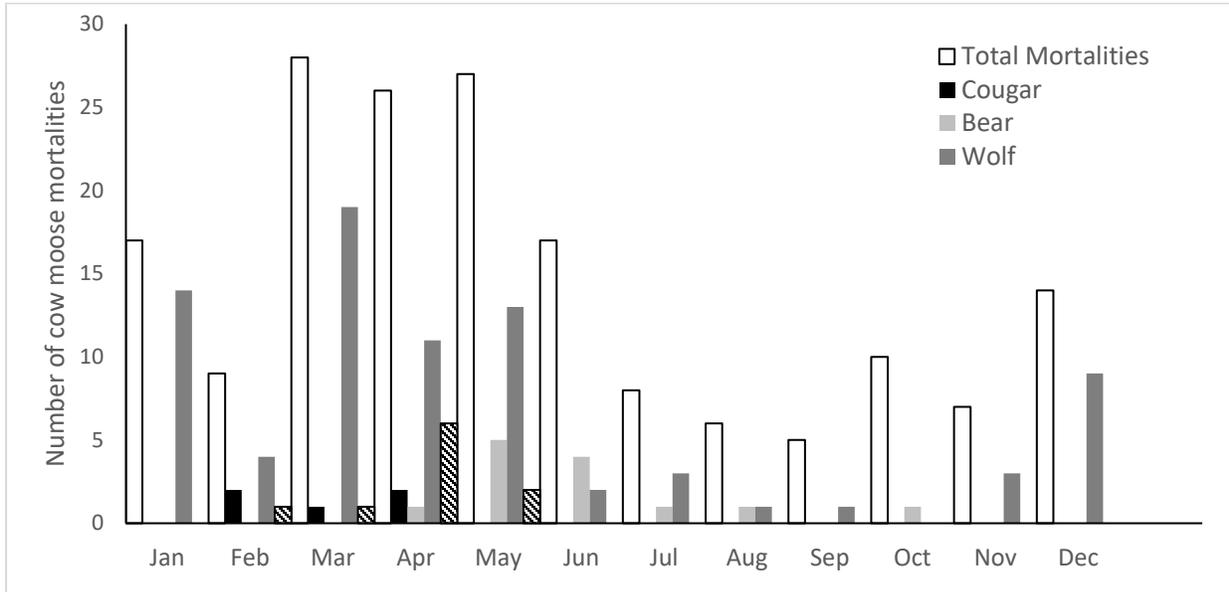


Figure 16. Month of death for radio-collared cow moose ($n = 174$) in central British Columbia, 01 February 2012–30 April 2022, showing seasonality in predation and apparent starvation.

Calf moose proximate cause of death – Of the 180 calf moose radio-collared and monitored between 2016 and 2021, there were 50 calf mortalities. Overall, of the calf mortalities observed to date, 80% were caused by predation, 18% were health-related, and 2% were accidents (Figure 17). In PGS, only one of 23 calf mortalities was apparent starvation; the rest were predation (including one failed predation attempt). In Bonaparte, 74% of 27 calf mortalities were from predation, 22% were health-related, and one calf was struck by a vehicle. Predation appears to be disproportionately affecting male calves in PGS, with 15 of 22 predation events on males, but the same pattern was not evident in Bonaparte and it is not clear whether this is a biologically significant pattern.

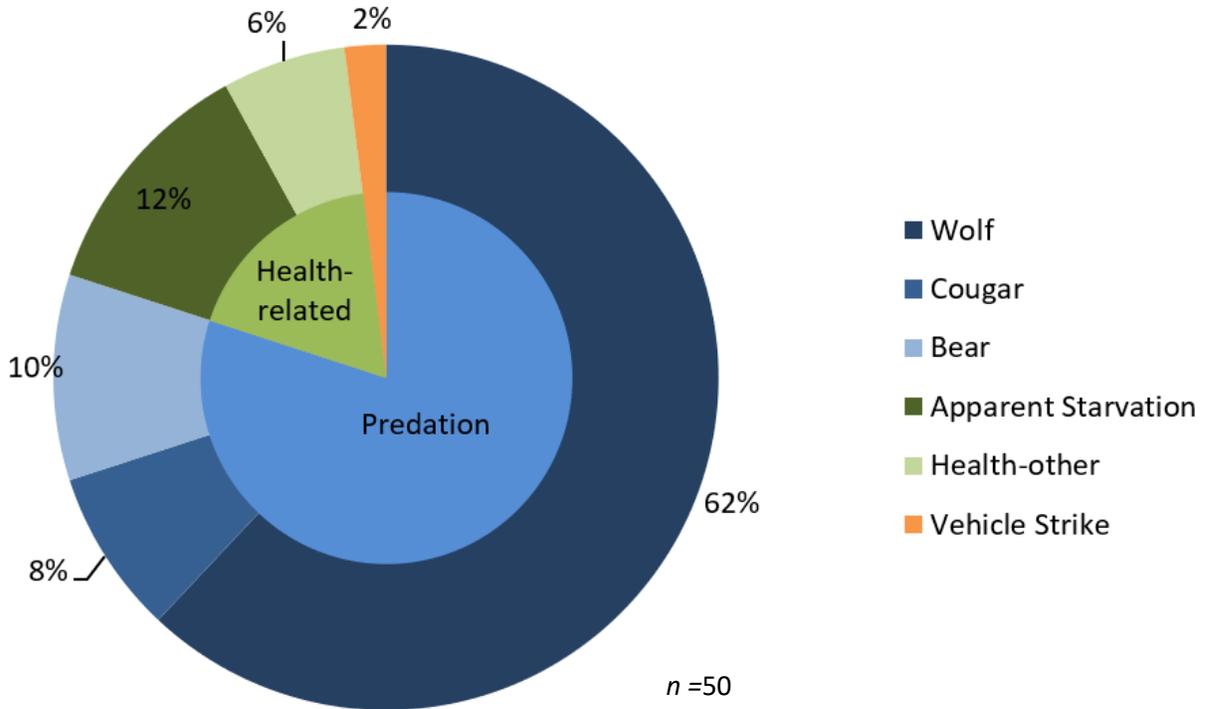


Figure 17. Probable proximate cause of death of radio-collared calf moose 8–12 months of age (*n* = 50) in central British Columbia, January 2017–22 May 2021.

Of the surviving calves that continued to be monitored as yearlings, we also recorded 24 yearling moose mortalities in PGS and Bonaparte. These were again dominated by predation (41%) but also included the first year at which bulls are vulnerable to licensed harvest, either through a limited entry hunt or spike-fork general open season. Hunting made up 22% of yearling moose mortality (Figure 18), but these data should be interpreted with caution due to small sample sizes.

