Factors Affecting Moose Population Declines in British Columbia

Summary and Recommendations, 2012-2022

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Cover Photo: Moose cow and calf crossing a mainline resource road north of Fort St. James, BC (Morgan Anderson).

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Summary

In 2012-13, 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 the effect of landscape change on adult female moose survival and population change. The project was extended in 2016 to evaluate the effect on calf recruitment as well. After a decade of monitoring moose populations, the Provincial Moose Research Project has tested hypotheses about mechanisms of moose decline, some of which were rejected and some of which were investigated more thoroughly. On-going work continues to address these remaining hypotheses.

We initially expected adult female survival to be the most important parameter in driving population change, however, adult female survival in most years and study areas was consistently high enough to maintain a stable population. Instead, calf recruitment, or the interaction of calf recruitment and marginal adult female survival, appears to have driven the population decline. Adult female survival was not higher in study areas with lower disturbance (considered as cutblocks <8 yrs old), but individual moose responded to disturbance features at the home range scale and within their home ranges. These responses included avoidance of new cutblocks and roads, but also varied extensively by individual, by season, and by study area.

The mechanism of decline was unknown, but hypothesized to be linked to increased hunting success, nutrition or health factors, or increased predation. After 10 years of mortality investigation, there was no evidence that hunting (licensed, legal First Nations harvest, or poaching) caused the decline. There were no infectious or non-infectious diseases driving population dynamics. There was some support for the role of nutrition and analysis is on-going to better understand how that may influence moose populations. Wolf predation was the primary cause of death for collared cows and 8-month-old calves. Wolf and moose behaviour and selection in a highly modified landscape have likely led to shifting predation patterns and trade-offs for moose between energy acquisition and risk avoidance.

Management recommendations based on work to date include maintaining landscape heterogeneity and connectivity, maintaining interior forest conditions for thermal/snow interception cover, encouraging deciduous stands and moose browse, maintaining dead standing pine for horizontal cover, reducing functionality of roads, and maintaining current licensed hunting opportunity.

Several aspects of the project are still under active investigation with final products expected in 2023-24. The results of this work are expected to further inform next steps for the project and provide management recommendations. Recommendations for the project moving forward include continuing to monitor cow survival, calf recruitment, and population change; additional investigation of the impacts of nutrition, climate, predation (including areas undergoing wolf control for caribou recovery), health, and wildfire; application of vital rates for population modelling; development and assessment of habitat enhancement trials; and refining survey methodology.

Introduction

Moose in British Columbia (BC) are highly valued for consumptive and non-consumptive purposes, evidenced by the concern expressed by First Nations, stakeholders, and the general public when moose populations decline (Gorley 2016, GOABC 2016). Some moose populations in BC declined by 50–70% between the early 2000s and 2010s, while other populations remained stable or increased (Kuzyk 2016, Kuzyk et al. 2018a). In BC's central interior, moose declines coincided with a mountain pine beetle (*Dendroctonus ponderosae*) outbreak, which resulted in widespread mortality of pine trees >30 years old, and subsequent extensive salvage logging of beetle-killed timber (Alfaro et al. 2015). The resulting large-scale landscape alterations included dense road networks and larger cut sizes with few reserves of mature timber, a disturbance pattern that likely affected moose distribution and abundance (Janz 2006, Ritchie 2008, Alfaro et al. 2015). In 2012-13, the BC Ministry of Forests, Lands and Natural Resource Operations (now Ministry of Forests) and its partners initiated a multi-year research project to examine causes of moose decline in interior BC.

Kuzyk and Heard (2014) proposed a landscape change hypothesis, which stated that habitat change, through increased salvage logging and associated road building, resulted in greater vulnerability of moose to predators and hunters. The primary predictions of the landscape change hypothesis were that moose survival will increase when forestry cutblocks regenerate to obstruct the view of predators and hunters, resource roads are rendered impassable, and moose become more uniformly distributed on the landscape (Kuzyk and Heard 2014). While calf recruitment was acknowledged as a potential population driver, the project initially examined adult female survival, as it was shown to have a larger, more immediate effect on population growth rates in similar systems (Gaillard et al. 1998). Accordingly, we assessed cow moose mortality by monitoring a minimum of 30 GPS radio-collared cow moose annually in each of five study areas across central BC with varying levels of disturbance (Kuzyk and Heard 2014). In 2016/17, we added additional research objectives to complement the adult female survival work by assessing drivers of moose calf recruitment in two study areas.

This report has four main objectives:

- Provide an overview and synthesis of work to date (2012-2022), with a focus on completed work from the first 5 years of the project and highlights of on-going research from the subsequent 5 years;
- Determine which hypotheses initially proposed to explain moose declines can be accepted or rejected or what additional information would be needed to do so;
- Provide management recommendations based on the completed research to date;
- Provide priorities for future research, including persistent knowledge gaps and new research directions.

Study Areas

We conducted research in five study areas across the Interior Plateau of central BC: Bonaparte, Big Creek, Entiako, Prince George South (PGS), and John Prince Research Forest (JPRF). We selected study areas to represent a range of MPB infestation and disturbance. With the exception of 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.

In addition to the five Provincial Moose Research Project study sites, the Peace-Williston Fish and Wildlife Compensation Program (PWFWCP) conducted a similar project on two additional study areas north of the interior plateau, West Parsnip and Moberly. These additional sites are summarized by Sittler (2021) and the West Parsnip study area was included in Mumma and Gillingham's (2019) survival analysis. Body condition data was also collected in 2021/22 from an additional area to the south, Pennask Plateau.

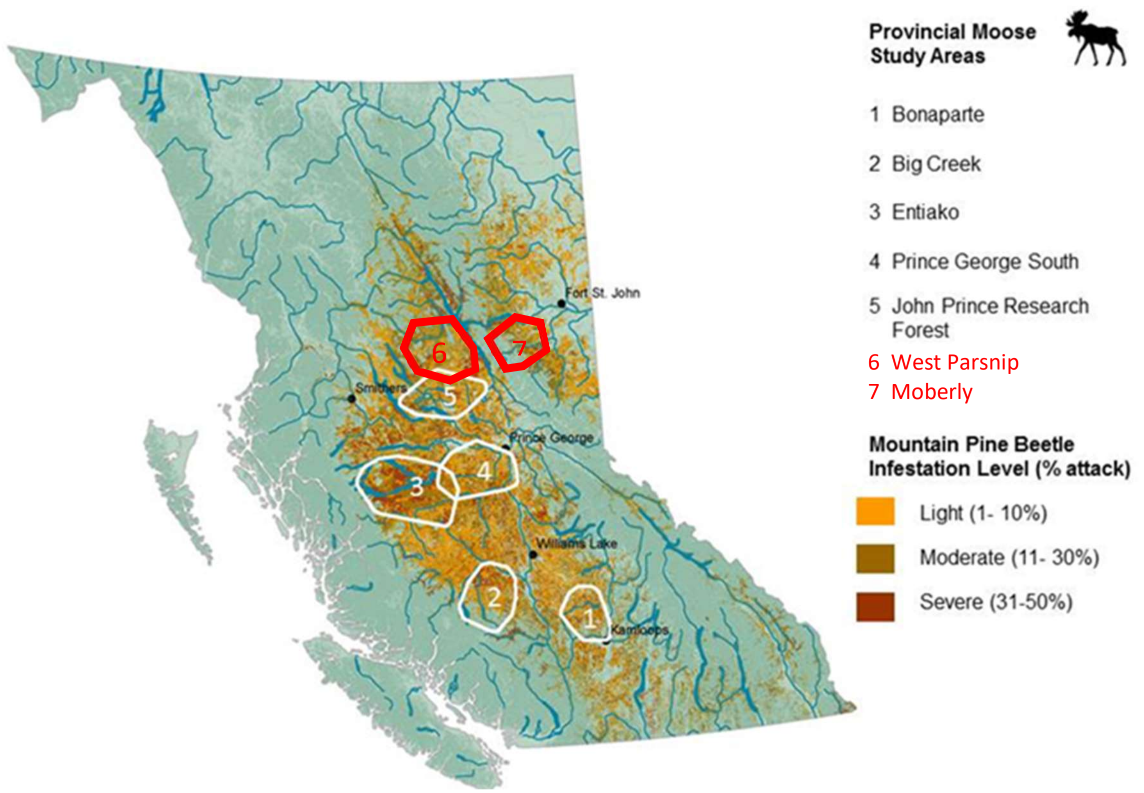

Figure 1. Map of moose research study areas in central BC overlaid on mountain pine beetle infestation as of 2016. PWFWCP study sites indicated in red.

Project Objectives

The objectives of the moose research project, based on Kuzyk and Heard's (2014) study design, were to assess causes and rates of adult female mortality, focusing on the impact of hunting, predation, and health/ nutrition, and the contributing spatiotemporal factors. Additional regional objectives were also defined, although not as the primary focus of the project (Table 1). Results to date have informed the original objectives, which have been either fully addressed (i.e. hypothesis rejected or not rejected) or partially addressed (i.e. unable to reject a hypothesis but other factors identified for investigation).

Table 1. Regional objectives specified for the moose research study areas by Kuzyk and Heard (2014). Specific study area objectives originally proposed for a study area are indicated by 'yes' while study areas for which those objectives were not originally prioritized are marked 'no.' 'Addressed' refers to study areas where work has been undertaken to address the objective, although not all have been fully addressed or answered.

Objective	Bonaparte	Big Creek	Entiako	PGS	JPRF
Determine impact of salvage logging on behaviour and mortality risk	Yes; addressed	No; addressed	Yes; addressed	No; addressed	No; addressed
Determine limiting factors for cow survival	Yes; addressed	Yes; addressed	Yes; addressed	Yes; addressed	Yes; addressed
Determine limiting factors for calf survival	Yes; addressed	No	Yes; not addressed	No; addressed	No
Determine climate effects on cow behaviour	Yes; not addressed	No	No	No	No
Determine sightability correction factors	Yes; not addressed	Yes; not addressed	No	Yes; not addressed	Yes; some analysis ongoing
Delineate population management units	No	No	Yes; not addressed	No	No
Inform caribou recovery objectives	No	No	Yes; analysis ongoing	No	No
Assess moose response to wildfire	No; analysis ongoing	No	Yes; not addressed	No	No

The objectives of the moose research project were refined by Kuzyk et al. (2019) to address knowledge gaps based on the first 5 years of the project. These objectives included:

- Continue monitoring adult female survival
- Conduct and evaluate forest management trials for moose enhancement
- Monitor true calf recruitment and population change
- Assess calf survival in relation to landscape change
- Assess calf survival in relation to adult female moose body condition
- Examine the role of nutrition and health in moose population change
- Examine the role of predation in moose population change

Hypotheses and Predictions

Kuzyk and Heard (2014) proposed a landscape change hypothesis in which logging features, especially from extensive salvage logging, led through some mechanism (hunting, predation, health) to reduced moose population growth rate and abundance. The original study design acknowledged the potential role of calf recruitment as a population driver but focussed on assessing adult female survival based on its role in population dynamics in other systems. Our first hypothesis therefore is that adult female survival was the dominant driver of population change. The mechanisms of decline can also be examined within the landscape change hypothesis overall, acting on either adult female survival or on calf recruitment: human hunting, predation, and health (nutrition, thermal stress, other health parameters). Tables 2 and 3 provide an overview of the hypotheses, predictions, data requirements and results supporting or refuting the hypotheses.

