

Understanding moose population declines in salvage-logged landscapes: Impacts of forest harvest on juvenile moose habitat use and survival, maternal strategies, and predator-prey interactions in interior British Columbia

By

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M.Sc., University of Alberta, 2018
B.Sc., University of Alberta, 2014

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We acknowledge and respect the ɫəkʷəŋən (Songhees and Esquimalt) Peoples on whose territory the university stands, and the ɫəkʷəŋən and W̱SÁNEĆ Peoples whose historical relationships with the land continue to this day.

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Abstract

Understanding how anthropogenic disturbances compound with natural stressors to influence wildlife during vulnerable life stages is critical for conserving biodiversity and informing management decisions. Juvenile ungulates, including moose (*Alces alces*) are often sensitive to disturbances that alter resource availability and predation risk, potentially leading to population declines. Across interior British Columbia, moose populations declined concurrently with extensive salvage logging following insect outbreaks – but the causes of these declines were poorly understood. In this dissertation, I sought to tease apart the mechanisms underlying moose population declines by examining how moose recruitment is shaped by habitat use, maternal habitat selection strategies, and predation in landscapes undergoing drastic changes from forest harvest, with a focus on vulnerable 7-8 month old calf moose. In Chapter 1, I investigated how the habitat selection and movement of wolf (*Canis lupus*), one of the main predators of moose in this system, is influenced by the cumulative effects of landscape change, and how forest harvest features are tied to wolf kill-sites of moose. The combined selection and movement responses by wolves to logging features, coupled with increased moose mortality sites associated with cutblocks, indicate that landscape change increases risk for moose. In Chapter 2, I explored how recruited (i.e., surviving from 7-8 months to 1 year old) and non-recruited juvenile moose move and select natural and anthropogenic features, and how this is influenced by maternal proximity. I found that while recruited juveniles avoided habitats with elevated predation risk and energetic costs, non-recruited juveniles lingered in these unsafe habitats, which likely reduced their survival. In Chapter 3, I assess seasonal habitat selection, maternal body condition, and previous recruitment success of adult female moose in relation to their success in recruiting older calves. Successful females exhibited riskier behavior, which likely offset nutritional deficits from previous recruitment successes and winter tick loads. In Chapter 4, I investigated how forest harvest features and silvicultural treatments shape predator and ungulate distributions, and their interactions, based on wildlife camera trap data. Predator and ungulate occurrences, and their spatial relationships, were linked to silvicultural treatments, not only patterns of forest harvest. In Chapter 5, I examine how use of forest harvest features influences juvenile moose survival, and whether this mortality risk was modified by body condition, long-term use, forage availability, weather, or predation risk from wolves and black bears (*Ursus americanus*). I demonstrated that

anthropogenic disturbances create risky landscapes for juveniles from predation and hunting, regardless of modifying factors, and in addition to natural stressors such as parasitism, reduce juvenile survival. Overall, I find that forest harvest increases juvenile mortality and contributes to moose population declines by altering wolf spatial distributions and hunting efficiency, increasing predation risk for juvenile moose lingering in high-risk cutblocks unlike their more experienced maternal females which benefit from using these habitats, reshaping predator and ungulate distributions and their interactions, and ultimately, creating risky landscapes that reduce juvenile survival.

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General Introduction

Globally, wildlife populations are declining at unprecedented rates, largely driven by anthropogenic disturbances such as resource extraction (1, 2). While landscapes naturally undergo changes, which many species are adapted to (3), human activities rapidly transform ecosystems across vast spatial scales, often greatly exceeding those impacts from natural disturbances (4). These drastic landscape changes expose species to intensified selective pressures, such as habitat fragmentation and loss, elevated predation risk, and reduced resource availability, which can lead to population declines and eventually, species extinctions (5-7). As human populations grow rapidly, undisturbed habitats have become practically non-existent due to resource extraction (e.g., forestry) and land conversion (8, 9). Consequently, alarming biodiversity declines have emerged worldwide, with extinction rates exceeding background rates, marking the aptly named Anthropocene extinction – the first mass extinction event driven by one species (10).