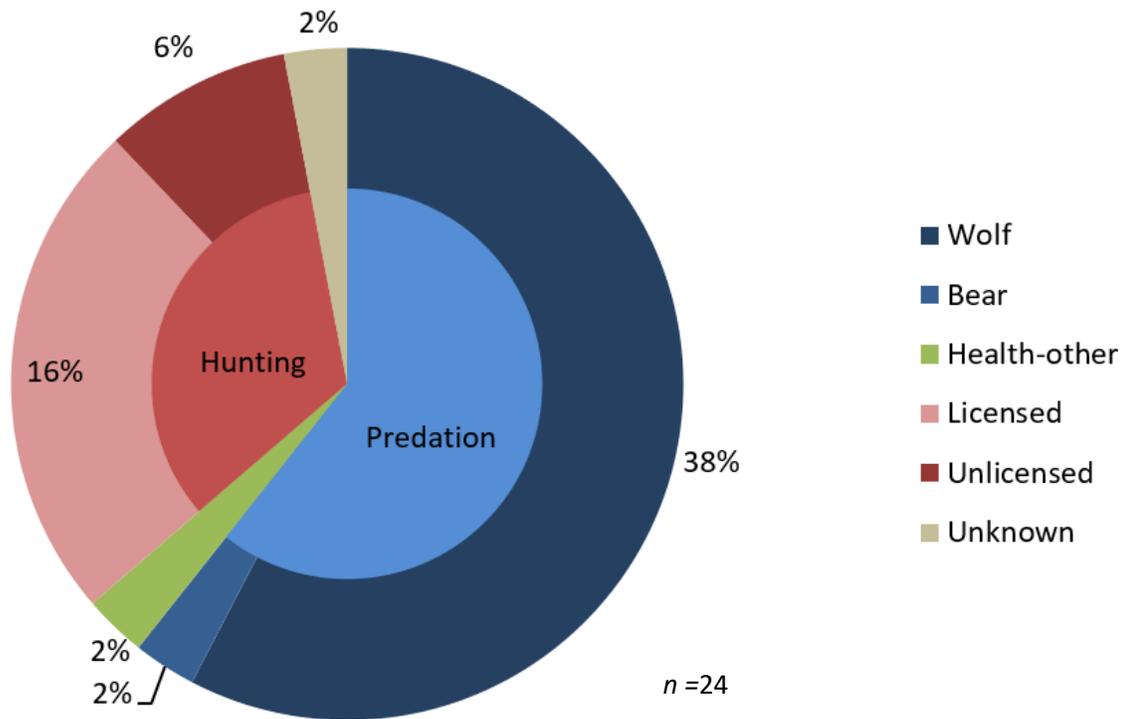


Figure 18. Probable proximate cause of death of radio-collared yearling moose 12–24 months of age ($n = 24$) in central British Columbia, January 2018–22 May 2022.

Marrow fat analysis – Assessments of bone marrow fat at time of death ($n = 118$) found that 49% of moose cows had high marrow fat content (>70% marrow fat), 21% were considered to be in poor condition (20–70% marrow fat), and 30% were in a state of acute malnutrition (<20% marrow fat). Notably, moose with marrow fat >70% are not necessarily in good condition, as marrow is the last fat store to be depleted, so provides only a partial assessment of body condition. Mortalities of cows with acute malnutrition generally occurred between April and June, while mortalities in the remainder of the year were generally moose with high marrow fat content, although some were considered to be in poor condition or in a state of acute malnutrition (Figure 16). Apparent starvation and health-related factors were the dominant cause of death for moose in a state of acute malnutrition, and all apparent starvation mortalities had marrow fat levels <10% (Table 3). Predation tended to be the primary cause of death for moose with high marrow fat content (Table 3). Hunter kills also generally represented moose with high marrow fat content, although that conclusion is based on a small sample size ($n = 6$; Table 3).

Table 3. Bone marrow fat content for cow moose mortality by proximate mortality type (n = 118) in central British Columbia, February 2012–30 April 2022. Acute malnutrition is associated with marrow fat <20%, poor body condition is associated with marrow fat between 21% and 70%, and high marrow fat content is associated with marrow fat >70%.

Probable Proximate Cause of Death	n	Average Marrow Fat %	Marrow Fat % Range
Predation - all	81	61.5	5 - 97
Predation - Wolf	64	66.4	5 - 97
Predation - Bear	12	40.7	7 - 84
Predation - Cougar	5	49.2	6 - 76
Apparent Starvation	10	6.5	5 - 9
Health - Other	12	29.8	7 - 85
Hunting	6	77.3	43 - 88
Natural Accident	3	8.5	5 - 10
Vehicle Strike	5	72.2	18 - 87
Unknown	1	78.5	n/a

The fat content of bone marrow in dead moose calves (n = 42) was assessed in Bonaparte and PGS, and all were classified as being either in poor body condition or in a state of acute malnutrition. Of the 20 marrow samples from Bonaparte, 55% had <20% marrow fat and 45% had 20-70% marrow fat. Of the 21 marrow samples from PGS, 62% had <20% marrow fat and 38% had 20-70% marrow fat.

Age at death - We collected 98 incisors (I1) from dead moose. The median age of cow moose at death was 10.4 years (range 1–18 years old). There were no significant differences in age of moose that died due to different probable proximate causes.

Health-related mortalities - Health-related factors were identified as the probable cause of death in several moose mortalities (6% of calf moose mortalities and 10% of cow moose mortalities) further described by Thacker et al. (2019). This preliminary evaluation of health data from capture and mortality samples suggested that the occurrence and potential impact of selected health determinants, including viral and bacterial pathogens, ectoparasites, and endoparasites, and non-infectious measures (e.g., body condition, pregnancy rates, long-term stress, and trace nutrient levels), varied among study areas. Although most health determinants evaluated to date are within ranges reported in moose populations elsewhere, there is evidence that some determinants have been directly responsible for morbidity or mortality in some age classes of moose in some study areas (e.g., gastrointestinal parasitism in calves in Bonaparte). No single factor, however, is identified as the proximal cause of apparent differences in the overall health status and/or performance of populations in these study areas at present. Likewise, the scope of this current moose health monitoring cannot adequately evaluate the potential sub-lethal or cumulative effects of various health determinants on the fitness of individual moose or the performance of moose populations in these study areas.

4.5 Calf Production, Survival, and True Recruitment

In Bonaparte and PGS, we observed variation across years in calf production, calf survival, and true recruitment at age 1. Due to mortality of calves in the late winter period, true recruitment at age 1 was consistently lower than recruitment indices measured during mid-winter aerial surveys, by an average of

30.0% (95% CI = 21.0%–39.0%), regardless of year or study area. However, 95% confidence intervals around both mid-winter calf ratios and calf ratios at age 1 generally overlapped (Table 11). Early calf survival from time of birth to late June calf surveys (Figure 34) indicate variability in neonate and summer survival among years (Table 11). Maximum pre-winter calf survival varied from 22 – 65% (Table 11). Calf production, survival, and recruitment parameters were generally similar between Bonaparte and PGS across the 5 years we monitored true recruitment rates. In 2019/20, both summer calf survival and true recruitment of 2019 calves was among the highest observed in both study areas since 2016/17 and calf survival and recruitment remained higher in the Bonaparte study area in 2020/21.

From 2014 to 2021, we conducted 26 late-winter (February and March) surveys across the five study areas to assess survival of calves associated with radio-collared cows. Results varied among study areas with calf/cow ratios ranging from 8–50 calves/100 cows (Table 4, Table 5, Table 6). The 2019 and 2020 late-winter calf survey survival results in Entiako, after implementation of wolf removals for caribou recovery, were the highest observed in that study area. Big Creek appears to have had the most consistent calf ratios through the duration of the study (Table 4).

The calf survival metrics (mid-winter recruitment or true recruitment at age 1) used to calculate lambda (population rate of change) unsurprisingly resulted in different estimates. A lambda estimate spanning one (e.g., 0.95–1.05) cannot be interpreted as either in decline, stable, or growing. In only one case did a change of recruitment metric result in change in the interpretation of lambda given imprecision in survival and recruitment estimates. In Bonaparte in 2019/20 and in both study areas in 2020/21, lambda as calculated using mid-winter recruitment was positive, but spanned zero when precision increased with the use of true recruitment (Table 6). Using true recruitment at age 1 reduced mean estimates of lambda by 0.07 (\pm 0.01 SE) across study areas and years (range 0.03-0.14, n = 9; Table 6). In all but one case, lambda estimates have lacked the precision required to definitively conclude whether populations have been growing or declining annually. The exception is Bonaparte in 2017/18, which saw population growth at a rate of 3–16% (Table 6).