Table 2. Hypotheses investigated by the Provincial Moose Research Project 2012-2022 with expected predictions and progress on accepting or rejecting the hypotheses.

Hypotheses	Predictions	Data Exist?	Result
Low adult female survival explains moose population change (included as a separate hypothesis because we initially assumed adult female survival would be most affected)	Adult female survival rates average <85%	Y	Not supported with pooled survival rates and in 3 study areas; supported in Entiako and weak support in PGS (Mumma and Gillingham 2019, Procter et al. 2020)
Hunting hypothesis: Direct hunting mortality of adult females caused low survival and/or excessive bull harvest caused low bull ratios and ultimately impaired reproduction	Adult female survival rates <85%; hunting as a dominant mortality factor for adult females	Y	Not supported in any study area (Mumma and Gillingham 2019, Procter et al. 2020)
	High second estrus pregnancy rates as first indicator of impaired reproduction; low bull:cow ratios	Y	Not supported (Procter et al. 2020 for PGS and Bonaparte, regional survey reports for bull:cow ratios)
Landscape change hypothesis: anthropogenic habitat changes arising from forest development led to unsustainable mortality of adult females and/or calf moose (may mediate or interact with other causes)	Dominant mortality factors of adult females and/or calves will be linked to features of landscape change (roads and cutblocks)	Y	Minimal support for cow survival for all study areas (Mumma and Gillingham 2019), ongoing for calf survival in PGS and Bonaparte (Boucher et al. in prep)
	Adult female survival rates will be inversely correlated with disturbance levels	Y	Ongoing but not currently supported over all study areas (Heard et al. in prep)
	Population rates of change will be inversely correlated with disturbance levels	Y	Ongoing but not currently supported over all study areas (Heard et al. in prep); migration work also expected to inform (Chisholm et al. 2021, Koetke et al. in prep)
Nutrition hypothesis: changes to forage quality/quantity due to environmental conditions, led to adult females in poorer condition and ultimately, poor calf survival and recruitment and/or adult female survival; may be confounded with landscape change (i.e., thermal cover or stress), health.	Adult females average <2mm early winter rump fat (per Ruprecht et al. 2016)	Y	Ongoing in PGS and Bonaparte, but currently not supported (Procter et al. 2020)
	Body fat of adult female moose will decline across a natural gradient of environmental conditions; calf ratios will also decline across the same gradient	Y	Ongoing for Bonaparte and Pennask Plateau, currently not supported (Anderson et al. in prep)
	Covariates explaining moose body fat levels suggest forage limitation	Y	Ongoing (UNBC - Jefferies), some support from diet analyses (Koetke et al. 2023)
	Calf survival and recruitment will be lower following years of warm, dry summer conditions (per Monteith et al. 2015)	Y	Ongoing but currently not supported (Boucher et al. in prep)
	Calf survival, as second indicator of poor nutrition, will be positively correlated with the condition of their mothers	Y	Not supported for calves <30 days old and <7-8 months old in PGS and Bonaparte; ongoing (UVic – Boucher)

Hypotheses	Predictions	Data Exist?	Result
Health hypothesis: poor health of moose led to poor adult female and/or calf survival. May be multiple causes (e.g., thermal stress, direct and specific health factors) and potentially confounded with nutrition or landscape change	Health-related causes of death, other than apparent starvation, will be a dominant ultimate mortality factor for adult females and/or calves	Y	Not currently supported in any study area (Thacker et al. 2019, Mumma and Gillingham 2019, Schwantje et al in prep)
	The majority of individuals dying from apparent starvation will have underlying health-related causes	Y	Not currently supported but analysis ongoing (Schwantje et al in prep)
	Health sampling at time of capture and/or time of death will indicate significant presence of important health-determinants	Y	Not currently supported (Schwantje et al in prep)
	Urine/fecal sampling will indicate important physiological health determinants	Y	Ongoing (UNBC – Jefferies)
Predation hypothesis: predation led to poor adult female and/or calf survival	Predation will be a dominant mortality factor and adult female survival rates will be < 85% on average for adult females OR	Y	Predation in all study areas, survival rates <85% supported in Entiako and weakly supported in PGS study areas, not others (Mumma and Gillingham 2019, Procter et al. 2020)
	Predation will be a dominant mortality factor for calves and recruitment rates will be insufficient to compensate for adult female mortality	Y	Predation supported for older calves (Procter et al. 2020, Boucher et al. in prep), all literature indicates predation is dominant factor for neonates, compensation for adult mortality needs analysis
	The majority of predated individuals would have otherwise survived (i.e., predation is an additive mortality factor)	Y	Ongoing (ultimate COD). Need to demonstrate that predation didn't just remove old and/or unhealthy individuals. Might be difficult for calves.
	Wolf densities correlate with timing of population declines and/or are inversely correlated to calf ratios	N	Needs analysis. Need a way to generate estimates of wolf abundance over time – integrated population model, population reconstruction based on harvest/ ungulate biomass? Alternatively track known changes moving forward with wolf removal in Entiako

Table 3. Expected responses of key moose population parameters under hypotheses explaining moose declines.

Hypotheses		Population Growth Rate (Lambda)	Cow survival	Dominant Mortality	Body Condition	Pregnancy	Calf Recruitment	Comments
Low adult female survival explains moose population change		Low	Low <85%					Assumes observed survival rates reflect survival rates during decline
Landscape change hypothesis: anthropogenic habitat changes arising from forest development led to population decline	Due to unsustainable mortality of adult female moose	Lower in the more disturbed study areas	Lower adult female survival in the more disturbed sites	Associated with landscape change features				Results will change depending on spatial and perhaps temporal scale, and with how disturbance is quantified.
	Due to unsustainable mortality of calf moose	Lower in the more disturbed study areas		Associated with landscape change features			Lower in the more disturbed sites	
Nutrition hypothesis: changes to forage quality, arising from environmental conditions, led to adult females in poor condition and ultimately, poor adult female and/or calf survival	Due to poor adult female survival	Lower where forage quality is lower	Lower where forage quality is lower	Health/ condition related	Lower where forage quality is lower	Lower where forage quality is lower		Requires forage quality/quantity analysis (how to measure, define, and separate those parameters would also be key). Likely at home range scale rather than study area scale.
	Due to poor calf survival	Lower where forage quality is lower		Health/ condition related	Lower where forage quality is lower	Lower where forage quality is lower	Lower where forage quality is lower	
Thermal stress hypothesis: warming temperatures or lack of functioning thermal cover led to adult females in poor condition or health and ultimately, poor adult female and/or calf survival	Due to poor adult female survival	Lower in more southerly/ warmer sites (or some other metric)	Lower in the thermal stress sites	Health/ condition related				Need to quantify number of openings, availability of functional thermal cover, climate data at meaningful scale, use of microsites, incorporation of lag effects

Hypotheses		Population Growth Rate (Lambda)	Cow survival	Dominant Mortality	Body Condition	Pregnancy	Calf Recruitment	Comments
	Due to poor calf survival	Lower in more southerly/ warmer sites (or some other metric)		Health/ condition related			Lower in the thermal stress sites	
Health hypothesis: poor health of moose led to poor adult female and/or calf survival	Due to poor adult female survival	Lower in sites where health factors identified	Health metrics are severe enough to impact adult female survival	Health/ condition related	Lower associated with health metrics	Could be impacted by health metrics		Health testing reveals high prevalence/ severity
	Due to poor calf survival	Lower in sites where health factors identified		Health/ condition related	Lower associated with health metrics	Could be impacted by health metrics	Health metrics impact calf recruitment	
Predation hypothesis: predation led to poor adult female and/or calf survival	Due to poor adult female survival	Lower where predator density/ predation rates higher	Insufficient to balance recruitment	Predation (as ultimate and proximate)				
	Due to poor calf survival	Lower where predator density/ predation rates higher		Predation (as ultimate and proximate)			Insufficient to balance adult female mortality	

Methods

Methods for capture, sampling, and monitoring were originally presented by Kuzyk and Heard (2014) and updated over the course of the project (Kuzyk et al. 2015, Kuzyk et al. 2016, Kuzyk et al. 2017, Kuzyk et al. 2018b, Kuzyk et al. 2019b, Procter et al. 2020). Cows have been captured annually since 2012 to maintain approximately 30 active collars on cows per study area. Eight-month-old moose calves were captured from winter of 2016/17 to winter 2020/21 in Bonaparte and PGS (20 calves per study area per year).

We collected biological samples from all captured moose and moose mortality sites following a standardized protocol that is updated annually (Thacker et al. 2019, Procter et al. 2020). We also assessed age class, body condition, tick load, and presence of calves. From 2018/19 to 2021/22 in PGS and Bonaparte, we measured maximum rump fat using a portable ultrasound machine. If non-random cows were captured (sometimes we targeted cows with calves for calf captures), their body fat measurements were excluded from the analyses.

We conducted mortality site investigations according to a standardized protocol to determine proximate and ultimate cause of death (Kuzyk and Heard 2014, Mumma and Gillingham 2019, Procter et al. 2020). The site investigations were conducted as soon as possible, typically 24-48 hrs after the mortality. In some cases, investigations were delayed, usually when predators or scavengers continued to move the collar post-mortem and delay a mortality beacon, and when collars that were buried or underwater sent delayed signals. 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 a proximate cause (Mumma and Gillingham 2019).

We calculated annual survival rates for cow moose based on a biological year (April 30 to May 1) intended to precede the average timing of parturition for moose in BC (Poole et al. 2007, Gillingham and Parker 2008). All cow moose were assumed to be random individuals and representative of the population with equal risk of mortality. 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% for stable moose populations (Bangs et al. 1989; Ballard et al. 1991, Bertram and Vivion 2002). Calf survival rates were calculated from date of capture (at about 8 months of age) to recruitment into the population (i.e. the average birth date, May 21) using a Kaplan-Meier estimator (Pollock et al. 1989, Bender 2006, Severud et al. 2015).

In addition to monitoring individual collared calves in two study areas, we monitored calf recruitment from collared cows. Calf parturition was determined by assessing daily cow movement rates 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 several days of very short movements constrained by the low mobility of calves immediately post-birth. Aerial surveys conducted 4-6 weeks post-parturition to locate collared cows and determine presence of a calf. In some years and study areas, calf-at-heel status was also determined in early winter during captures and 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 birth date. We assumed that cow deaths were too few to substantially alter the cow/calf ratios between mid-winter and recruitment of calves to 1 year of age. 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 following Hatter and Bergerud (1991).