While biodiversity loss is wide in scope, certain taxa experience disproportionate adverse pressures from human disturbance, while some benefit, resulting in biotic communities with ‘few winners and many losers’ (11). Among those often negatively impacted are large-bodied herbivores, which require extensive habitats, exhibit low fecundity over relatively long lifespans, and are sensitive to disruptions of both the ‘bottom-up’ (e.g., resource availability) and/or ‘top-down’ (e.g., predation pressure) regulatory processes that influence their population dynamics (12-15). Many large herbivores (e.g., ungulates) are ecologically, economically, and/or culturally important species. Their population declines have broad-scale impacts that cascade through ecosystems (15), including disruption of valuable ecosystem services (e.g., nutrient cycling) (16), modified predator-prey dynamics and predator population declines due to prey depletion (17), and alteration of vegetation communities from reduced browsing (18). Declining herbivore populations also have socio-economic impacts, such as reduced subsistence hunting and loss of cultural practices (15, 19, 20). Thus, large herbivore population declines are concerning – even when their overall population numbers remain relatively high across their range, such as in the case with moose (*Alces alces*).

Although moose are not a threatened species, their populations are declining across many parts of their circumpolar temperate and boreal forest range, particularly along the southern edge but also in highly disturbed areas (20-25). Moose population declines are linked to a variety of potential causes, including but not limited to habitat changes (26), climate-induced stress (27), predation pressure (28), disease and parasitism (23, 29), and resource limitation (30). One such region experiencing significant declines – but with poorly understood mechanisms – is central British Columbia, where drastic moose population declines were identified between the early 2000s and 2010s (20, 31). Hunter harvest, which highly correlates with population estimates, declined by almost half from 1995 to 2014, despite sustained search efforts (31). While some wildlife management units (WMUs) had stable or increasing populations, 71% of examined WMUs exhibited decreasing moose populations from 2006 to 2015, with some regions reaching declines of 50-70% (20, 31). Mechanisms for these declines were unknown, although the suspected cause was landscape change from salvage logging following a widespread insect outbreak (32).

Starting in the late 1990s and early 2000s, a severe mountain pine beetle (*Dendroctonus ponderosae*) outbreak spread across much of interior British Columbia (33). Mountain pine beetle (MPB) colonize *Pinus* spp. host trees, which are predominantly mature lodgepole pine (*P. contorta*) in western Canada (34, 35). Female beetles tunnel galleries into the host tree to lay eggs, weakening trees by introducing blue stain fungi (Ophiostomatales species) and the larva later feeding upon the tree's phloem (34). MPB are native to western North America, with its population dynamics and range typically limited by availability of susceptible hosts and climate (33, 36). While small populations often will not kill trees, mass attacks by many beetles do – as in the case of the outbreak in BC. Following favourable weather and decreased wildfire activity (which would remove mature host trees), mountain pine beetle populations peaked in British Columbia, impacting about 731 million m³ of pine (33).

Following, the annual allowable cut was raised for salvage logging of beetle-impacted trees. Salvage logging is harvesting post-disturbance, with the intent to recover economic value from damaged timber but also to potentially reduce hazard from further disturbances, such as insect outbreak or wildfires (37). However, salvage logging operations in British Columbia can often bypass forest management plans set in place to promote sustainability of harvests. Salvage logging often exceeds standard cutblock size limitations (often 40 hectares) or disregards

adjacency/green-up constraints (wherein cutblocks must exceed a certain threshold of tree growth prior to harvesting adjacent blocks) (38). Additionally, while salvage logging is intended to recover damaged timber, often both live and dead trees are harvested and little retention within the cutblock is left standing (38). Thus, following the massive MPB outbreak, salvage logging transformed extensive areas of potentially suitable moose habitat into a patchwork of new cutblocks, generally clearcuts with little retention, linked by networks of resource roads – leaving little remaining mature forest interspersing these features.