Table 4. Calf production, summer calf survival, and true calf recruitment in the Bonaparte and Prince George South study areas, May 2016–June 2021. Estimates of error are 95% confidence intervals. Sample size (*n*) is the number of cows from which the estimate is derived.

Year	Study Area	Minimum No. Calves/100 Cows at Birth ^a	No. Calves/100 Cows Mid-June ^b	No. Calves/100 Cows Mid-winter ^c	Maximum Calf Pre-winter Survival (%) ^d	No. Calves/100 Cows Mar.31 ^b	True Recruitment Rate (No. Calves/100 Cows at age 1) ^e
2016/17	Bonaparte	59 (46 – 72) (<i>n</i> = 59)	n/a	13 (7 – 19) (<i>n</i> = 184)	22% (15 – 26)	16 (<i>n</i> = 32)	6 (3 - 9)
2017/18	Bonaparte	76 (64 – 88) (<i>n</i> = 46)	64 (<i>n</i> = 47)	32 (23 – 41) (<i>n</i> = 194)	42% (36 – 47)	38 (<i>n</i> = 40)	27 (20 – 35)
2017/18	PGS	79 (62 – 96) (<i>n</i> = 24)	n/a	34 (29 – 39) (<i>n</i> = 280)	43% (39 – 46)	26 (<i>n</i> = 35)	24 (20 – 27)
2018/19	Bonaparte	80 (68 – 92) (<i>n</i> = 41)	51 (37 – 65) (<i>n</i> = 47)	28 (17 – 39) (<i>n</i> = 116)	35% (25 – 42)	n/a	22 (14 – 31)
2018/19	PGS	70 (48 – 85) (<i>n</i> = 20)	65 (44 – 86) (<i>n</i> = 20)	31 (21 – 41) (<i>n</i> = 128)	65% (62 - 70)	n/a	23 (16 – 30)
2019/20	Bonaparte	78 (64 – 88) (<i>n</i> = 46)	55 (41 – 69) (<i>n</i> = 45)	49 (38 – 59) (<i>n</i> = 84)	63% (51 - 75)	n/a	34 (25 – 43)
2019/20	PGS	76 (60 – 88) (<i>n</i> = 34)	45 (29 – 62) (<i>n</i> = 31)	41 (29 – 62) (<i>n</i> = 61)	54% (48 – 70)	n/a	27 (20 – 34)
2020/21	Bonaparte	86 (71 – 94) (<i>n</i> = 35)	62 (45 – 76) (<i>n</i> = 34)	50 (41 – 60) (<i>n</i> = 105)	58% (48 – 68)	n/a	43 (34 – 49)
2020/21	PGS	69 (53 - 85) (<i>n</i> = 32)	50 (33 - 67) (<i>n</i> = 36)	35 (31 - 40) (<i>n</i> = 505)	51% (39 - 62)	n/a	28 (23 - 33)

^a Estimated from movement analyses for collared cows and assumes all cows had only one calf (i.e., no twinning).

^b Estimated from aerial searches of collared cows and their calves.

^c Estimated from aerial composition surveys in respective study areas.

^d Estimated by comparing survey-based calf ratio mid-winter to estimated calf ratio at birth; should be considered the maximum calf survival estimate as twinning rate at birth not known.

^e True recruitment = mid-winter calf ratio x calf survival from mid-winter to age 1 (estimated from collared calves).

Table 5. Calf surveys to determine presence of calves with radio-collared cow moose in central British Columbia, March 2014–March 2021. The number of collared cows observed is presented parenthetically.

Study Area	No. Calves/100 Cows in Late Winter							
	2014	2015	2016	2017	2018	2019	2020	2021
Bonaparte	-	25 (40)	26 (68)	16 (32)	38 (40)	-	-	-
Big Creek	28 (41)	37 (43)*	33 (43)	27 (41)	32 (37)	34 (29)	-	47 (30)
Entiako	-	-	14 (44)	9 (35)	15 (26)	27 (30)	37 (27)	50 (32)
PGS	-	39 (18)	27 (44)	40 (49)	26 (35)	-	-	
JPRF	-	8 (13)*	17 (36)	40 (42)	37 (38)	-	-	30 (33)

*Indicates that the survey was completed in February; all others occurred in March of associated year.

Table 6. Comparison of moose population rate of change (lambda) estimated using recruitment indices from mid-winter surveys and survival rates from collared cows and calves to recruitment at age 1. Lambda was calculated as $S/(1-R)$ where S is cow survival and R is female calf/cow ratio (Hatter and Bergerud 1991). Lambda values <1 indicate declining populations and values >1 indicate increasing populations.

Year	Study Area	Lambda-Survey-based Mid-winter (95% CI)	Lambda-True Recruitment Age 1 (95% CI)
2016/17	Bonaparte	0.98 (0.82 – 1.07)	0.93 (0.78 – 1.01)
2017/18	Bonaparte	1.14 (1.06 – 1.19) *	1.11 (1.03 – 1.16) *
2017/18	PGS	0.92 (0.79 – 1.04)	0.88 (0.75-1.01)
2018/19	Bonaparte	1.08 (0.96 - 1.17)	1.05 (0.94 - 1.13)
2018/19	PGS	0.95 (0.82 - 1.06)	0.92 (0.79 - 1.04)
2019/20	Bonaparte	1.16 (1.02 – 1.27) *	1.08 (0.97 – 1.19)
2019/20	PGS	1.07 (0.95 - 1.18)	0.98 (0.87 - 1.08)
2020/21	Bonaparte	1.21 (1.12 – 1.31)*	1.08 (0.85 – 1.19)
2020/21	PGS	1.14 (1.08 - 1.22)*	1.01 (0.90 - 1.11)

* Indicates estimates that do not span 1 and thus can be interpreted as reflective of a growing (>1) or declining (<1) population.

4.6 Density Surveys

At the initiation of the study, moose densities ranged from 0.17 to 0.77 moose/km² among study areas, and every study area has experienced population declines (Figure 19). Updated abundance/density estimates are generally planned every 5 years; Big Creek and Bonaparte are planned for winter 2022/23, Entiako is planned for 2023/24. JPRF and PGS are planned to be surveyed in 2025/26; the most recent survey was in 2020/21 and suggests an increasing population trend for both study areas (Scheideman and Anderson 2021).