Analysis techniques have relied on a wide variety of explanatory variables including remote sensing data, topography, forest harvesting and silvicultural treatments, stand type, infrastructure, and land cover type. The specific analysis methods are fully described in the respective reports and publications.

Results

Adult female survival as primary population driver

Adult female survival was generally high enough to maintain stable moose populations (>85% annual survival) in all study areas and years of the project. In some study areas in some years, adult female survival rates were sufficiently high to indicate expanding moose populations if normal recruitment rates were observed at the same time. If we assume that adult female survival during this study was representative of adult female survival in the years of greatest decline that occurred prior to monitoring, consistently low adult female survival was not the primary driver of population change. And, given we have monitored female survival rates for 10 years in several different areas, we also assume that we have captured the natural range of variation in this parameter for interior BC. In some years and some study areas (PGS and Entiako) adult female survival was relatively low and may have contributed to decline. We do not know whether survival rates have changed from before or during the decline to 2012/13 when the project was initiated, although the mechanism (if mediated through landscape change) would be expected to be consistent.

Adult female survival was predicted to be the primary driver of decline because it is a key parameter in population dynamics of long-lived ungulates (Gaillard et al. 1998). Rapid declines without a lag effect are more likely associated with reduced adult female survival and its immediate impact on the population; slower declines that show evidence of a lag effect would suggest recruitment as the driving mechanism of population change. Moose population abundance is not monitored annually, and calf recruitment is highly variable among years, so the actual nature of the decline curve is hard to estimate (Werner 2020).

In PGS, moose abundance has been estimated every 5 years since 1991 with nearly annual monitoring of demographics using less intensive composition surveys since 1972. These data were used in a population reconstruction for PGS, in which composition data was used to infill and backcast abundance estimates between surveys conducted every 5 years. Adult female survival and calf recruitment were both strongly related to population growth rate and relative importance could not be assessed (Werner 2020). The relationship weakened with increasing time lags to 4-5 years (Werner 2020). The conclusion based on the population modelling was that different habitat conditions may have become limiting following extensive salvage logging (Werner 2020). If that was the case, the mechanisms of population change during the decline and recovery may not be the same (Werner 2020).

Calf recruitment as primary population driver

Early calf survival (4-6 weeks post-parturition) is generally around 50% wherever it has been examined, with most mortality attributed to predation. This project did not attempt to quantify early calf survival, but the combination of pregnancy and parturition data, June calf-at-heel surveys, and monitoring of older calves either through mid- and late winter calf-at-heel surveys or collaring, does allow us to infer some patterns in calf recruitment. In the years for which calves were collared and monitored in PGS and

Bonaparte, recruitment to age 1 was highly variable, with predation as the leading mortality factor. We assume that patterns of calf survival and mortality observed during the monitoring period can be applied to the period during the population decline, which may not be the case.

The calf data that we do have prior to the decline is limited to mid-winter composition surveys. Based on the calf survival work, late winter/spring survival can be highly variable, so mid-winter ratios may not be indicative of calf recruitment the following spring (Kuzyk et al. 2019, Procter et al. 2020). Calf ratios have been variable among years, but in PGS where composition surveys have been flown almost annually since 1972, calf ratios appeared to be higher (~50 calves:100 cows) prior to the moose declines in the 2000s and have remain lower since (~35 calves:100 cows). The lower recent calf ratios could be expected to maintain a stable population but may not be sufficient when late winter calf mortality is considered or in years with lower adult female survival. First, the number of female calves recruited might not balance the number of adult females dying if adult female mortality was elevated. Second, if mortality factors affected all age and sex classes, we would not expect any change in the demographic ratios, because the lower calf numbers would be counteracted by lower cow numbers. This is unlikely however, as most mortality factors (with the exception of human-caused mortality) have a higher impact on juveniles. Similar declines in average mid-winter calf ratios have been observed in the Bonaparte study area, where calf ratios have declined from an average of approximately 45 calves/100 cows prior to 2010 to 27 calves/100 cows since, excluding the higher mid-winter recruitment rates observed since 2020, which have averaged 46 calves/100 cows.

Landscape change hypothesis

At the broadest scale, i.e. among study areas, this project set out to determine whether lower moose population growth rates and lower adult female survival coincided with areas of higher disturbance. At the broadest scale, adult female survival was not lowest in study areas with the highest disturbance. Adult female survival was unexpectedly lowest in study areas with the least disturbance, as it was defined for our analysis. Individual moose did respond to landscape attributes associated with the extensive disturbance following mountain pine beetle salvage logging, and use of these features influenced their risk of mortality from hunting, predation, and apparent starvation. These responses at a smaller scale may still provide guidance for wildlife managers seeking to enhance moose habitat.

Moose are not distributed at random on the landscape, and the habitats and landscape features that moose use are expected to impact their survival and reproductive success. Observed habitat use and selection is the result of trade-offs encountered by individuals, including maximizing energy intake, minimizing energy expenditure, and minimizing predation risk (Fryxell et al. 1988, Dussault et al. 2005). Selection at the coarsest scale is expected to address the most important limiting factors for an animal (Johnson 1980). We examined patterns of habitat selection at the study area, home range, and within home range scales to better understand the hierarchy of limiting factors for moose, focusing on PGS, Bonaparte, Big Creek, and Entiako (Scheideman 2018, Francis 2020, Francis et al. 2020, Mumma et al. 2020).

Seasonal home ranges and movement rates were smallest in late winter and largest in summer (Scheideman 2018, Francis 2020). Home range size was generally not associated with road density or proportion of cutblocks in PGS, Big Creek and Entiako (Scheideman 2018). Mature forest (usually dead standing pine-leading) generally made up the largest proportion of habitat in moose home ranges in all study areas, although new cutblocks (harvested since 2000, when cutblocks became larger with reduced reserve zones) were the predominant land cover in PGS home ranges in early winter. Moose in PGS, which had the highest road density, selected home ranges with lower road densities while moose in Big Creek and Entiako did not show consistent selection or avoidance of road density in their home range placement (Scheideman 2018), and road density was not an important variable for Bonaparte moose habitat selection (Francis 2020). Although cutblocks were not consistently avoided in home ranges, moose did select home ranges with a variety of habitat types and 50-60% mature forest (Scheideman 2018). PGS moose had more variable home range selection than moose in Big Creek or Entiako, suggesting that multiple selection strategies may be employed by individuals in a highly modified landscape (Scheideman 2018).

Selection within home ranges is expected to address less critical limiting factors than selection at the home range scale (Johnson 1980, Leblond et al. 2010, Street et al. 2016). Selection within home ranges was generally consistent with selection at the home range scale (Scheideman 2018). Remaining beetle-killed pine stands were used extensively, especially in summer (Scheideman 2018, Francis 2020). Moose in Big Creek and Entiako selected for conifer stands in fall, and these forest types were important to Bonaparte moose in summer (Scheideman 2018, Francis 2020). Moose in Big Creek, PGS, and Entiako selected deciduous stands in all seasons (Scheideman 2018) and Bonaparte moose selected deciduous and mixed deciduous-coniferous stands in spring, calving, and fall (Francis et al. 2020). Moose in Big Creek selected forest edges, although selection for edge was less consistent in PGS and Entiako (Scheideman 2018). Moose did not consistently select areas near or far from roads within the home range (Scheideman 2018, Francis 2020), although at the study area scale moose in PGS and Bonaparte selected areas farther from roads (Mumma et al. 2020).

Moose responses to cutblocks varied by season, cutblock age, and site characteristics, and this complexity may also have contributed to our inability to observe a relationship between disturbance and adult female survival at the between-study-area scale. New cutblocks were generally considered to have been harvested following salvage logging practices after 2000 (Scheideman 2018) or based on age since harvest for approximately the same timeframe (0-14 years since harvest, Francis 2020), although Francis et al. (2020) also considered 0-2 years since harvest as new cutblocks to better assess predation risk. Moose avoided old cutblocks (harvested prior to 2000) except in late winter and in summer in PGS, and response to new cutblocks (harvested since 2000) varied by study area, with avoidance in Big Creek, selection in fall and early winter in Entiako, selection in PGS except in summer (Scheideman 2018). In Bonaparte, new cutblocks (0-14 years since harvest) were selected in spring and new cutblocks (0-2 years since harvest) were selected in every season except spring (Francis et al. 2020). The reason for such a divergent response to new cutblocks could be a combination of vegetation regeneration and regeneration times, silvicultural differences, or an artifact of how new cutblocks were defined. Wetlands were selected in Big Creek and Entiako in early and late winter, and in summer in PGS and Bonaparte (Scheideman 2018, Francis 2020).

Mumma et al. (2021) undertook a more refined assessment of selection and use of cutblocks of varying ages since harvest to refine our definition of 'new' cutblocks. Moose used new (1-8 years since harvest) cutblocks less than their availability (except in early winter), used regenerating cutblocks (9-24 since harvest), and did not select for cutblocks older than 25 years (Mumma et al. 2020). PGS moose were less likely to avoid regenerating cutblocks than moose in Bonaparte, and consistently selected for regenerating cutblocks in early and late winter (Mumma et al. 2020). Leading species also affected moose selection, with moose in PGS and Bonaparte using cutblocks in spruce stands relatively more than in Douglas-fir stands. Compared to Douglas-fir cutblocks, moose used fir-dominated cutblocks relatively more in spring, fall, and late winter, pine cutblocks more in early winter, and cutblocks dominated by broadleaf species more in early and late winter (Mumma et al. 2020).

Adult female survival alone, if the rates we measured during this work are reflective of survival rates during the decline, does not appear to have been the driving factor in the population decline, so a lack of relationship between adult female survival and disturbance at a study area scale would not be surprising. Moose also clearly respond to salvage logging features at smaller scales, including at the home range scale and within their home ranges, but responses varied by study area and season and among individual moose. This response could still have important fitness consequences, but not be reflected by how we measured adult female survival or how we quantified disturbance, as not all cutblocks provide the same value or risk to moose. It is likely that the effect of landscape change on adult female survival could not be detected across study areas due to a combination of factors.

Hunting hypothesis

We evaluated the contribution of hunting to adult female mortality throughout the project, combining licensed harvest by BC resident and non-resident hunters, legal unlicensed harvest by First Nations, and illegal unlicensed harvest through poaching. Cow moose were more likely to be harvested by hunters if using high road density areas on a given day or a high proportion of new cutblocks over the previous week (Mumma and Gillingham 2019). Hunting accounted for 11% of 181 cow moose mortalities investigated between 2013 and 2022. It was not a leading mortality factor in any year or study area and was not sufficient to cause moose population declines.