These forest changes were hypothesized to negatively impact moose populations by increasing their vulnerability through multiple mechanisms: reduced hiding cover that enhances predator and hunter search efficiency, concentration of moose in remaining habitats, greater thermal stress, and increased energetic costs due to reduced snow interception (32). Through a multi-year project, the Government of BC began an investigation of these declines, with a focus on adult female moose survival due to the rapid nature of the population declines (32). However, monitoring of adult female moose indicated that while forest harvest impacted their habitat use and was often negatively linked to their survival (39-41), their survival rates were indicative of a stable population (26) – suggesting that juveniles may play a greater role in population declines than previously expected. Juvenile ungulates have highly variable survival rates and in cases where limiting factors intensify, such as in disturbed environments, recruitment can drive population changes (42, 43). Often, the main mortality source for juveniles is predation, and their survival is also dependent on maternal care (44-46). Thus, understanding how these forest harvest features impact the habitat selection, movement, and survival of juvenile moose and their maternal females, as well as their predators, is critical in understanding the mechanisms of these population declines.

In this dissertation, I investigate the mechanisms driving moose population declines with a focus on juveniles, given their importance in ungulate population dynamics (42), and their predators, which are a main mortality source for juvenile ungulates (43). To do so, I use a combination of collared older (7-8 months) calf moose and their maternal females, collared wolves (*Canis lupus*), and predator/ungulate data collected from wildlife camera trap arrays. My research focuses on two study areas, Prince George South and the Bonaparte Plateau, which are both representative of the declining moose population trend and are characterized by extensive salvage logging following the mountain pine beetle outbreak and extensive road networks.

In Chapter 1, I investigated how forest harvest impacts predation risk for moose by assessing the cumulative impacts of salvage logging and associated resource roads on GPS-collared wolf movement, habitat selection, and predation patterns. This chapter provides a foundation for understanding how one of the main predators of juvenile moose, wolf, is impacted by forest harvest, altering its spatial distribution and reshaping the predation risk that moose are exposed to across disturbed landscapes. In Chapters 2 and 3, I shift the focus back to moose. Chapter 2 explores how semi-independent moose calves navigate human-altered landscapes, in relation to their maternal female, and how these habitat use strategies differ between their survival outcomes. While habitat selection is expected to be ideal, improving an individual's fitness (47), this may not be the case for inexperienced juveniles – particularly in novel landscapes exposing them to both anthropogenic and natural pressures. While older calves are becoming independent, their survival and movement behaviors are still tied to their maternal female (48). Thus, in Chapter 3, I link maternal body condition, previous rearing success, and resource selection across multiple seasons – from the summer prior to parturition through to the calf's first winter – to the survival of older calves. This chapter highlights the importance of maternal investment and habitat use strategies in determining juvenile recruitment outcomes. Chapter 4 evaluates how silviculture (i.e., managing trees to meet resource objectives through treatments such as site preparation, reforestation, and stand tending) – which is fundamental for forestry but often overlooked in wildlife ecology studies – impacts predator-prey dynamics in multi-predator, multi-prey systems using wildlife camera traps. Here, I demonstrate the importance of considering silvicultural treatments, not only harvest successional stages, as playing a role in altering wildlife community interactions. Finally, Chapter 5 assesses how forest harvest, and its interactions with body condition, predation risk, and forage availability, impact juvenile mortality hazard. This chapter directly links juvenile survival to risk factors, to improve our understanding of juvenile mortality in relation to both natural and anthropogenic stressors. Together, these investigations offer insights into mechanisms driving moose population declines in forest harvested landscapes, with implications for resource management that can be implemented to support populations.