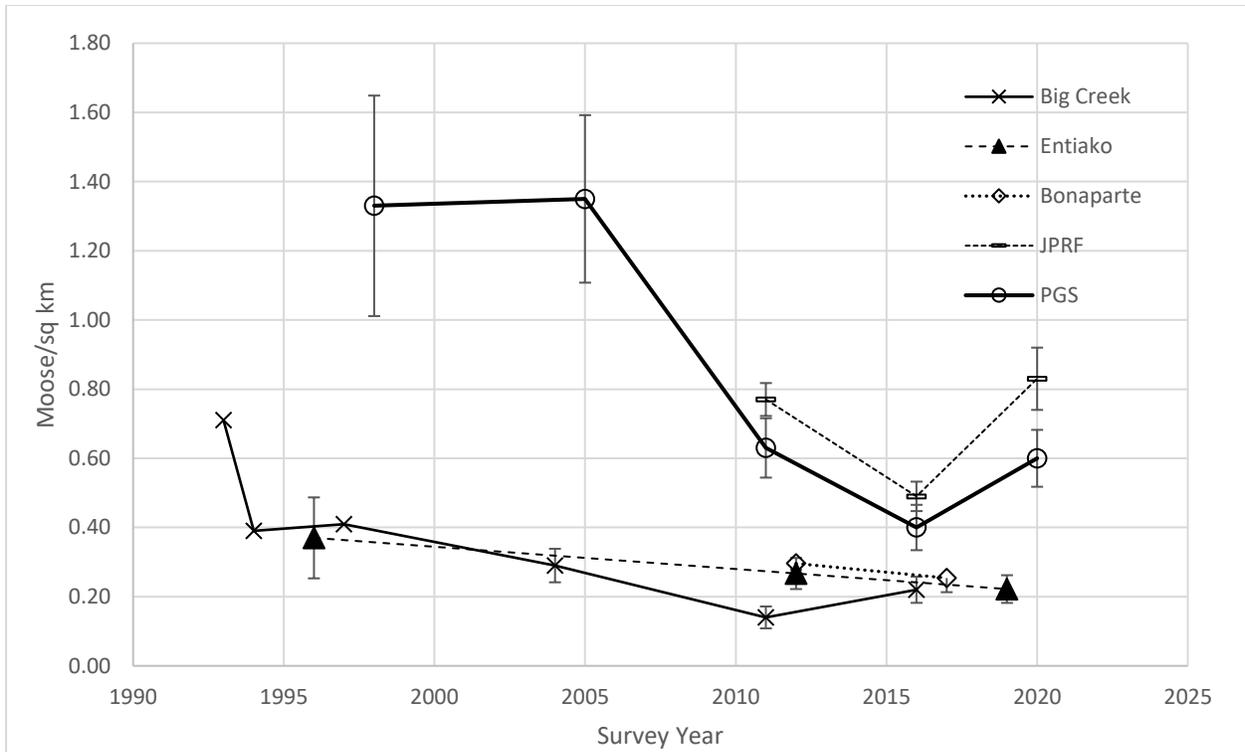


Figure 19. Sightability-corrected moose density estimates for survey areas coinciding with the Provincial Moose Research Project study areas (see Appendix 1). Error bars are 90% confidence intervals. Survey conditions in Big Creek in the 2011/12 survey were not ideal; temperatures were $>0^{\circ}\text{C}$ with sparse snow cover in more than half the survey blocks.

5. DISCUSSION

This research was originally designed to test the landscape change hypothesis (Kuzyk and Heard 2014) by evaluating the causes, rates and locations of adult female moose mortality. We found that adult female survival was generally high enough to maintain stable to increasing moose populations, and we transitioned to investigating drivers of poor calf recruitment. In doing so, we have accumulated data on the health, vital rates, and key mortality factors and factors contributing to mortality of moose populations in our study areas. While survival rates were the primary objective, we have also established an enhanced understanding of the habitat use, health status, predation patterns, movements, and population dynamics of moose populations that are fundamental to understanding and interpreting survival data and population trend. Our challenge going forward is to complete ongoing analyses and begin integrating the various data streams together to gain an understanding of the primary drivers of moose population dynamics to generate recommendations to meet objectives for moose populations in the province. The importance of understanding moose population drivers is as important now, if not moreso, than when the project was initiated. While some answers will be provided in the next 1-2 years by work currently underway at UNBC and UVic, other questions remain unaddressed and new avenues of investigations are expected.

5.1 Biological Assessments and Sampling

Cow body condition - At the time of capture, most cow moose were mid-aged adults and assessed as being in good body condition, although condition varied considerably among years and study areas. A higher proportion of moose were captured in poor condition in 2016/17 and in PGS overall. For those cows for which we measured rump fat, the subjective body condition scores generally correlated with the rump fat measurements, although the subjective scores may not be precise enough at a fine scale or variable enough across the population to correlate with important vital rates like pregnancy. In 2020/21 and 2021/22, we estimated average percent IFBF of about 7-11% for PGS and Bonaparte. We consider these early winter body condition estimates to be reflective of summer habitat conditions and characterize the condition of adult females entering winter in near peak condition. Some cows were captured in January due to unsuitable weather conditions in early December, which is later than desired to represent peak condition; however, the unsuitable weather (very little snow) through December and early January was such that we assumed cows did not appreciably lose fat during that time. Cows that had calves present at time of capture were generally thinner than cows without calves, presumably due to the energy expenditure associated with lactation (Cook et al. 2013). Some variation in body condition at time of capture for those cows without calves is likely explained by when their calves died through the summer and fall, and the consequent influence on lactation period.

Much of the moose body condition data that exist in the literature were collected in very different systems, in different years, at different times during the year (e.g., late winter), and usually with different subspecies of moose. This variation in body condition data and methodology challenges our ability to directly compare our data to a known baseline. Results from other studies do indicate that it is biologically possible for moose to be in better condition than we observed in any study area for any year monitored. Testa and Adams (1998) observed rump fat on cow moose in 1994–1995 prior to winter in Alaska and found that reproductive cows had an average rump fat of 29 mm and non-reproductive cows had an average rump fat of 42 mm—substantially higher than observed in this study. Our observed early-winter body fat levels were similar to those observed in a declining moose population in Minnesota, but those measurements were taken in late February and early March, when body fat levels are expected to be lower (IFBF 9.8%; DelGiudice et al. 2011). This suggests that moose in PGS and Bonaparte are in poorer body condition than moose monitored in Minnesota, but PGS moose populations have been increasing recently and calf survival has improved in recent years in the Bonaparte, suggesting an increasing population there as well.

In 2021/22, we estimated body fat levels of moose in two other areas south of Kamloops (Pennask Plateau and HVC) to help interpret body fat estimates generated through this research in the PGS and Bonaparte study areas. Pennask and HVC moose had very similar body fat, despite key differences in moose population status. The Pennask Plateau moose population did not experience the same declines observed elsewhere in interior BC despite living in some of the warmest climates in the province and in a landscape with similar disturbance levels (Procter and Iredale 2014). Pennask moose occur at 2-3 times the density of moose in Bonaparte and are consistently characterized by high calf ratios, often up to 50 calves/100 cows in mid-winter (Procter and Iredale 2014). HVC moose have also had generally higher calf ratios than those observed in Bonaparte and naturally occur at lower densities given much of the area is lower elevation sub-optimal moose habitat (Procter and Iredale 2017). Despite the observed differences in calf survival and population trajectory, body fat measurements in PGS, Bonaparte, HVC, and Pennask were all similar. More consistent body condition monitoring at HVC and Pennask, or in other relevant moose populations, might provide additional insight, but the body condition data for 2021/22 and from previous years does not suggest it is a primary driver of recruitment or population performance in any of the study areas. Differences in predation may also factor into the difference in population trajectory. Analyses are ongoing evaluating the factors that contribute to moose body condition and how maternal condition might be contributing to calf survival and moose population change in British Columbia.