The other mechanism through which moose harvest could impact the population would be excessive harvest of bulls leading to insufficient bull density to effectively breed cows on their first estrous. If this was the case, we would record unusually low bull ratios on surveys and would detect unusually high proportions of second estrous calves. Bull ratios prior to decline and throughout the study period have been generally adequate, i.e. >30 bulls:100 cows for the population densities in the study areas (Stahlberg 2005, Davis 2012, Grimson 2017, Lemke 2013, Thiessen et al. 2013, Cadsand et al. 2013, Klaczek et al. 2017, Procter and Iredale 2018, Scheideman and Anderson 2020). Although some study areas in some years have had low pregnancy rates, the observed pregnancy rates include second estrous pregnancies and are more likely due to other factors. We have also assessed cow movement rates to determine parturition status and calving date each year – although in some years and study areas this analysis is completed prior to expected second estrous calving events about 20 days after first estrous calves (Schwartz et al. 1994). There have been relatively few (<10%) second estrous calving events detected with the movement analysis or observed on June calf-at-heel surveys, when second estrous calves are noticeably smaller than first estrous calves. This is within the range of reported second estrous calves (11% Edwards and Ritcy 1958, 17% Schwartz and Hundertmark 1993). Furthermore, licensed moose harvest has remained within the range of sustainable harvest rates for bull-biased harvest set out in the Provincial Framework for Moose Management in BC (BC FLNRO 2015). Overharvest of bulls therefore does not appear to be driving population change.

Health hypothesis

The importance of health-related mortality varied by study area, with more health-related mortality observed in Bonaparte and relatively few observed in Entiako and JPRF (Thacker et al. 2019). However, we have not detected the occurrence of any specific health determinant that is expected to have population-level consequences for moose populations in interior BC. Assessment of moose health is further challenged by a lack of baseline health data on these moose populations to understand whether health status has changed and whether observations made during this research are extraordinary. Apparent starvation cases (moose in extremely poor body condition) made up 7% of cow moose mortalities to April 30, 2022, with most cases observed in PGS and Bonaparte and during earlier years of research. The health hypothesis was further examined after a significant number of apparent starvation cases to determine why the moose were in such poor body condition, as several factors could be responsible (Werner and Anderson 2017). Poor body condition could be caused by either insufficient energy intake or too much energy expenditure, or a combination of the two. Insufficient energy intake could be due to poor quality forage (digestible protein, trace nutrients, toxins), insufficient quantities of forage, or behaviour limiting access to forage (e.g., forage-predation trade-offs), and diet work suggests these trade-offs are present in a highly modified landscape (Koetke et al. 2023). Excessive energy expenditure could be due thermal stress, increased movement rates (especially in deep/crusted snow), or parasites or disease (e.g., winter ticks).

Other health-related mortalities (infection, non-infectious disease) made up 10% of cow moose mortalities over the same timeframe. Health assessments to date have relied on a piece-meal approach with inconsistent sampling, usually from individuals showing outward signs of poor health, and are not representative of general population health. As the first health monitoring for moose in BC, this project provides a baseline but without any comparison for moose health in BC historically. Although standardized sampling at capture and mortality sites now provide better data, samples are deficient from many mortalities. This is often the case when predators consume most of the carcass, so the true health status at time of death is not known for many individuals.

Wildlife health is a complex term that reflects many interacting factors at varying spatiotemporal scales affecting individuals and populations and is likely best approached from a cumulative effects perspective (Thacker et al. 2019). Assessing the population-level impact of health concerns is not always straightforward because of these interacting factors, and work currently underway seeks to further assess the implications of health parameters monitored to date for moose population change in BC (Schwantje et al. in prep).

Forage limitation

Bottom-up processes and nutrition can drive moose population dynamics, especially where moose are at high densities and predation pressure is low; moose are expected to operate in a density-dependent manner with growth and reproduction more sensitive to energetic limitation than adult mortality (Sæther 1997, Gaillard et al. 1998, Ferguson et al. 2000, Boertje et al. 2007). Quantifying forage quality, quantity, and availability to moose can be difficult, and the links between forage characteristics, moose condition, and population-level effects can be tenuous. The depth of data available on this project has allowed us to address several knowledge gaps around moose nutrition, particularly in the PGS study area where apparent starvation mortalities were unexpectedly high in the early years of the project.

Secondary compounds produced by plants can limit the availability of digestible nitrogen, especially in open early seral habitats, making them lower quality forage and suppressing body condition (Bø and Hjeljord 1991, Jonasson et al. 1986, Lenart et al. 2002, McArt et al. 2009, Spalinger et al. 2010). Werner (unpubl.) assessed digestible energy and protein in several important moose browse species in shaded understory environments and found reduced nutritional quality at increasing distances of forest edge into open cutblocks in PGS, especially later in the growing season. The results of that work would need to be considered in the context of amount of shaded or edge habitat available and used by moose, account for additional forage types that were not analyzed (e.g. aquatic vegetation), and link to changes in survival and recruitment for individual moose that would be expected to drive population change.

Moose in Bonaparte trade off predation risk and forage availability, avoiding roads but using new cutblocks during calving, but selecting areas near roads in winter and spring, apparently favoring forage acquisition over risk avoidance seasonally in winter, spring, and summer (Francis et al. 2020). If moose select for areas like new cutblocks that provide forage associated with a higher risk of predation, Francis et al. (2020) suggest that an ecological trap could be established. However, across all study areas, moose cows were more likely to die from apparent starvation if they used high road density areas over the previous year and higher proportions of new cutblocks over the previous 180 days (Mumma and Gillingham 2019), suggesting that new cutblocks are not associated with significantly higher nutritional benefits. Additional work on diet in PGS and JPRF also suggests new cutblocks may not provide high quality forage (Koetke et al. 2023).

Moose with suboptimal forage resources may also need to expand their diet to make up for deficiencies in forage quality. Moose in the more highly disturbed landscape of PGS had a wider dietary niche than moose in less disturbed JPRF (Koetke et al. in prep). This could indicate that PGS moose have expanded their diet to make up for lower forage quality in the more disturbed landscape (Koetke et al. 2023).

We initiated the collection of body fat measurements using ultrasonography to better understand the nutritional status of adult female moose and how their condition may affect calf survival. Winter had previously been considered the time of greatest nutritional stress limiting body condition in ungulates, but recent research indicates that ungulates can mitigate winter condition loss by accumulating sufficient fat reserves over the summer. The ability to build up fat reserves from spring to fall is more important from a population productivity perspective (Tollefson et al. 2010, Cook et al. 2013, Cook et al. 2021). Female moose body fat levels monitored in PGS and Bonaparte indicated lower ingesta-free body fat (IFBF) levels compared to other populations (e.g., Alaska), especially for cows with a calf-at-heel during early winter captures (Procter et al. 2020). However, comparing these data to other studies is challenged by differences across sub-species, differing moose densities, timing of measurements during the year and specific years of study. In PGS and Bonaparte, body fat levels have been higher than that required to maintain normal pregnancy rates (Ruprecht et al. 2016). This is expected to be one of the first parameters affected by poor nutrition and low body condition, along with calf survival, followed lastly by poor adult female survival if body condition declines enough (Gaillard et al. 2000). Currently, we have not detected a relationship between maternal condition and calf survival to approximately 30 days of age in the subsequent year (Anderson et al., in prep) or during their first winter (Boucher et al. in prep). Further, preliminary investigation of body condition in moose populations in southern BC, characterized by warmer climates, similar levels of landscape change, stable to increasing densities and consistently high mid-winter calf ratios (e.g., 40-55 calves/100 cows) in recent years has shown similar body fat levels as those measured in PGS and Bonaparte, suggesting the condition of moose is likely not driving moose population change. Analysis is currently ongoing to determine the effect of habitat selection on body condition and the affect of maternal body condition on calf survival (UVic – Nicole Boucher).

Parasites, disease, and trace element concentrations

Baseline herd health monitoring has not suggested widespread direct mortality attributed to the infectious diseases examined to date, which were prioritized for assessment based on their importance in other moose populations (Macbeth 2017, Thacker et al. 2019). These included viral pathogens (parainfluenzavirus-3, bovine viral diarrhea virus, bovine herpesvirus-1, infectious bovine rhinothracheitis), bacterial pathogens (*Mycobacterium avium ssp. paratuberculosis, Erysipelothrix rhusiopahiae*), gastrointestinal parasites (nematodes Ostertagiinae, Trichostrongylinae, Nematodirinae, Trichurinae; cestodes; trematodes; coccidia), and tissue-dwelling protozoans (*Neospora caninum, Toxoplasma gondii*). Relatively high prevalence of *N. caninum* in Bonaparte calves could be a factor in a reproductive failure observed in that study area (Thacker et al. 2019). Brainworm (*Parelaphostrongylus tenuis*) has been implicated in moose declines elsewhere in North America, but is not present in BC, and giant liver fluke (*Fascioloides magna*) was not detected in the study areas (Thacker et al. 2019).

Levels of trace minerals examined (manganese, iron, cobalt, copper, zinc, selenium, and molybdenum) were generally within levels detected in other healthy populations (Thacker et al. 2019). One moose in PGS did have toxic levels of copper, the cause of which was not determined.

In the eastern and southern portions of their North American range, late winter/spring moose mortalities are often associated with heavy winter tick (*Dermacenter albipictus*) loads (Jones et al. 2017, 2019). The impact of ticks on moose populations in BC is less certain, although some tick mortalities have been reported on this project. Tick burdens appear to be highest on PGS and Bonaparte moose, and lowest in JPRF and Big Creek (Thacker et al. 2019). Fieldwork has been initiated to better understand the interacting role of climate, landscape change, and winter tick dynamics on moose populations (UNBC – Ben Spitz).

Thermal stress

Thermal stress has also been considered as a potential contributing factor to moose health and as a factor driving behaviour and distribution. Renecker and Hudson (1986) identified heat stress thresholds for moose in winter at -5°C and 14°C in summer, with acute heat stress above 0°C in winter and above 20°C in summer. Heat stress was predicted to be greatest for moose in April-May, which also coincides with annual minimum body condition (Schwartz and Renecker 1997, Werner 2022). Operative temperature measured in forest and cutblocks in PGS indicated much higher daily and seasonal variability in temperature in open areas (Werner 2022) and other investigators report an average of 6°C warmer temperatures in open areas than conifer cover (Pigeon et al. 2016). Van Beest and Milner (2013) linked moose body condition with thermoregulatory behaviour.

Moose using areas over winter with high proportions of new cutblocks, burns, and pine (mostly dead and providing little canopy cover) were more likely to die from apparent starvation, suggesting snow interception and thermal cover may be important (Mumma and Gillingham 2019). Avoidance of new cutblocks in Big Creek in all seasons could be partially due to reduced browse opportunities on dry sites with longer regeneration times, or to higher thermoregulation costs (Scheideman 2018). The importance of water features and coniferous stands to Bonaparte moose in summer could also reflect behavioural responses to thermal stress (Francis 2020). Moose using wetted areas and new cutblocks more during twilight than mid-day may also suggest thermoregulatory behaviour (Scheideman 2018), although balanced against reduced energy intake (Renecker and Hudson 1986, Murray et al. 2006, Kuzyk et al. 2016).