Chapter 1: Cumulative effects of widespread landscape change alter predator-prey dynamics

Boucher, N.P., Anderson, M., Ladle, A., Procter, C., Marshall, S., Kuzyk, G., Starzomski, B.M. and Fisher, J.T., 2022. Cumulative effects of widespread landscape change alter predator–prey dynamics. Scientific Reports, 12(1), p.11692.

1.1 Introduction

Anthropogenic landscape change modifies predator-prey dynamics, which has implications for both predator and prey populations (49, 50). Predators respond to prey through numerical responses (changes in predator density) and functional responses (changes in consumption rate), and mathematical models describing the functional response identify limits to the rate of prey consumption, prey encounter rate, and handling time (51, 52). Holling’s disc equation, which models the functional response, postulates that kill rate is limited by handling time at high prey densities, but by search efficiency at low prey densities (51, 52). Growing evidence indicates that anthropogenic landscape change influences predator search efficiency and thus, predator-prey encounter rate by facilitating predator movement and/or altering prey vulnerability (49, 53, 54). Unless prey alter their behavior to avoid predation (e.g. sheltering in human-created refugia (55)) or landscape change bolsters prey populations by increasing habitat quality (e.g., increasing available forage), anthropogenic landscape change could lead to declining prey populations due to increased predator foraging efficiency.

Predators exploit specific anthropogenic features to increase search efficiency, which intensifies predation risk for prey (7). Large carnivores often select and travel quickly on linear features, which improves foraging efficiency by increasing potential predator-prey encounters (49, 53, 56). Logging – which creates both roads and cutblocks – increases predator travel efficiency, reduces hiding cover, concentrates prey in remaining patches, and creates predictable, small areas for predators to search (57, 58). Additionally, prey species are attracted to polygonal features such as cutblocks, where early seral vegetation offers abundant forage (40, 59, 60). If predators hunt more efficiently due to linear features linking cutblocks (53, 61), these anthropogenic features could function cumulatively to increase predation risk for prey across disturbed landscapes.

Predation risk could be elevated if prey select for cutblocks (e.g. for increased forage) but logging features also increase predator search efficiency, possibly leading to an ecological trap (62-64). In areas with extensive logging, such as forests infested with outbreaks of bark beetles (Scolytinae) which are subsequently logged to salvage timber (36, 65), the opportunity for such scenarios to manifest may be intensified (62-64). Landscapes highly modified by salvage logging of beetle-killed forests are characterized by cutblocks that are significantly larger than conventional cutblocks, linked by extensive linear feature networks and interspersed with patches of forests relatively homogeneous in structure, age, and composition (66, 67). If functioning cumulatively to increase predation risk, salvage logging features could lead to prey population declines. This may be the case in the western sub-boreal, where extensive salvage logging of forest killed by mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreaks linked to climate change coincided with declines in moose (*Alces alces*) populations (20, 31, 36, 68).

One mechanism hypothesised for the moose population decline within interior BC could be increased movement rates of wolves (*Canis lupus*) – a primary predator of moose – and altered habitat selection, resulting in increased predation risk for moose near logging features (68). Evidence suggests that anthropogenic landscape change – particularly, linear feature networks – facilitates predation by wolves (49, 53, 69). Selection for linear features increases wolf movement efficiency, affecting predator-prey encounter rates and subsequent predation rates on ungulates (49, 53, 56, 70-73). Additionally, wolves select forest edges, cutblocks, and areas with new forage created by logging, due to increased availability of prey associated with these features (40, 61, 74, 75). We argue that anthropogenic features facilitating wolf travel and creating predictable prey locations is a concern for moose inhabiting areas undergoing extensive logging.