Pregnancy rates - Average pregnancy rates observed in this study over 10 years ranged from 47-100%, with the lowest average rates observed in Bonaparte and PGS study areas, and with Big Creek, Entiako, and JPRF frequently over 90%. In some years where estimated pregnancy rates were low, parturition rates measured by cow movement rates were higher, which suggests the estimates of pregnancy rate may not have been representative of the population, likely due to error from small sample sizes in some years and in some study areas. For example, in 2021/22, the estimated pregnancy rate from captured individuals was 64% in the Bonaparte study area, but the parturition rate estimated from all collared cows was 86%. Moose pregnancy rates in North America are variable, generally 60-100% depending on nutritional status, and average 84% (Boer 1992, Gasaway et al. 1992, Schwartz 1998, Ruprecht et al. 2016, Jensen et al. 2018). Data on moose pregnancy rates across North America generally suggests a close relationship between pregnancy rates and moose population nutritional status.

Using data provided by Ruprecht et al. (2016), we calculated that approximately 6% IFFB was required to achieve a high and normal probability of pregnancy and the probability of pregnancy did not increase with increasing body fat levels beyond this threshold. Average body fat in both Bonaparte and PGS was above this threshold in all years. In Alaska, Testa and Adams (1998) found that approximately 10% body fat is required to achieve a probability of pregnancy of 85%, which is approximately the average observed in studies across North America (Boer 1992). Average body fat levels of moose in this study were generally below this threshold. However, both thresholds were developed with different subspecies of moose (*A. a. shirasi* in Ruprecht et al. 2016 and *A. a. gigas* in Testa and Adams 1998) and maximum rump fat/body fat relationships vary with body size (Cook et al. 2010).

However, other factors such as age can influence pregnancy rates for moose (Heard et al. 1997, Murray et al. 2006). Age data from our study also suggest that moose populations are trending toward older age distributions, which could reduce population productivity. Health-related factors, such as suboptimal trace mineral levels, can also influence moose pregnancy, parturition and calf survival rates, and ultimately recruitment as well (Thacker et al. 2019, Newby and DeCesare 2020). Considering the observed pregnancy

rates and body condition, additional analyses, particularly around trace nutrient levels, are required to assess the importance of these factors for moose in this study.

The abundance of bull moose is often suggested as a potential cause of low pregnancy rates and calf recruitment. In BC, most moose populations are managed to maintain a minimum of 30 bulls/100 cows post-hunt. In both PGS and Bonaparte, where we detected low pregnancy rates in some years, we also measured bull/cow ratios below the objective in some years (e.g., PGS 21-42 bulls/100 cows since 2000). A population-level effect of low bull ratios is most likely to manifest in higher incidence of second estrus pregnancy, delayed primiparity, and lower pregnancy rates in yearlings (Clutton-Brock et al. 1982, Aitken and Child 1993, Noyes et al. 1996, Komers et al. 1999, Solberg et al. 2002). Altered bull ratios or age structure could contribute to population effects because second-estrus calves are born 22-28 days later and are consequently smaller and less likely to survive their first winter (Schwartz and Hundertmark 1993, Schwartz et al. 1994, Hundertmark et al. 2000, Saether et al. 2003). However, in this study, we have been estimating the parturition date for collared cow moose based on their movement rates on an annual basis in the Bonaparte and PGS study areas, and second-estrus pregnancies appear to occur at a low rate. For example, of 91 and 219 pregnancy events observed in the PGS and Bonaparte study areas in recent years, 3% and 5% were second-estrus pregnancy events, respectively, which appears normal. Furthermore, second-estrus pregnancies would still be detected when serum collected at the time of capture is tested for pregnancy, so pregnancy rates could appear normal even if there was a higher proportion of second estrus pregnancies. Our study is not directly monitoring bull moose, but our data suggest it is unlikely that the low pregnancy rates we detected are due to low bull/cow ratios.

Calf body weight – We assessed the size of moose calves as an index to the nutritional status of moose populations. Most of the 175 8-month-old captured calves assessed for body condition were in fair (38%) or good (58%) condition. The average estimated weight of all calves 8 months of age in Bonaparte and PGS for all years was 172 ± 3 kg (95% CI). This is at the lower end of the range reported in Alaska over several years for 9- to 10-month-old calves (167.5–191.4 kg; Keech et al. 2011) but larger than average weights of 9- to 10-month-old calves reported elsewhere in Alaska (148.9 kg, Keech et al. 1999; 157–170 kg, Boertje et al. 2007) and smaller than the average weight of 7-month-old calves reported in North Dakota (196 kg; Jensen et al. 2013). Keech et al (1999) attribute the low average weight of 9- to 10-month-old calves to poor nutritional status of their study moose population due to high moose densities. Similarly, Jensen et al. (2013) attribute the higher average weight of calves in their North Dakota population to high nutritional status of the moose population arising from use of high-quality forage in agricultural areas. Boertje et al. (2007) also indicated their average weights varied with nutritional status, and suggested that average calf weights of >190 kg are predictive of high nutritional status. Calves in this study appear to be a normal size; they are smaller on average than those from populations characterized by high, albeit potentially supplemented, nutritional status, but larger than those known to be from populations characterized by poor nutritional status.

Although the size of older moose calves observed in this study appears normal, caution is required interpreting these data. Calf weights in the literature are reported from 7 to 10 months of age, and the time of the year calves were weighed may introduce variation that is reflective of the time of year as opposed to true differences in calf weights. Differences in weight could also be partially reflective of phenotypic differences among populations, especially when comparing moose of different subspecies that are known to differ substantially in size and weight (Franzmann and Schwartz 2007). We suspect that comparing calf weights between geographically distinct populations may be of limited utility, although it

provides context for the range of sizes expected under various conditions. A final concern with interpreting these data is that calf size may influence survival earlier in the year. The calves monitored at 8 months of age were those that survived their first 8 months and the smallest calves may have already died. If this were true, we would expect cows in poorer condition to lose their calves earlier than those in better condition given positive relationships between maternal condition and the size of calves at birth. To date, we have not observed this pattern and there does not appear to be a relationship between maternal condition and early calf survival to 30 days of age. The probability of overwinter survival may be a function of calf size entering winter (Cook et al. 2004), however, an analysis of the relationship between calf size entering winter and survival to June 30 (following their first birthday to ensure all winter-related mortality was captured) indicated this was not significant, although those calves surviving to June 30 in the Bonaparte study area tended to be larger. Overall, although the size of moose calves observed in this study do not indicate anything out of the ordinary and initial work has not indicated a relationship between neonate survival and maternal condition, the interaction of maternal body condition, calf size and condition, and habitat use patterns are expected to provide a better assessment of the linkages between factors driving maternal condition and calf survival, and this work is ongoing.

5.2 Survival Rates

The landscape change hypothesis proposed that moose declines coincided with an MPB outbreak where habitat changes and increased salvage logging and roadbuilding resulted in greater vulnerability to moose, primarily from hunters and predators (Kuzyk and Heard 2014). We assessed cow survival rates initially to evaluate the landscape change hypothesis because cow survival was predicted to have a greater proportional effect on population change than calf survival and was therefore expected to best explain the observed rapid population declines (Kuzyk and Heard 2014). Given that several studies report stable moose populations with cow survival rates greater than 85% (Bangs et al. 1989, Ballard et al. 1991, Bertram and Vivion 2002), we established an 85% cow survival rate threshold to evaluate and interpret survival rates observed in this study. Annual pooled cow survival rates for all study areas were greater than 85%, although confidence intervals overlap 85% in some years, and were higher than those estimated for cow moose in studies from the Northwest Territories (85%; Stenhouse et al. 1995) and northern Alberta (75–77%; Hauge and Keith 1981).