The effect of higher temperatures on moose populations was not initially an objective of this project, and there are no control study areas where moose did not decline to assist with assessing the influence of climate. Thermal stress has been implicated in poor moose population performance elsewhere in North America in recent years (Lenarz et al. 2009, Lenarz et al. 2010). However, in BC, moose have generally not declined in the warmest climates in the province (e.g., Okanagan; Kuzyk et al. 2018b) and many of these moose populations experience higher temperatures in all seasons and are characterized by habitat experiencing similar levels of landscape change arising from mountain pine beetle timber salvage, consistently high calf recruitment, and stable to increasing moose densities during the same time frame declining moose populations were observed in research study areas. One of these areas is the Pennask Plateau and body fat measurements on adult female moose collected there during winter 2021/22 indicated they were in similar body condition as measured in PGS and Bonaparte. These observations suggest that thermal stress and temperature alone are unlikely to have caused population decline (especially given that 2021/22 coincided with record high summer temperatures), but it may act as a contributing factor. Notably, predator communities differ among many survey areas in southern BC and the study sites discussed here. Additional work on cortisol and thyroid metabolites is underway to examine the differential impact of forage limitation and thermal stress on body condition (UNBC – Carl Jefferies).

Glyphosate

Glyphosate has been used as a silvicultural practice to reduce competition between coniferous crop trees and deciduous species and would also be expected to impact forage quality and quantity. The effects of herbicide application on moose habitat use and browse have been mixed (Cumming 1989, Kennedy and Jordan 1985, Hjeljord 1994, Santillo 1994, Raymond et al. 1996), so additional work has been undertaken to better understand the impact of herbicide on moose in our study areas.

Glyphosate has been demonstrated to persist longer than previously known in northern environments (Botten et al. 2021). Plants sprayed in late summer that survive to the following year had higher levels of digestible protein than in unsprayed blocks (Werner et al. 2022). This may be problematic because the higher quality forage may attract moose and expose them to higher levels of chronic glyphosate exposure, the effects of which are unknown. It is also not a long-term increase in forage quality, because protein levels and digestible energy decline after several years (Milner et al. 2013, Werner et al. 2022).

The direct effects of glyphosate on moose were not considered in this study, and the effects of low-level chronic exposure on wildlife are unknown. Herbicide application was not a significant predictor of adult female moose survival (Mumma and Gillingham 2019). Regardless of any effect on moose health, the demonstrated effect of glyphosate on moose browse species make widespread herbicide application contrary to moose enhancement objectives.

Predation hypothesis

Prime adult moose are large, aggressive, and less vulnerable to predators than calves and animals in poor condition. Predation was the dominant mortality factor observed in this research for both adult females and calves older than 8 months. Predation could alter population trajectories by either influencing the adult female survival rate or calf recruitment or both, and landscape features that provide greater movement of predators or that enhance detectability or vulnerability of prey could result in a shift in predator-prey dynamics. Changing predation dynamics were considered a potential driver of population change, so additional work on wolf predation was undertaken in PGS and JPRF (Anderson in prep). Cougar and bear predation was assessed through the mortality site investigations in all study areas, but camera trapping work currently underway may further inform predation risk from these species (UVic – Nicole Boucher).

Moose that used areas of low road density over the previous year were more likely to die from wolf predation (Mumma and Gillingham 2019), despite wolves using roads to facilitate movement and killing moose closer to roads than expected at random (Boucher et al. 2022). Wolf responses to roads and road density vary (Kittle et al. 2017, Newton et al. 2017, Muhley et al. 2019), and wolves in PGS selected roads but did not select areas of high road densities (Boucher et al. 2022). Wolves selected new cutblocks and wolf-killed moose were associated with new and regenerating cutblocks (Boucher et al. 2022). The combination of moose survival and selection patterns, wolf selection and movement patterns, and characteristics of wolf kill sites suggest that moose and wolves use salvage logging features differently and where roads and new cutblocks are extensive, wolf selection patterns may be favored. As cutblocks regenerate, or in areas with extensive deciduous stands, moose selection patterns may be favored.

Trade-offs between forage acquisition and avoidance of predation risk are often presented as a dichotomy, but moose and wolf selection patterns in PGS suggest that some habitat types can provide both forage resources and lower predation risk. Moose selected deciduous stands in all seasons in PGS, Big Creek, and Entiako (Scheideman 2018) and these were also often selected in Bonaparte (Francis 2020). Deciduous stands are associated with year-round forage and, based on wolf habitat selection and moose kill site locations in PGS, less exposure to wolf predation risk (Boucher et al. 2022).

Population reconstruction modelling for PGS hypothesized that moose populations could be maintained at a different, lower state due to predation, in which case substantial intervention would be required to shift the population to an alternate steady state of higher moose density (Werner 2020). Given the uncertainty in model parameters for the population reconstruction and lack of reliable historic data for assessing predation (Mowat et al. 2022), it would be difficult to evaluate the presence of multiple predator-maintained population states for moose in our study areas, most of which have less intensive monitoring data than PGS.

Wolves were observed to be a major proximate cause of death for cow moose in all study areas, making up 48% of cow mortalities to April 30, 2022 (Anderson et al in prep). Where calves were monitored from 8 months of age in PGS and Bonaparte, wolf predation was the proximate cause of death for 62% of calf mortalities (Anderson et al in prep). Adult female survival was generally high, but wolf predation is the major component of mortality for cows that do die, and an important factor driving calf recruitment to one year of age. This could be due to a numerical response (i.e. higher wolf density) and/or a functional response of wolves to a highly modified landscape. Further work in this regard should be focused on understanding the extent to which the predation observed on moose in this research is considered an additive mortality factor. If predation was focused on individuals that had a low probability of otherwise surviving, there may be other dominant factors ultimately responsible.

Conclusions

Landscape features associated with the MPB epidemic and subsequent salvage logging drive adult female moose habitat selection at multiple scales, but the population-level effect on adult female survival was not apparent among study areas. This could be because landscape change drives the population through lower or more variable calf recruitment, or because adult female survival monitored during this study is not reflective of survival rates during the population decline, or because the decline was due to a combination of adult female survival and calf recruitment.

Work to date has allowed us to reject some of our hypotheses for the primary mechanisms driving moose population change. Hunting does not appear to have driven the decline, nor were any infectious or non-infectious diseases examined in this assessment considered to be major contributors to population dynamics. Although temperatures frequently exceed seasonal thermoneutral thresholds for moose in the central interior, differing population trends and recruitment rates in the southern interior where temperatures are even higher suggest that thermal stress alone is not driving population decline. There has been some support for the role of nutrition and predation in moose declines in BC's central interior. Trade-offs between energy acquisition and risk avoidance mean it will likely be difficult to fully separate the importance of either factor. On-going work is focussed on further refining support for these remaining hypotheses to better understand the mechanisms of moose population change, understanding that they may not be mutually exclusive.

- Hunting hypothesis (high adult female hunting mortality or low bull ratios) – rejected
- Landscape change hypothesis (adult female mortality related to amount of disturbance in study areas) – rejected, with caveat that adult female survival does not appear to have been the primary driver of population change; work on-going assessing landscape change and calf mortality relationships
- Nutrition hypothesis (low body fat corresponding to low calf recruitment, covariates suggest forage limitation) – work on-going
- Health hypothesis (other than apparent starvation) – likely rejected, some work on-going
- Predation hypothesis (high adult female/calf predation mortality) – likely contributed to population declines, some work on-going

Management Recommendations

Management recommendations reported here assume that the objective is to maintain or increase moose populations. Broader discussions about species and ecosystem objectives will dictate whether the desired outcome is more moose on the landscape in a given area. For example, Entiako overlaps the Tweedsmuir caribou herd, where lower moose densities should be maintained to meet caribou recovery objectives.

While the recommendations below may seem counter to our rejection of the landscape change hypothesis at the broadest scale examined (among study areas) for the dependent variable chosen (adult female survival), we also recognize that other population parameters like calf survival are likely impacted by habitat changes, and that individual and population responses are often scale-specific. Many of these recommendations were developed at the scale of the study area, home range, or within home range, that may be more relevant to local moose populations and operations on the land base. Examining calf recruitment instead of or alongside adult female survival will also provide a more complete view of the landscape change hypothesis. Additional recommendations can be expected from the work currently underway.

1. Maintain or increase landscape heterogeneity

Home range selection is expected to address limiting factors that influence animal fitness, and as such, habitat and home range selection Moose select home ranges with a diversity of forest types and are often associated with mature timber edges within their home ranges. Home range size provides some guidance as to the scale at which heterogeneity needs to be maintained. Home range sizes vary, around 20-70 km^2 with most restricted movement in late winter when home ranges can be 10-20 km^2.

Heterogeneity in the case of interior BC would be increased by maintaining mature timber on the landscape and managing reforestation to include a variety of species, especially deciduous. This could include harvesting smaller clearings, maintaining greater proportions of intact forest between cuts, and maintaining leave patches in cutblocks. Landscapes with the highest road densities and proportions of new cuts were avoided. Wolf kill sites of moose were associated with new cutblocks, which tend to be large and provide good sightlines and movement for a primarily visual hunter. New cutblocks (0-8 yrs old) were also mostly avoided by moose in most seasons and study areas. New blocks adjacent to existing blocks should be harvested once the existing blocks have regenerated to provide cover (5 m height recommended).

Moose tend to be associated with edges of mature forest and minimizing large open areas would provide more effective moose habitat. Dash distances for moose are generally considered 200-400 m, so blocks should be designed with irregular boundaries to minimize areas >400 m from forest edge or large leave patch. Thermal/snow interception cover is important (mature timber cover – stand age >60 yrs and canopy closure >40-65%) and security cover (>5m vegetation height) and needs to be dispersed across the landscape at the scale of a moose home range. Leave patches need to be large enough to provide interior forest conditions (>3-5ha).

2. Maintain connectivity

It is important to consider that a proportion of moose in a given population may be migratory with distinct seasonal ranges (5-60 km apart based on JPRF moose, Chisholm et al. 2021). This requires consideration of habitat needs both within home ranges and across the landscape. Connectivity of habitat between seasonal ranges and habitat patches used by moose has been identified as important, especially for migratory moose populations. Maintaining connectivity would mean maintaining areas without roads and large cutblocks, which were avoided by moose and associated with kill sites of moose by wolves.

Connectivity is not currently well-defined in the context of moose movement in a highly modified landscape. Areas of horizontal cover between important habitat features like wetlands and thermal cover may be achievable on a small (within seasonal home range) scale, but corridors between seasonal home ranges should also be considered. Corridors should provide sufficient lateral cover (5 m height and 100 m wide) between important habitat features.

3. Maintain deciduous stands on the landscape

Moose selected deciduous stands in all seasons, which provide year-round forage and less exposure to wolf predation based on both wolf habitat selection and lower probability of wolf-killed moose in these stands. Deciduous stands therefore provide both forage and refuge for moose, and maintaining or enhancing deciduous-leading stands would be expected to increase moose habitat suitability.

Deciduous stands were consistently selected by moose in all seasons and across study areas and deciduous trees and shrubs make up an important component of moose forage. Areas of intermediate regrowth (which provide more forage) were generally selected, and the strength of selection depended on specific site characteristics. Herbicide application should not be used, to allow browse species to be retained. Important browse species for moose on the central interior plateau include saskatoon, red osier dogwood, willow species, subalpine fir, trembling aspen, beaked hazelnut, paper birch, and cottonwood/poplar.