We examined whether the two dominant forms of anthropogenic landscape change associated with salvage logging – linear features and cutblocks – work to cumulatively influence wolf movement and habitat selection, and are tied to moose kill-site locations within our study area – interior British Columbia (BC), Canada. We ask: (i) do wolves select for salvage logging features; (ii) do salvage logging features facilitate wolf movement; and (iii) are salvage logging features linked to wolf kill-sites of moose? We hypothesized that the impacts of cutblocks and linear features function together to affect predator-prey dynamics. Specifically, we predict that

wolves will select for cutblocks and linear features and have increased movement rates associated with these disturbance features. We expect that cutblock age and size will influence wolf habitat selection, with increased selection for smaller, regenerating (9 – 24 years since harvest) cutblocks due to increased prey availability (40, 41, 76). Lastly, we expect these landscape features to facilitate wolf predation on moose, such that there is a positive relationship between salvage logging features and wolves' kill-sites of moose.

1.2 Methods

Study area

BC's Interior Plateau has experienced the cumulative effects of significant land conversion and habitat loss, with impacts to forests including a recent severe MPB outbreak (77-79). This outbreak began in the 1990s, killing over 53% of merchantable pine (723 million m³ of pine) (77, 78, 80). To mitigate economic effects, the Government of BC increased the annual allowable cut (timber amount sustainably harvested per year for a region) by approximately 30% from levels prior to the outbreak, resulting in extensive linear feature networks and the removal of large areas of beetle-killed trees (78).

Our study area, Prince George South (PGS), is located southwest of the city of Prince George, on BC's Interior Plateau (Fig. 1.1; Appendix 1). PGS is one of five study areas in a long-term provincial moose monitoring project, selected for additional research on predation dynamics due to its continued moose declines and the identified role of wolves as a leading cause of mortality for both adult females and 8-12 month old calves (68).

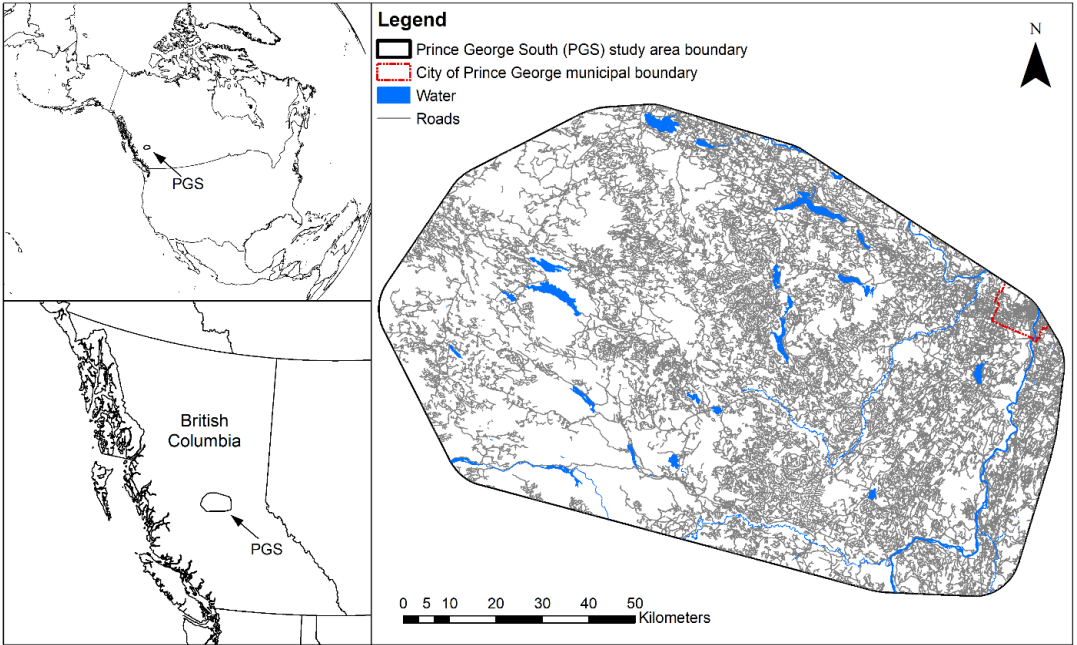


Figure 1.1 Map of the Prince George South study area where wolf habitat selection and movement research was conducted. The Prince George South (PGS) study area, located in interior British Columbia, Canada. PGS is heavily altered with linear features (in grey) and cleared forest. The municipal boundary for the city of Prince George is outlined in red. Waterbodies are shown in blue.