On an individual study area basis, Big Creek and JPRF study areas were characterized by cow survival above 85% although 95% confidence intervals sometimes overlap the threshold. This suggests that adult cow moose survival cannot be ruled out as a contributing factor but is not likely the primary driver of moose population declines in those study areas. Where moose populations have declined through the first ~10 years of the research (Bonaparte and JPRF), low calf recruitment and survival is likely the primary influence on moose population dynamics over time. In comparison, we observed survival rates above 85% in the Entiako study area starting in 2019/20 but below the threshold in the previous 4 years, indicating that low cow survival was likely contributing to population decline in this study area, at least in some years. Although we do not have estimates of true calf recruitment at age 1 in this study area, low female survival rates in combination with low calf recruitment could cause significant moose population changes over time, especially when those years of lower cow survival interact with years of low calf survival, which likely occurred in at least 2015/16 and 2016/17, and which may explain observed declines through this period. Adult female survival and calf recruitment to late winter in Entiako has increased since 2019, when wolf reduction in support of caribou recovery efforts for the Tweedsmuir herd was implemented. Cow survival was most variable in PGS, and survival rates were below 85% in 3 years and very near the threshold in 2

additional years, which again indicates that low cow survival could be contributing to moose population decline over time. March calf recruitment rates were higher than Entiako (prior to wolf reduction), and calf recruitment estimates at age 1 did not appear alarmingly low. This suggests the importance of lower cow survival and interactions between cow and calf survival rates in any given year may even be of more importance in PGS than Entiako for explaining moose population dynamics.

When all study areas were combined, cow survival rates over all years were not indicative of moose population declines and were inconsistent with the cow survival component of the landscape change hypothesis, suggesting that calf survival and recruitment is the primary factor influencing moose population change in most areas. However, it is becoming increasingly apparent that temporal interactions between these key vital rates are important to understand to explain moose population change in some areas.

5.3 Cause-specific Mortality

Our second objective in testing the landscape change hypothesis was to determine the mechanisms influencing cow survival (Kuzyk and Heard 2014). We accomplished this by assessing relationships between the causes and locations of moose mortality and features of landscape change over various time periods prior to death. Since initiation of this research, 58% of cow moose mortalities were determined to be due to predation (proximate cause of death), with the majority of those killed by wolves. Mumma and Gillingham (2019) found that moose in this study were more likely to be killed by wolves in areas of lower road density, and no relationship between salvage-logged cutblocks and wolf predation was found. Similar analyses are currently ongoing to assess moose calf mortality relative to landscape disturbance features associated with intensive forest management. Predation by wolves occurred in all study areas, and predation by bears occurred in three study areas (Big Creek, PGS and Entiako). Predation by cougars occurred in Bonaparte, PGS, and Big Creek. Wolves were the only predator documented to have killed radio-collared moose in JPRF, despite moderately high densities of black bears and grizzly bears. All cougar kills were recorded between February and April, and most bear kills were between April and June. Although wolf kills were recorded in every month except October, most were during winter. Snow conditions favouring wolf movements and impeding moose movement likely contribute to increased vulnerability to wolf predation later in the winter (Mech 1977, Fritts and Mech 1981, Huggard 1993, Jedzrejewski et al. 2002, Husseman et al. 2003).

Hunting was initially assumed to be one of the main factors, along with predation, influencing moose population change because increased road access and reduced visual cover in large contiguous cutblocks would make moose more vulnerable to hunters (Kuzyk and Heard 2014). Moose in this study were more vulnerable to hunting in proximity to cutblocks and in areas of higher road density (Mumma and Gillingham 2019); however, only 11% of proximate cow moose mortalities were due to hunting, suggesting that other factors play a greater role in explaining moose population dynamics. There is potential for bias associated with hunters seeing radio-collared moose and choosing against harvesting those moose despite outreach requesting the opposite. We believe this bias is of low importance because the collars (belting and housing) are black with an internal antenna making them very difficult to see on moose, even at close range.

The second most frequent proximate cause of cow moose mortality was health-related (17%). MacBeth (2017) and Thacker et al. (2019) provided more details regarding health-related mortalities up to October 2019. Additional testing is under way with the gradual lifting of COVID-19 restrictions and increased lab

capacity after backlogs. Health-related causes of death included septicemia secondary to wounds, an unusual copper toxicity, dystocia/abortion, high tick burdens, complications of failed predation attempts, cancer, an extreme gastrointestinal parasite burden in a calf, and emaciated body condition (apparent starvation). Since initiation of this research, approximately half of the health-related mortalities were attributed to apparent starvation. Moose in this study were more likely to die from apparent starvation if they used areas with higher road densities and higher proportions of cutblocks (Mumma and Gillingham 2019), suggesting that intensive forest development may be influencing moose health. Fewer apparent starvation mortalities have been observed in recent years. More research is required in this regard to determine the specific mechanisms explaining how landscape change may be affecting moose health.

When compared to many other moose mortality studies in northern Canada and Alaska our results similarly identified predation as the primary mortality factor, although bears were the primary predator in many studies (Larsen et al. 1989, Ballard et al. 1991, Gasaway et al. 1992, Bertram and Vivion 2002). Other studies also identified wolf predation as the primary cause of mortality (Gasaway et al. 1983). The relevance to our study varies, as they present results from different geographic areas, habitats, moose subspecies, and time periods. In Minnesota, Carstensen et al. (2017) reported a significant proportion of moose mortalities were health-related (61%), three times that observed in this study. Although wolves were the principal predators, less wolf predation was reported (32%) and at least 40% of the moose killed by wolves had underlying health issues that may have predisposed them to predation. Timing of most mortality was like our study (April and May peak mortality), for both health-related and predation mortality.

Our study is continually increasing the sample size of bone marrow fat samples from radio-collared cows at time of death. Nearly half these cow moose were characterized by high marrow fat content; however, almost a third were in a state of acute malnutrition. Mortalities from a state of acute malnutrition occurred mainly between April and June and likely reflect the normal annual cycle of body condition of moose, since their poorest body condition occurs naturally during late winter/early spring (Franzmann and Arneson 1976, Fong 1981, Ballard 1995). DelGiudice et al. (2011) suggested that variation in the condition of moose in declining populations in Minnesota entering winter might also be affected by summer conditions in some years. In these cases, moose are not able to accumulate sufficient reserves to survive to green-up the following spring. If true, we would expect annual variation in the frequency of death by apparent starvation, dependent on previous summer conditions. Variability in apparent starvation deaths is consistent with our observations in this study, with apparent starvation in PGS and Bonaparte being more prevalent in some years than others. Our data also indicate that health-related mortalities occurred at a higher rate earlier in this research than in recent years, which suggests that moose populations may have gone through a time when health had a bigger influence than observed recently. Interestingly, in the Bonaparte study area, this time period may have coincided with the time period when much of the salvage logging was completed, but more specific analyses are required in this regard. Investigating moose health factors (pathogens, body condition, stress, parasites) and their interactions and cumulative effects within the context of landscape change is currently ongoing.