Trade-offs between risk and forage availability were apparent, especially where the impacts of salvage logging were most pronounced. Maintaining or enhancing browse and restocking deciduous species in areas of lower predation risk (near forest edges, away from roads) and on less productive sites is likely to have the greatest benefits for moose without exposing them to added mortality risk. Depending on site characteristics and browse species present, light scarification, burning, or crushing vegetation with machinery may encourage proliferation of moose browse.

4. Consider site attributes in determining cutblock value to moose

Not all cutblocks are used by moose in the same way. In drier locations, pine cutblocks were avoided, and similarly, spruce cutblocks were selected compared to Douglas fir cutblocks. This is likely partly due to the forage species present in the different site series and the different regeneration times. Moose selected for regenerating cutblocks (9-24 yrs old) but did so more in areas with higher regrowth. Recent cutblocks (0-8 yrs after cut) are generally avoided, although in some study areas and seasons there can be selection for very recent blocks. Older cuts (25-40 yrs) are generally avoided. Maintaining a diversity of cutblock ages at the scale of a moose home range would allow the staggered entry of cutblocks into the age bracket preferred by moose.

5. Maintain dead standing pine on the landscape

Moose used home ranges with high proportions of uncut pine and used areas within their home ranges that were dominated by pine. These stand types were common on the landscape. Although dead standing pine does not provide cover for snow interception, these sites still contain high levels of stocking, add vertical and horizontal structure, and provide a diversity of understory browse species. Dead standing pine should also be retained on a home range scale (20-70 km^2).

Effectively reduce road functionality

Distance to road was an important factor in moose mortality risk. Moose were more likely to be killed by hunters if they were near roads on a given day or in new cutblocks (often associated with roads and long sightlines) the previous week, and in areas of higher road density. Moose selected areas away from roads within their home ranges. While both forage availability and mortality risk best predicted habitat selection in all seasons, risk (defined as distance to linear features) best predicted moose selection during calving and fall. Moose using areas of higher road density over the previous year and areas with higher proportions of new (0-8 yr old) cutblocks over the previous 180 days were more likely to die of apparent starvation.

There is an interesting interaction between road density over the landscape and wolf predation risk. Areas of higher road density were not associated with higher risk of moose being killed by wolves. This is despite wolves using roads as travel corridors. Other factors, like increased human harvest of wolves or lower local wolf density, may explain this seemingly contradictory result. In areas of higher road density, wolves may also be less likely to use any road, resulting in lower predation risk for moose near a particular road compared to areas with few roads that are reliably frequented by wolves. Roads should be located away from key habitat elements (wetlands, security cover, forest edge) or preferentially deactivated and rehabilitated when 200-400 m from those habitat features.

Impacts of hunting can be mitigated with access management, avoidance of loop roads, and deactivation. Only physical access management (gates, barricades, deactivation) can be expected to reliably affect hunter access; access regulations do not apply to all hunters and suffer high rates of non-compliance.

Recontouring and replanting are necessary to address the greater movement rates of predators that may be influencing moose populations. Full rehabilitation of roads is difficult and expensive, and many roads cannot be rehabilitated because access needs to be maintained for infrastructure, public safety, wildfire control, or because of ongoing work. Similarly, the investment in road rehabilitation is difficult to secure because roads are re-opened when they provide access for new projects or when the public, used to the access they previously enjoyed, maintain their functionality. However, in-block roads should be deactivated immediately after harvesting, including by moving debris onto the road to reduce functionality, and other roads should be deactivated following silviculture obligations.

Maintain licensed hunting opportunity

Results of work to date suggest that current harvest levels (licensed hunting, legal First Nations harvest, and illegal poaching) did not drive moose declines in the study areas. Changing current hunting regulations to be more restrictive is therefore unlikely to address concerns over moose abundance. In fact, the data provided by this project suggests that moose populations could sustain higher harvest levels and harvest on other sex/age classes, i.e. limited cow and calf harvest as well as bull harvest. Whether this is socially palatable enough to be an effective management tool or provide the conditions for any harvest-related experiments is uncertain, but higher harvests could be supported from the standpoint of biological sustainability.

Even without any changes to regulations or harvest, monitoring moose harvest and populations continues to be important to ensure that human harvest of moose remains sustainable. There is often little information on First Nations harvest and traditional moose management varies by community, including when most moose should be harvested, how many, and what sex and age classes should be taken or avoided. Working with Nations to better understand traditional management strategies and their application would provide a more complete understanding of different moose harvest patterns on the landscape.

Recommendations for Next Steps

Any additional work should follow the approach of the project so far, that is, with a focus on addressing critical knowledge gaps to inform management of moose and moose habitat, specifically providing direction to apply management levers that are within scope for resource managers (Table 4). Immediate next steps are the completion of currently ongoing work, which may identify knowledge gaps not addressed here and prioritize research for the next phase of the project. A persistent challenge in wildlife ecology and management is making clear linkages between results at different scales, from within-individual (physiological responses, health) to individual (behaviour, selection) to population (growth rate, abundance), and it would be well worth integrating the results that this project has provided at these various scales once on-going work has been completed.

Table 4. Overview of management levers available to resource managers to address moose population and habitat objectives, modified from Kuzyk et al. (2019).

Management Lever	Legal Authority to use Management Lever	Research Approach that Informs Lever
Hunting Regulations	Authorized through *Wildlife Act*, supported by regulations and policy	Adult female survival True calf recruitment rates Calf survival and maternal body condition Nutrition and health
First Nations Harvest	In the absence of a clear conservation concern, First Nations harvest will most likely be managed through agreements with First Nation governance bodies. Harvesting contrary to agreements may be enforced through the *Wildlife Act*. Increased participation of First Nation in wildlife management (not just First Nations harvest) is expected.	Adult female survival True calf recruitment rates Calf survival and landscape change Calf survival and maternal body condition
Predator Management	Hunting and trapping of predators is authorized through *Wildlife Act*, although predator control to enhance ungulate hunting opportunities is not supported by current policy ("Control of Species Policy")	Adult female survival Calf survival and landscape change Calf survival and maternal body condition Wolf predation
Access Management	Access restrictions authorized through *Wildlife Act* supported by regulations and policy, also general recreation closures through the *Forest and Range Practices Act*. This will likely require working with other Ministries (Transportation and Infrastructure; Energy, Mines and Low Carbon Initiatives; Environment and Climate Change)	Adult female survival Calf survival and landscape change Calf survival and maternal body condition Wolf predation
Habitat Enhancement and Protection	Numerous Acts involved with limited authority under *Wildlife Act*	Adult female survival Calf survival and landscape change Calf survival and maternal body condition Nutrition and health
Environmental Assessment and Mitigation	Provincial government staff review land-use applications and can influence mitigation measures to benefit moose (e.g., moose habitat supply through Timber Supply Reviews)	Adult female survival True calf recruitment rates

1. Continue to monitor cow survival

While adult female survival was not identified as the sole driver of population change, in some years and study areas it likely interacted with low calf recruitment to maintain low moose densities. Patterns in survival and mortality as population dynamics shift may allow us to determine whether adult female survival rates measured during this study could be applied at different phases of decline or increase. As large areas of the landscape shift from the age classes unfavorable to moose to stands that moose select, we expect to see increases in survival and recruitment, because moose should select habitats that maximize their lifetime fitness. As these stands transition out of selected age classes, moose densities will likely continue to change in response to changing habitat. Monitoring adult female survival during the increase in populations that appears to be occurring in some study areas over the last couple years may provide expected survival rates associated with the growth phase and provide context for what has been monitored for the lower population densities to date.

Changes in cow survival could be expected in response to other management changes in the study areas as well – any change to hunting regulations or access, wolf control for caribou recovery, and following extensive wildfires. Changes in cause-specific mortality with changing population trajectory are also important indicators of limiting factors.

- Maintain sample size of 30 collared cows per study area to track annual survival and cause-specific mortality in the 5 study areas

2. Continue to evaluate calf recruitment

If calf recruitment is a primary driver of population change in the study areas, which seems to be supported by project results so far, maintaining collars on cows in the study area would allow us to continue to track parturition, neonate survival, twinning rates, and late winter recruitment. Changes in recruitment patterns may be particularly informative as populations begin to increase, and in Entiako, where wolf removals change the predator-prey dynamic. More frequent calf-at-heel surveys (June, mid-winter, late winter) would also allow us to assess variation in calf survival seasonally. Critically, the work on calf survival that is currently underway has not been completed and is expected to provide further clarity on the most effective strategy for population monitoring moving forward.

- Conduct annual movement analysis to determine parturition rates for collared cows
- Conduct calf-at-heel surveys in June to assess neonate survival and in late winter to assess recruitment (which can be adjusted to true recruitment with calf survival data collected 2016-2021)
- Assess impact of maternal condition and habitat selection on neonate survival and calf recruitment to 1 year of age (UVic; manuscripts anticipated spring 2024).

3. Maintain monitoring of population trends as pine salvage blocks recruit into selected age classes

Much of the landscape in the study areas was harvested 10-20 years ago and is now being recruited into the age class that moose are more likely to select or less likely to avoid, based age class selection determined for these stands determined by this project. In some study areas (PGS, JPRF, Bonaparte), we are starting to see increasing moose populations again. Monitoring moose populations through abundance estimates and composition surveys, conducted by regional staff independent of this project, is expected to continue, but linking population status and trend with the legacy of salvage logging will provide a better understanding of how habitat and moose populations change.

- Coordinate with regional staff conducting abundance and composition surveys to link landscape attributes, calf recruitment, adult female survival, and population trajectory

4. Assess vital rates through population modelling

Vital rates are measures of life stages within a population (pregnancy, parturition, recruitment, survival), and the project has accumulated an impressive dataset of vital rates for moose in interior BC. Given that most vital rates in most years are generally in the normal range for stable moose populations, it is likely that moose population declines resulted from interactions among vital rates, which vary substantially among study areas and years. A matrix model incorporating sensitivity and elasticity analyses, or similar approach, may allow for a more in-depth examination of the influence of multiple vital rates. We recommend more in-depth analyses in this regard once data collection ends for some aspects of this research; vital rates associated with known population increase will also likely be informative. Understanding which vital rates are contributing, and how they combine to affect observed moose population declines, is important for informing management.

- Use a matrix model or similar approach to ascertain influence of different vital rates on population trajectory
- Incorporate vital rate data in integrated population modelling approaches to predict population responses to perturbations and inform population monitoring provincially
- Incorporate results of (currently on-going) nutrition, health, and predation work combined with climate variables in model development to determine how these factors may interact to drive moose population trajectories

5. Additional investigation of nutrition

Work to date on forage quality and quantity has focused on nutritional composition of forage species in cutblocks and persistence of herbicide in moose forage, which are important parameters but need to be linked to moose survival and recruitment. Analysis of changes in moose diets in highly and moderately disturbed landscapes provides additional context.