Integrated step selection analysis

Adult wolves were captured using standard protocols for aerial darting or net-gunning (December-March), or soft-catch, foot-hold trapping (June-July), 2018-2020 (Appendix 1). All wolf captures and protocols were completed following Canadian Council on Animal Care and Animal Research: Reporting In Vivo Experiments (ARRIVE) guidelines, as well as BC Ministry of Environment Standards for Live Animal Capture and Handling. Approval for experimental protocols and animal care guidelines was issued in accordance with the British Columbia Wildlife Act and BC Ministry of Forest, Lands and Natural Resource Operations Animal Care Ethics Committee (permit: PG17-272811).

Captured wolves were fitted with satellite GPS collars (Vectronic Aerospace, Berlin) with a 60-min fix rate and 2-year drop-off mechanisms. Wolf movement data was divided into ‘winter’ (October 1-March 31; snow present, no pups) and ‘summer’ (April 1-September 30; denning, rearing pups, ungulate calving, snow-free) periods. We were interested in wolf habitat selection and movement during all periods except those associated with denning and rendezvous sites, where we assumed there would be limited prey searching behaviors by wolves (81). We

removed wolf locations within 1 km of these sites (82), determined using GPS cluster analysis (83) and ground truthing. We removed GPS locations within the first 48-hours after capture to account for altered behavior following handling and only included wolves with >7 days of movement data.

Integrated step selection analyses (iSSA) compare used (1) to available (0) locations of steps (connection between successive relocations), integrating habitat selection and movement within a conditional logistic regression model framework (84). We used the R package ‘amt’ (Animal Movement Tools Version 0.0.6.) to generate ten random steps for every used wolf step (85, 86), drawn from population-level parametric distributions of step lengths (Euclidean distance between successive relocations) and turn angles (angle between consecutive relocations). Because we had a limited sample size of wolves and packs, we used individual wolves as the sampling unit and retained all individuals regardless of pack within the analysis. While this decision could lead to biased results due to pseudo-replication and territory restrictions, there is evidence suggesting that individual resource use varies between pack members (87).

We included the following habitat covariates: cutblock use (new cutblock [0-8 years since harvest], regenerating cutblock [9-24 years since harvest] or outside of cutblock [reference category] (41)) and size; distance to, and density of, linear features; distance to edge habitat; land cover type (deciduous-leading stands, coniferous-leading stands, mixed forest stands, pine-leading stands, and non-forest); plant productivity (normalized difference vegetation index, NDVI); and distance to the nearest waterbody (Appendix 1). All environmental covariates that were included as an interaction with $\ln(\text{Step length})$ were extracted from the start of the step, while all other covariates were extracted from the end of the step. Distance covariates were log-transformed to account for skewness.

We developed candidate models with each model representing a competing hypothesis (Table 1.1), and modeled iSSAs for each individual in each season separately (84, 88). As step length may vary with time of day, we created a harmonic interaction term, hereafter referred to as $\sin(\text{hour})$, to represent activity peaks at dawn and dusk, using the following formula:

$\sin\left(\frac{4*\pi*(\text{hour}-6)}{24}\right)$ (89, 90). All models included $\ln(\text{Step length})$ and an interaction between $\sin(\text{hour})$ and $\ln(\text{Step length})$ to control for varying movement rates at different times of day (Fig. A1.1).

Table 1.1 Candidate models for the integrated step selection analysis examining wolf (*Canis lupus*) movement and habitat selection in Prince George South, 2018-2020. $\ln()$ = log-transformed covariate. SL = step length. LF = linear feature. NC = new cut. RC = regenerating cut.