There are limitations to assessing body condition based only on bone marrow fat, especially for animals that are not in poor condition (Mech and DelGiudice 1985). Marrow fat is one of the last fat storage sites to be mobilized such that individuals could lose other fat stores and still have high levels of marrow fat. It is also unclear how quickly marrow fat can decline from 100% to acute malnutrition in moose. Marrow fat levels also vary with the specific bones selected for analysis (Spears et al. 2003). We tried to maintain

consistency with the bones collected but when preferred bones were not available, alternates were used. Marrow fat levels may be overestimated due to weather conditions and length of exposure prior to collection and freezing, or from samples being frozen too long, because the porous bones gradually dry out. We tried to minimize these biases by collecting samples as soon as possible and by proper storage in airtight or vacuum-sealed bags. Ballard (1995) suggested that general body condition of the larger moose population (not just those that are dead) could be inferred by comparing the condition of those dead by mortality causes independent of body condition, like vehicle collisions. Unfortunately, our sample size of these mortalities is insufficient to make inferences at this time. Our results suggest that most calf moose were in poor condition at time of death based on marrow fat levels. However, calf moose are naturally characterized by low marrow fat levels because energy intake is invested in body growth rather than in accumulating fat storage. Therefore, marrow fat may not reliably indicate nutritional status or (by extension) habitat condition for calves. Given this uncertainty, our results should be interpreted with caution (Fong 1981, Spears et al. 2003).

Age at death of cow moose varied between 1 and 18 years of age, and there appeared to be no patterns in proximate cause of death by age. The ages at death observed in this study suggest that cow moose typically died at an older age (median of 11.5 years), regardless of cause. Survival senescence, decreased survival with age, is a widespread occurrence in large herbivores (Gaillard et al. 2000). Despite the survival senescence, the bias towards older mortalities might suggest that: 1) the random sample of cow moose captured and monitored reflected an older standing population age structure; 2) older moose are more vulnerable to all causes of mortality (Peterson 1977, Montgomery et al. 2014), although some mortality factors operate independent of age (Ericsson and Wallin 2001); or 3) we captured a biased sample of older moose from the population. The latter is unlikely given the current large sample size and limited number of recaptures to replace collars. Analysis of moose ages from hunter-harvested moose from 1982 to 2003 and ages from mortalities from this study found the average age of random cows harvested from 1982–2003 ($n = 2,016$; age = 3.84, SD = 3.03) to be much younger than the small sample of cows dying from all causes (i.e., hunter harvest, health, predation, natural accident) during the decline ($n = 47$; age = 10.93, SD = 3.72) (Kuzyk et al. 2020). This suggests that moose populations prior to this research were likely characterized by a younger age distribution. The possible shift from a younger to older age structure is likely a result of reduced recruitment sustained over several years. The average age of wolf-killed non-collared adult cow moose from a concurrent predation study in PGS and JPRF (10 ± 0.9 yrs 95% CI, range 2–17 yrs, $n = 71$; Anderson et al. 2023) was the same as for wolf-killed radio-collared cow moose in PGS and JPRF in this study (10 ± 1.6 yrs 95% CI, range 1–16 yrs, $n = 20$).

5.3 Calf Production, Survival, and True Recruitment

Late-winter survival rates of calves from 8 to 12 months (age 1) varied from 45 to 85% across years and study areas (PGS and Bonaparte), with 65% survival in both study areas in 2019/20 and 80% and 85% survival in 2020/21 in PGS and Bonaparte respectively. On average, calf survival from 8 to 12 months of age was 74%, suggesting an average 30% lower recruitment at age 1 compared to mid-winter recruitment surveys. This is important because true recruitment is capable of changing population trends on an annual basis, especially in years where lower calf recruitment may interact with years of lower cow survival or years when mid-winter calf ratios are near the threshold required to maintain stable moose populations. Data collected to date in this study suggests that mid-winter recruitment ratios generated from aerial surveys better reflect early calf survival than recruitment to age 1, and that mid-winter recruitment ratios need to be corrected to account for late winter and early spring mortality to better understand the

influence of recruitment on moose populations. Calf recruitment from 8 months to 1 year is also highly variable among years. Relatively constant cow survival paired with variable calf recruitment in this study is consistent with observations of many other ungulate populations (Gaillard et al. 1998, Gaillard et al. 2000).

Since 2016/17, 50 of the 180 collared 8-month-old calves died before reaching age 1. Probable proximate causes of mortality of calves were primarily predation (31 wolf kills, 5 bear kills, 4 cougar kills), health-related (6 apparent starvation and 3 other health-related) and one vehicle collision. More than half of the total mortalities were from wolves. We recorded a significantly higher proportion of health-related mortalities (particularly apparent starvation) in 2017 (45%) in the Bonaparte study area than has been observed since (25% in 2018 and 0% from 2019-2021). The lack of recent apparent starvation mortalities is of interest as it may relate to our work on maternal body condition as a potential driver of calf survival. Moose may have been in poorer condition in the earlier years of this research than they have been in subsequent years, and ongoing work with this dataset will provide insight on the influence of maternal condition on calf survival and recruitment. Very few data exist in other studies on mortality causes of older moose calves (8–12 months of age), but the proportion of predation mortalities observed in this study (80%) is similar to that observed in Minnesota for neonatal calves (84%; Severud et al. 2019). Wolves were responsible for 78% of predation-caused mortality in our study, which was also similar to rates recorded in Minnesota (77%; Severud et al. 2019). In Bonaparte, male and female calves were predated in approximately equal numbers (9 females, 10 males), but in PGS, more than twice as many male calves were killed by predators than females (6 females, 15 males). We currently cannot explain this, but it does not seem to be related to the size of moose calves as both male and female calves were of similar size, and the pattern was not observed in Bonaparte. We hypothesize that cow/calf bonds and/or separation timing or rates vary between male and female calves, such that male calves spend more time farther from their cows and separate earlier, making them more susceptible to predation, especially if snow conditions are favorable for wolves during this time. If true, however, we would expect to see similar patterns across study areas. A more thorough analysis of the movements of collared cow-calf pairs may provide a better assessment of sex-specific predation risk on moose calves.

In addition to mortality causes for 8- to 12-month-old calves, we also monitored surviving calves between ages 1 and 2. Small sample size ($n = 24$) precludes strong inferences from the data, but we do see similar rates of predation mortalities in yearlings (40%) and adult cows (48%). Only 2% of yearling mortalities were health-related (compared to 17% for cows and 18% for calves) which could suggest that either this age class is less susceptible to health-related mortalities, or the sample size was insufficient to detect them. The yearling age class is also when bulls are susceptible to licensed harvest through either general open season for spike-forks or limited entry hunting, and we saw much higher hunting mortality in this age class. This is likely partly due to regulations (very limited cow/calf hunting opportunities are available to licensed hunters) and hunter preference (unquantified and likely variable for unlicensed harvest). Additional investigation on yearling mortality may be of interest in areas with low bull ratios given 22% of yearling mortality is associated with hunter harvest, but as noted previously, bull ratios do not appear to drive moose population change in our study areas. In PGS, the proportion of yearlings that are spikeforks and survive to the post-hunt period in midwinter was about half, and the yearling cohort was the second largest class on surveys, after sub-prime bulls, which includes a greater age range (Carriere and Scheideman 2023).

We have not assessed cause-specific neonate mortality in the project design to date, due to competing priorities for data acquisition, budget and capacity constraints, and safety and animal care concerns. As a result, we do not know the causes of neonate calf mortality in our study areas. We have observed summer calf survival rates averaging 41% (22–65%), indicating variation in that parameter and that there are important mortality factors influencing early calf survival that likely influence true recruitment rates. Studies of neonate moose calf mortality in North America consistently identify predation as the most important mortality factor for neonate calves, although the dominant predator varies (Ballard et al. 1981, Larsen et al. 1989, Ballard et al. 1991, Osborne et al. 1991, Testa et al. 2000, Keech et al. 2011, Patterson et al. 2013, Severud et al. 2019). Maternal condition, with IFBF as a proxy, did not appear to predict calf survival through the neonate period (~30 days), however, none of the cows we have assessed to date have been close to maximum body fat (~25%). We are currently examining landscape features that enhance or impede early calf survival based on parturient cows that raise a calf to approximately 1 month of age, compared to those whose calves do not survive the neonatal period. We assessed parturition for individual cows in Bonaparte and PGS based on movement rates and have calf-at-heel survey data on which cows retained their calves 4-6 weeks later. This approach will allow us to make landscape-level recommendations for enhancing early calf survival, regardless of the direct cause of neonate mortality.