- Assess linkages between habitat use, nutritional stress, body condition, and survival and recruitment (UNBC; manuscript anticipated fall 2023)
- Forage availability may also be a driver of migratory strategies (UNBC; manuscript expected spring 2024)

6. Additional investigation of climate impacts

Work to date on thermal stress has been tangential to population impacts, providing excellent data on the physical properties of cutblocks and forested areas but without the next required linkage to moose physiology. The persistence of stable moose populations with high calf recruitment in areas of high disturbance and consistently higher temperatures suggests that thermal stress is not the primary driver of decline in our study areas. However, climate change is expected to increasingly act on wildlife populations and ecological communities, and a better understanding of how climate variables may drive those shifts will be key to long-term planning in wildlife and habitat management.

- Assess linkages between habitat use, thermal stress, body condition, and survival and recruitment (UNBC; manuscript anticipated spring 2024).
- Determine conditions under which moose populations remain stable even at high temperatures, including an understanding of predator communities in these areas

7. Implications of health monitoring

The sampling conducted to date has provided a critical dataset for evaluating moose herd health in interior BC. Interpretation and application of this information is still lacking, and wildlife veterinarians are currently working on summarizing implications for moose populations where health monitoring has been conducted. In addition to the impact of climate variables directly on moose, winter ticks are highly susceptible to changes in temperature, humidity, and snow cover. Winter ticks have been responsible for moose declines elsewhere in North America, and other pathogens implicated in moose declines are not present in our study areas but changing parasite distributions are expected. The Wildlife Health Team coordinates many harvest monitoring and sampling programs, including the samples from this project.

- Determine implications of observed health parameters for moose populations (manuscript expected spring 2024)

- Determine limiting factors for winter tick populations and the impact on moose in interior BC (UNBC; manuscripts expected fall 2024)
- Coordinate with Wildlife Health Team on monitoring pathogen distribution (UNBC; manuscripts expected fall 2024)
- Additional health assessments should be expected given the rapid range expansions, accelerated life cycles, and host-switching observed in many pathogens under changing environmental conditions
- Evaluate the impact of chronic glyphosate exposure

8. Effect of wolf predation on moose populations

Wolf control has been undertaken in the Entiako study area as a recovery action for the Tweedsmuir caribou herd. This provides an opportunity to examine moose behaviour and demographics when predation risk is largely reduced, which could further refine our understanding of trade-offs between predation risk and forage limitation. It would also provide an opportunity to assess shifts in predation patterns, for example, whether bear predation increases in absence of wolves. Close working relationships already exist between Ministry of Forests staff involved in moose research and Caribou Program staff (Ministry of Land, Water and Resource Stewardship), and these should be further developed and strengthened.

Given that we are not able to back-cast precise wolf densities from available data (harvest, ungulate biomass), questions related to moose population performance under different predation scenarios may need to be addressed across different areas of wolf density, not over a timescale for which wolf densities may or may not have changed. While wolf control for non-species-at-risk is not currently supported by government policy, there may be situations where stakeholders and First Nations want to see it implemented. A better understanding of predation dynamics would be important for decision makers considering wolf control.

- Develop a wolf predation risk layer for moose
- Determine how wolf predation affects moose migratory behaviour (UNBC; manuscript expected fall 2023)
- Coordinate with Caribou Program where moose data may inform caribou objectives as well
- Assess the impact of wolf removal on moose populations (adult female survival, calf recruitment, abundance, cause-specific mortality)

9. Develop and assess habitat enhancement trials

Habitat quality is a critical consideration for moose populations and any long-term moose enhancement actions needs to account for habitat. However, enhancement work is usually focused on relatively small areas, due to budgetary, logistical, or other constraints, and the realized impact on populations is difficult to measure and requires long timeframes to accurately assess.

Habitat enhancement work was proposed and undertaken in PGS, although the scale is unlikely to affect population abundance in the study area. A range of harvesting practices has been applied in JPRF and is also being assessed for relative use. Monitoring relative use of these enhancement sites will provide additional recommendations to improve moose habitat. The Interior Broadleaf Working Group is exploring approaches for maintaining deciduous stands on the landscape. Similar work could be considered for other study areas, particularly Big Creek where the drier environment and slower regeneration times may require a different approach to habitat enhancement. Lessons learned from the PGS work and on-going analysis in JPRF should be incorporated in plans for additional habitat enhancement work.

- Examine how moose use different silvicultural treatments (UNBC; manuscript expected fall 2023)
- Habitat enhancement in PGS is led by the ministry of Water, Land and Resource Stewardship (WLRS); maintain coordination to ensure evaluation of established habitat enhancement measures (WLRS lead) and develop enhancement in other areas

10. Response to wildfire

Several study areas have recently been impacted by large high-intensity wildfires. While there are similarities between forest harvesting and wildfire as disturbance types, there are also critical differences. The response of moose in these study areas to wildfire compared to salvage harvesting could provide insight on limiting factors. Furthermore, the ecological impacts of wildfires are increasingly relevant with climate change predictions for longer more intensive fire seasons. Existing wildfire impacts provide natural experiments that could be further investigated to determine moose response to another large-scale disturbance likely to increase in extent and impact.

- Examine moose body condition, survival, and recruitment as related to movement, selection, and use of areas affected by large wildfires

11. Refine survey methodology

Refining survey methodology is an operational deliverable that has not been a primary objective of moose research to date, but the current structure of the moose research project provides opportunities to explore improvements in survey methodology as a side project. The methods we use to estimate abundance and trend, although well-established, are generally expensive and often contentious when implicated in management decisions, so constant evaluation and improvements are undertaken as technology, analysis methods, and modelling approaches improve to better represent the systems we manage. The utility of remote camera grids, which are increasingly used for other research and monitoring objectives and could represent efficient multi-species monitoring tools, could be further investigated for moose population abundance and trend. Refining sightability correction factors (SCFs) was previously identified as an important objective for some study areas but has not been undertaken to date. If there is still a need for refined SCFs, resources should be earmarked to conduct the trials in conjunction with survey work. Priority should be to the study area(s) for which existing SCFs are demonstrably inadequate.

- Compare moose survey methodologies like SRBs and camera trapping to assess utility for monitoring moose populations (UNBC; manuscript expected fall 2023)

References

Alfaro, R.I., L. van Akker, and B. Hawkes. 2015. Characteristics of forest legacies following two mountain pine beetle outbreaks in British Columbia, Canada. Canadian Journal of Forest Research 45: 1387-1396.

Ballard, W. B., J. S. Whitman, D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs 114: 3–49.

Bangs, E. E., T. N. Bailey, and M. F. Portner. 1989. Survival rates of adult female Moose in the Kenai Peninsula, Alaska. Journal of Wildlife Management 53: 557–563.

Bender, L. C. 2006. Uses of herd composition and age ratios in ungulate management. Wildlife Society Bulletin 34: 1225–1230.

Bertram, M. R., and M. T. Vivion. 2002. Moose mortality in eastern interior Alaska. Journal of Wildlife Management 66: 747–756.

Bø, S., and O. Hjeljord. 1991. Do continental moose ranges improve during cloudy summers? Canadian Journal of Zoology, 69(7): 1875-1879.

Boertje, R., K. A. Kellie, C. Seaton, M. Keech, D. D. Young, B., Dale, and A. Aderman. 2007. Ranking Alaska moose nutrition: signals to begin liberal antlerless harvests. The Journal of Wildlife Management, 71(5): 1494-1506.

Botten, N., L. J. Wood, and J. R. Werner. 2021. Glyphosate remains in forest plant tissues for a decade or more. Forest Ecology and Management 493: 119259.

British Columbia Ministry of Forests, Lands and Natural Resource Operations (BC FLNRO). 2015. Provincial Framework for Moose Management in British Columbia. BC Ministry of Forests, Lands, and Natural Resource Operations, Victoria, BC.

Cadsand, B., D. C. Heard, J. Courtier, A. Batho, and G. Watts. 2012. Moose density and composition in the Southern Omineca Region, Winter 2011-2012. Ministry of Forests, Lands and Natural Resource Operations. 40 pp.

Chisholm, J. D., D. P. Hodder, S. M. Crowley, R. V. Rea, and S. Marshall. 2021. Seasonal movements of migratory and resident female moose (*Alces alces*) in north-central British Columbia, Canada. Mammal Research 66: 419-427.

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. McCorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. Briggs Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1 45.

Cook, R. C., J. Oyster, K. Mansfield, and R. B. Harris. 2021. Evidence of summer nutritional limitations in a northeastern Washington moose population. Alces 57: 23-46.

Cumming, H. G. 1989. First year effects on moose browse from two silvicultural applications of glyphosate in Ontario. Alces, 25:118 132.

Davis, L. 2012. Big Creek (MU 5-04) 2012 winter moose inventory. Prepared by Davis Environmental Ltd. for BC Ministry of Forests, Lands and Natural Resource Operations, Williams Lake, BC. 41 pp.

DeMars C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecology and Evolution 3(12): 4149–4160.

Dussault, C., J. Ouellet, R. Courtois, J. Huot, L. Breton, H. Jolicoeur, and D. Kelt. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Edwards, R. Y., and R. W. Ritcy. 1958. Reproduction in a moose population. Journal of Wildlife Management 22: 261-268.

Ferguson, S. H., A. R. Bisset, and F. Messier. 2000. The influences of density on growth and reproduction in moose *Alces alces*. Wildlife Biology 6(1): 31-39.

Francis, A. 2020. Evaluating habitat use of female moose in response to large scale salvage logging practices in British Columbia, Canada. MSc thesis. University of Victoria.

Francis, A. L., C. Procter, G. Kuzyk, and J. T. Fisher. 2020. Female Moose prioritize forage over mortality risk in harvested landscapes. Journal of Wildlife Management 85(1): 156–168.

Fryxell, J. M., J. Greever, and R. E. Sinclair. 1988. Why are migratory ungulates so abundant? The American Naturalist 131: 781–789.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13(2): 58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31: 367-393.

Gillingham, M. P., and K. L. Parker. 2008. The importance of individual variation in defining habitat selection by moose in northern British Columbia. Alces 44: 7-20.

Grimson, C. 2017. Big Creek (MU-504B) winter moose survey 2017. BC Ministry of Forests, Lands and Natural Resource Operations, Williams Lake, BC. 23 pp.

Hatter, I. W., and W. A. Bergerud. 1991. Moose recruitment, adult mortality and rate of change. Alces 27:65–73.

Hjeljord, O. 1994. Moose (*Alces alces*) and mountain hare (*Lepus timidus*) use of conifer plantations following glyphosate application. Norwegian Journal of Agricultural Science 8:181-188.

Janz, D. W. 2006. Mountain pine beetle epidemic – hunted and trapped species sensitivity analysis. B.C. Ministry of Environment, Environmental Stewardship, Prince George, BC.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Jonasson, S., J. P. Bryant, F. S. Chapin III, and M. Andersson. 1986. Plant phenols and nutrients in relation to variations in climate and rodent grazing. American Naturalist: 394-408.