Model name	Covariates
Prey	$\ln(SL) + \ln(SL):\sin(\text{hour}) + \text{Pine} + \text{Deciduous} + \text{Mixed Forest} + \text{Coniferous} + \ln(\text{Distance to water}) + \text{NDVI} + \ln(\text{Edge in}) + \ln(\text{Edge out})$
LF network	$\ln(SL) + \ln(SL):\sin(\text{hour}) + \text{LF density} + \ln(\text{Distance to LF}) + \ln(SL):\ln(\text{Distance to LF}) + \ln(SL):\text{LF density}$
Cutblock	$\ln(SL) + \ln(SL):\sin(\text{hour}) + NC + RC + NC:\text{Cut size} + RC:\text{Cut size} + \ln(SL):NC + \ln(SL):RC + \ln(SL):NC:\text{Cut size} + \ln(SL):RC:\text{Cut size}$
Prey + LF network	$\ln(SL) + \ln(SL):\sin(\text{hour}) + \text{Pine} + \text{Deciduous} + \text{Mixed Forest} + \text{Coniferous} + \ln(\text{Distance to water}) + \text{NDVI} + \ln(\text{Edge in}) + \ln(\text{Edge out}) + \text{LF density} + \ln(\text{Distance to LF}) + \ln(SL):\ln(\text{Distance to LF}) + \ln(SL):\text{LF density}$
Prey + Cutblock	$\ln(SL) + \ln(SL):\sin(\text{hour}) + \text{Pine} + \text{Deciduous} + \text{Mixed Forest} + \text{Coniferous} + \ln(\text{Distance to water}) + \text{NDVI} + \ln(\text{Edge in}) + \ln(\text{Edge out}) + NC + RC + NC:\text{Cut size} + RC:\text{Cut size} + \ln(SL):NC + \ln(SL):RC + \ln(SL):NC:\text{Cut size} + \ln(SL):RC:\text{Cut size}$
LFN + Cutblock	$\ln(SL) + \ln(SL):\sin(\text{hour}) + \text{LF density} + \ln(\text{Distance to LF}) + \ln(SL):\ln(\text{Distance to LF}) + \ln(SL):\text{LF density} + NC + RC + NC:\text{Cut size} + RC:\text{Cut size} + \ln(SL):NC + \ln(SL):RC + \ln(SL):NC:\text{Cut size} + \ln(SL):RC:\text{Cut size}$
Global	$\ln(SL) + \ln(SL):\sin(\text{hour}) + \text{Pine} + \text{Deciduous} + \text{Mixed Forest} + \text{Coniferous} + \ln(\text{Distance to water}) + \text{NDVI} + \ln(\text{Edge in}) + \ln(\text{Edge out}) + \text{LF density} + \ln(\text{Distance to LF}) + \ln(SL):\ln(\text{Distance to LF}) + \ln(SL):\text{LF density} + NC + RC + NC:\text{Cut size} + RC:\text{Cut size} + \ln(SL):NC + \ln(SL):RC + \ln(SL):NC:\text{Cut size} + \ln(SL):RC:\text{Cut size}$

Akaike’s Information Criterion (AIC) was used to determine the best-supported model for each individual wolf in each season. Performance of models was assessed using cross-validation, with data subset by step ID. For model selection, we determined the best overall model for each season by assessing the distribution of AIC weights. Then, we used bootstrapping to estimate population β coefficients and associated confidence intervals from the best-supported model (88, 89, 91, 92). This two-stage approach of fitting separate individual models and then post-hoc estimating population averages via bootstrapping is commonly used for iSSAs when sample sizes for individual steps are sufficient (84). This approach allows for unbiased estimation of habitat selection variability and fewer assumptions than mixed-effects models (84, 88). For bootstrapping, we weighted samples by individual wolf i.d., which ensured equal probability of sampling for each individual wolf. From 2000 repetitions, we obtained the median and confidence interval for beta coefficient estimates (using 2.5th and 97.5th quantiles) which were used for population-level inferences. To quantify selection responses, we calculated relative

strength of selection which estimates probability of selecting one resource unit over another (93) (Appendix 1).