Vital rates are measures of life stages within a population, for example, pregnancy, parturition, and adult death rates. Pooled vital rates observed in this study so far, including cow survival, pregnancy and parturition rates, and calf survival rates do not appear alarmingly low in most years. As such, moose population declines observed in this study are likely resulting from interactions among vital rates, and these vital rates can often vary substantially between study areas and years. A matrix model approach with sensitivity and elasticity analyses might allow for a more in-depth examination of the influence of multiple vital rates, and to isolate the most influential vital rates, on population trends (Caswell 2001). This approach may also provide more precise estimates of lambda. We recommend more in-depth analyses in this regard once data collection ends for some aspects of this research. Understanding which vital rates are contributing, and how they combine to affect observed moose population declines, is important for informing management.

5.4 Density Surveys

Aerial surveys were not completed in our study areas in 2021/22. PGS and JPRF were flown in 2020/21. Surveys are typically on a 5-year rotation. Survey conditions were not suitable in 2021/22 to fly Big Creek; SRBs are scheduled for Big Creek and Bonaparte in winter 2022/23 and for Entiako in 2023/24. Most study areas experienced population declines from 2.8-7.3% annually since the early-2000s, with increases in PGS and JPRF detected on the 2020/21 survey and expected in Bonaparte based on consistently high calf recruitment.

5.5 Ongoing Analyses

Important knowledge gaps have been identified over the course of the research project and by investigators working on the in-depth analyses of space use, selection, and survival. We are currently working with the University of Victoria, University of Northern BC, and our other collaborators to address these gaps in accordance with our updated research design (Kuzyk et al. 2019a). Some of the highlights include:

- Overall evaluation of the landscape change hypothesis
- Mechanisms affecting moose migration
- Shifts in moose diet in disturbed landscapes

- Comparison of SRB and camera trapping surveys to estimate moose density
- Response of moose to different silvicultural practices
- Influence of maternal habitat use/selection and condition on calf survival
- Landscape features influencing neonate survival
- Interactions among body condition, stress hormones and landscape change
- Interactions among landscape, climate, and ungulate community on winter tick
- Development of predation risk layers using wolf telemetry data, moose kill sites, and predator detections on remote camera arrays

6. MANAGEMENT RECOMMENDATIONS

Management recommendations were presented by Procter et al. (2020) and Anderson et al. (in prep). They are based on the theses and research products that had been completed to date and are directed to areas where the management objective is enhancing moose populations. On-going work is expected to provide further recommendations.

1. Increase local landscape heterogeneity by maintaining intact stands of mature timber, creating smaller clearings, and reducing areas with a high proportion of new cutblocks (Scheideman 2018; Mumma and Gillingham 2019; others in prep).
2. Identify and protect movement and migration corridors (Chisholm et al. 2021).
3. Consider migration patterns when assessing the abundance, density, and use by moose of seasonal ranges, including maintaining consistent monitoring protocols that take these seasonal movements into consideration (Chisholm et al. 2021).
4. Maintain and encourage deciduous stands on the landscape (Scheideman 2018, Boucher et al. 2022, Anderson et al. 2023).
5. Increase browse in areas that are otherwise managed to reduce predation risk (i.e., road deactivation and access management) to reduce the risk of creating an ecological trap (Francis 2020, Francis et al. 2020, Koetke et al. 2023). Reduce herbaceous and shrub stand-tending where regeneration is slow, incorporate deciduous species in re-stocking post-harvest in dry sites, and include palatable species near edges (Scheideman 2018).
6. Cutblocks do not necessarily provide high-quality habitat for moose, and to maintain stable moose populations, managers should consider vegetation composition and regrowth during forestry planning (Mumma et al. 2020).
7. Retain dead standing pine stands along with moose habitat to preserve horizontal and vertical structure and understory species diversity while maintaining high stocking standards (Scheideman 2018).
8. Reduce road access for predator and human traffic by limiting construction of new roads and rehabilitating roads following harvesting (recontouring, replanting, deactivating), and by reducing road density, particularly near important habitat features (Scheideman 2018; Mumma and Gillingham 2019; Francis et al. 2020).
9. Current licensed bull hunting opportunity appears to be sustainable in the study areas and not driving population trajectories; reductions in licensed bull harvest opportunity may be considered in some areas based on different objectives, but is not supported based on calf production data collected by this project.

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APPENDIX 1: MOOSE DENSITY SURVEYS

Table 7. Moose density estimates from prior to the early-2000s moose decline to the most recent surveys for five study areas in interior BC. For details on survey results and methodology, refer to the survey reports indicated.

Study Area	Survey Area	Survey Year	SCF-adjusted density (moose/km ²)	90 % CI for SCF density	Unadjusted density (moose/km ²)	Bulls: 100 cows	Calves: 100 cows	Reference
Big Creek	5-04	1993	0.71		0.510	18.0	40.0	Youds and Dielman 1994
Big Creek	5-04	1994	0.39		0.280	26.0	43.5	Dielman et al 1995
Big Creek	5-04	1997	0.41		0.296	37.7	49.3	Stahlberg et al. 1998
Big Creek	5-04	2004	0.29	0.048	0.222	56.3	36.5	Stahlberg 2005
Big Creek	5-04	2011	0.14	0.032	0.123	40.5	27.9	Davis 2012
Big Creek	5-04	2016	0.22	0.038	0.183	41.5	30.2	Grimson 2017
Bonaparte	3-29, 3-30	2012	0.30	0.018				Procter et al. 2020
Bonaparte	3-29, 3-30	2017	0.25	0.041				Procter et al. 2020
Entiako	Tweedsmuir/Entiako	1996	0.37	0.117	0.286	51.0	31.0	Marshall 1997
Entiako	Tweedsmuir/Entiako	2012	0.267	0.045	0.230	54.0	19.0	Thiessen et al. 2013
Entiako	Tweedsmuir/Entiako	2019	0.222	0.04	0.200	32.0	18.0	Schindler et al. in prep
JPRF	Fort St James	2011	0.77	0.048	0.757	30.0	30.0	Cadsand et al 2013
JPRF	Fort St James	2016	0.49	0.043	0.421	25.0	35.0	Klaczek et al 2017
JPRF	Fort St James	2020	0.83	0.090	0.725	38.8	21.0	Scheideman and Anderson 2021
PGS	PGE, PGW, TFL30	1998	1.33	0.319	0.667	36.0	47.0	Heard et al 1999
PGS	PGE, PGW, TFL30	2005	1.35	0.242	0.834	26.0	36.0	Walker et al 2006
PGS	PGW	2011	0.63	0.086	0.493	27.0	28.0	Cadsand et al 2013b
PGS	PGW	2016	0.4	0.066	0.339	27.0	32.0	Klaczek et al 2017
PGS	PGW	2020	0.6	0.082	0.563	31.0	35.0	Scheideman and Anderson 2021