Jones, H., P. J. Pekins, L. E. Kantar, M. O'Neil, and D. Ellingwood. 2017. Fecundity and summer calf survival of moose during 3 successive years of winter tick epizootics. Alces 53: 85–98.

Jones, H., P. Pekins, L. Kantar, I. Sidor, D. Ellingwood, A. Lichtenwalner, and M. O'Neal. 2019. Mortality assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermacenter albipictus*) epizootics in New Hampshire and Maine (USA). Canadian Journal of Zoology 97: 23-30.

Kennedy, E. R., and P. A. Jordan. 1985. Glyphosate and 2,4 D: the impact of two herbicides on moose browse in forest plantations. Alces 21:1 11.

Klaczek, M., S. Marshall, A. Batho, and M. Anderson. 2017. Density and Composition of Moose (*Alces alces*) within the Southern Omineca Region, central British Columbia. Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Prince George, BC. 39pp.

Kuzyk, G. W., I. Hatter, S. Marshall, C. Procter, B. Cadsand, D. Lirette, H. Schindler, M. Bridger, P. Stent, A. Walker, and M. Klaczek. 2018b. Moose population dynamics during 20 years of declining harvest in British Columbia. Alces 54:101-119.

Kuzyk, G., and D. Heard. 2014. Research design to determine factors affecting moose population change in British Columbia: testing the landscape change hypothesis. B.C. Minist. For., Lands and Nat. Resour. Operations. Victoria, BC. Wildl. Bull. No. B-126. 16pp.

Kuzyk, G., S. Marshall, M. Klaczek, and M. Gillingham. 2015. Determining factors affecting moose population change in British Columbia: testing the landscape change hypothesis. B.C. Minist. For., Lands and Nat. Resour. Operations. Victoria, BC. Wildl. Working Rep. No. WR-122. 9pp.

Kuzyk, G., S. Marshall, M. Klaczek, C. Procter, B. Cadsand, H. Schindler and M. Gillingham. 2016. Determining factors affecting moose population change in British Columbia: testing the landscape change hypothesis. 2016 Progress Report: February 2012 – 30 April 2016. B.C. Minist. For, Lands and Nat. Resour. Operations. Victoria, BC. Wildl. Working Rep. No. WR-123. 26pp.

Kuzyk, G., S. Marshall, C. Procter, B. Cadsand, H. Schindler, M. Klaczek, H. Schwantje, and M. Gillingham. 2017. Determining factors affecting moose population change in British Columbia: testing the landscape change hypothesis. 2017 Progress Report: February 2012–April 2017. B.C. Minist. For., Lands and Nat. Resour. Operations and Rural Dev. Victoria, BC. Wildl. Working Rep. No. WR-125. 34pp.

Kuzyk, G., S. Marshall, C. Procter, H. Schindler, H. Schwantje, M. Gillingham, D. Hodder, S. White, and M. Mumma. 2018a. Determining factors affecting moose population change in British Columbia: testing the landscape change hypothesis. 2018a Progress Report: February 2012–April 2018. B.C. Minist. For., Lands and Nat. Resour. Operations and Rural Dev. Victoria, BC. Wildl. Working Rep. No. WR-126. 64pp.

Kuzyk, G., C. Procter, S. Marshall, and D. Hodder. 2019. Factors Affecting Moose Population Declines in British Columbia: Updated Research Design. B.C. Min. For., Lands and Nat. Res. Operations and Rural Dev. Victoria, B.C. Wildl. Bull. No. B-128. 17pp.

Leblond, M., C. Dussault, and J. P. Ouellet. 2010. What drives fine-scale movements of large herbivores? A case study using moose. Ecography 33: 1102–1112.

Lemke, S. L. 2013. Thompson Region Moose Stratified Random Block Population Surveys in Management Units 3-30 (Zone B) & 3-29. Unpublished report to Ministry of Forests, Lands, and Natural Resource Operations, Kamloops, BC. 17pp.

Lenart, E. A., R. T. Bowyer, J. V. Hoef, and R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. Canadian Journal of Zoology 80(4): 664-678.

Lenarz, M. S., M. E. Nelson, M. W. Schrage and A. J. Edwards. 2009. Temperature mediated moose survival in northeastern Minnesota. Journal of Wildlife Management 73(4): 503-510.

Lenarz, M. S., J. Fieberg, M. W. Schrage, and A. J. Edwards. 2010. Living on the edge: viability of moose in northeastern Minnesota. Journal of Wildlife Management 74(5): 1013-1023.

Macbeth, B. 2017. British Columbia Moose Health Assessment Program Summary of Ongoing Work. Unpublished report to Government of British Columbia Provincial Moose Research Project Team, BC Ministry of Forests, Lands, Natural Resource Operations, and Rural Development, Victoria, BC. 78 pp.

McArt, S. H., D. E. Spalinger, W. B. Collins, E. R. Schoen, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology 90(5): 1400-1411.

McGraw, A. M., J. Terry, and R. Moen. 2014. Pre-parturition movement patterns and birth site characteristics of Moose in northeast Minnesota. Alces 50:93–103.

Milner, J. M., F. M. van Beest, and T. Storaas. 2013. Boom and bust of a moose population: a call for integrated forest management. European Journal of Forest Research 132: 959-967.

Mowat, G., L. Vander Vennen, M. Anderson, M. Bridger, S. White, S. Marshall, K. MacAulay, and S. O'Donovan. 2022. An evaluation of the accuracy of licensed wolf harvest data and the correlation with population trends in British Columbia. Province of BC Technical Report 137, Victoria, BC.

Mumma, M. A. and M. P. Gillingham. 2019. Determining factors that affect survival of moose in central British Columbia. Technical Report to the Habitat Conservation Trust Foundation.

Mumma, M. A. Gillingham, M. P. Marshall, S. Procter, C. Bevington, A. R. and M. Scheideman. 2021. Regional moose (*Alces alces*) responses to forestry cutblocks are driven by landscape-scale patterns of vegetation composition and regrowth. Forest Ecology and Management 481: 118763.

Obermoller, T. R. 2017. Using movement behavior of adult female Moose to estimate survival and cause-specific mortality of calves in a declining population. MSc thesis. University of Minnesota, Minneapolis, MN.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53: 7–15.

Poole, K. G., R. Serrouya, and K. Stuart-Smith. 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88: 139–150.

Procter, C. and F. Iredale. 2018. Moose population density and composition on the Bonaparte Plateau. BC Ministry of Forests, Lands, and Natural Resource Operations, Kamloops, BC. 15 pp.

Procter, C., M. Anderson, M. Scheideman, S. Marshall, H. Schindler, H. Schwantje, D. Hodder, and E. Blythe. 2020. Factors affecting moose population declines in British Columbia, 2020 Progress report: Feb 2012-May 2020. Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Victoria BC. Wildlife Working Report No. WR-128.

Raymond, K. S., F. A. Servello, B. Griffith, and W. E. Eschholz. 1996. Winter foraging ecology of moose on glyphosate treated clear-cuts in Maine. Journal of Wildlife Management 80: 753-763.

Ritchie, C. 2008. Management and challenges of the mountain pine beetle infestation in British Columbia. Alces 44: 127-135.

Sæther, B.E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology & Evolution 12(4): 143-149.

Santillo, D. J. 1994. Observations on moose, *Alces alces*, habitat and use on herbicide treat-ed clearcuts in Maine. Canadian Field Naturalist 108: 22-25.

Scheideman, M. C. 2018. Use and selection at two spatial scales by female moose (*Alces alces*) across central British Columbia following a mountain pine beetle outbreak. M.Sc. Thesis, University of Northern British Columbia, Prince George, BC.

Scheideman, M., and M. Anderson. 2020. Prince George West Moose Composition Survey, Winter 2019-20. Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Prince George, BC. 9 pp.

Schwartz, C. C., and K. J. Hundertmark. 1993. Reproduction in Alaskan Moose. Journal of Wildlife Management 57: 454-468.

Schwartz, C. C., and L. A. Renecker. 1997. Nutrition and energetics. In: Franzmann, A. W. and C. C. Schwartz, eds. Ecology and management of the North American moose. Smithsonian Institution, Washington. D.C. pp. 441–478.

Schwartz, C. C., K. J. Hundertmark, and E. F. Becker. 1994. Growth of moose calves conceived during first versus second estrous. Alces 30: 91-100.

Severud, W. J., G. D. Giudice, T. R. Obermoller, T. A. Enright, R. G. Wright, and J. D. Forester. 2015. Using GPS collars to determine parturition and cause-specific mortality of moose calves: GPS monitoring of female moose and calves. Wildlife Society Bulletin 39(3): 616–625.

Spalinger, D.E., W. B. Collins, T. A. Hanley, N. E. Cassara, and A. M. Carnahan. 2010. The impact of tannins on protein, dry matter, and energy digestion in moose (*Alces alces*). Canadian Journal of Zoology 88(10): 977-987.

Stahlberg, M. 2005. 2005- Big Creek (5-04) Winter Moose Inventory. Prepared by Intrepid Biological Contracting for BC Ministry of Water, Land, and Air Protection, Williams Lake, BC. 31 pp.

Street, G. M., J. Fieberg, A. R. Rodgers, M. Carstensen, R. Moen, S. A. Moore, S. K. Windels, and J. D. Forester. 2016. Habitat functional response mitigates reduced foraging opportunity: implications for animal fitness and space use. Landscape Ecology 31: 1939–1953.

Thacker, C., B. J. Macbeth, G. Kuzyk, S. Marshall C. Procter, and H. Schwantje 2019. British Columbia Provincial Moose research project health assessment summary 2013-2018. Prep. for B.C. Minist. For., Lands, Nat. Resour. Operations and Rural Dev. Victoria, BC. 83 pp.

Thiessen, C., D. Peard, and B. Jex. 2013. Entiako/North Tweedsmuir mid=winter moose density estimate: January 2013. BC Ministry of Forests, Lands, and Natural Resource Operations, Smithers, BC. 22 pp.

Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler, N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. The Journal of Wildlife Management 74(5): 974-986.

Van Beest, F. M., and J. M. Milner. 2013. Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. PLoS ONE 8(6): e65972. doi:10.1371/journal.pone.0065972

Werner, J. 2020. Moose population reconstruction for the PG West area: draft technical analysis. BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Prince George, BC. 23 pp.

Werner, J. 2022. Forest condition, thermal regimes, and the health of a temperature sensitive ungulate. Submitted to PeerJ.

Werner, J., and M. Anderson. 2017. An approach to investigate ‘apparent starvation’ in moose populations: a preliminary scoping. BC Ministry of Forests, Lands, and Natural Resource Operations, Prince George, BC. 19 pp.

Werner, J. R., L. J. Wood, N. Botten, and A. Fredeen. 2022. Potential lasting impacts of industrial herbicides on ungulate nutrition. Canadian Journal of Forest Research 52(7): 1098-1109.