Moose kill-site analysis

Moose mortality sites were determined by ground-truthing potential kill-sites identified by cluster analysis of wolf GPS locations, using the Find Points Cluster Identification Program Version 2 (83) (Appendix 1). We used logistic regressions to compare habitat features at sites of successful wolf kills of moose to random sites selected within the study area. We used variance inflation factors (VIF) to check for multicollinearity and excluded variables with $VIF > 4$. We weighed evidence for competing hypotheses relating landscape features to sites where moose were killed by wolves, following a set of *a priori* candidate models similar to the iSSA set (Table A1.2), and selected the best supported model using AIC. For the top model, we used k-fold cross validation with $k = 10$ and Spearman’s rank correlation (r_s) to assess model fit (94).

1.3 Results

We deployed satellite GPS collars on ten wolves in five packs (Table A1.1) and collected hourly location data between February 24, 2018 and July 31, 2020. Wolf collars were staggered in deployment and end date, so data was not available from all individuals through the study duration (Table A1.1).

For both seasons, the ‘Global’ model outperformed the alternate models (Fig. 1.2, Table A1.3), indicating wolf movement and habitat selection is influenced by a combination of cutblocks, linear features and natural features. All remaining models received minimal support based on AIC weights.

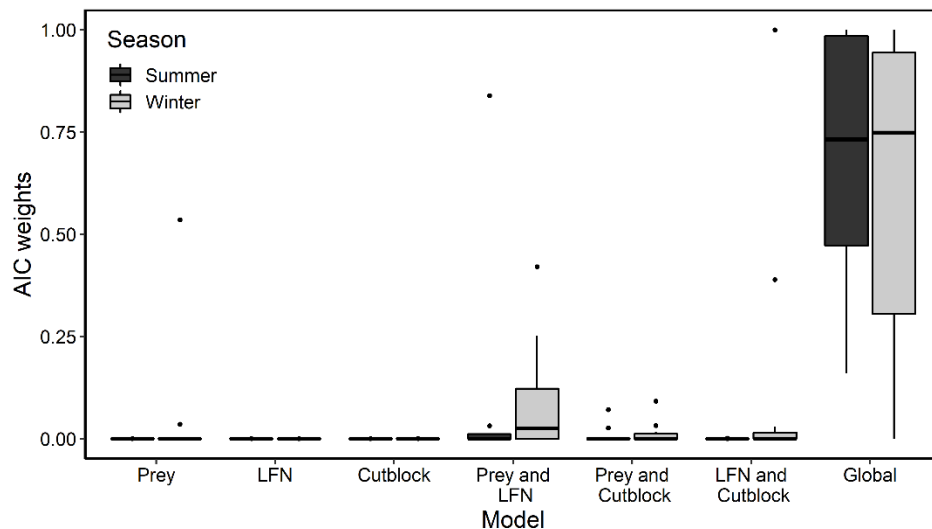


Figure 1.2 Model selection determining top seasonal integrated step selection models for wolves. Akaike's information criterion (AIC) weight distribution for summer (April 1–September 30) and winter (October 1–March 31) integrated step selection analysis candidate models for Prince George South, 2018-2020. Outliers are represented by points.

Wolf selection for salvage logging features

In both seasons, wolves selected habitat closer to linear features (Table 1.2, Fig. 1.3). There was no clear trend in selection of varying linear feature densities for both seasons (Table 1.2). Wolf selection of logged areas was dependent on cutblock size and age in summer, but only on cutblock age in winter (Table 1.2). In both seasons, wolves selected for new cutblocks. In summer, selection of new cutblocks decreased as cutblock size increased. There was no clear trend in wolf selection of regenerating cutblocks during both seasons.

In summer, coniferous-leading forests were selected, and in winter, wolves selected for areas with high NDVI values (Table 1.2). Edge habitats and areas closer to water were selected for in both seasons.

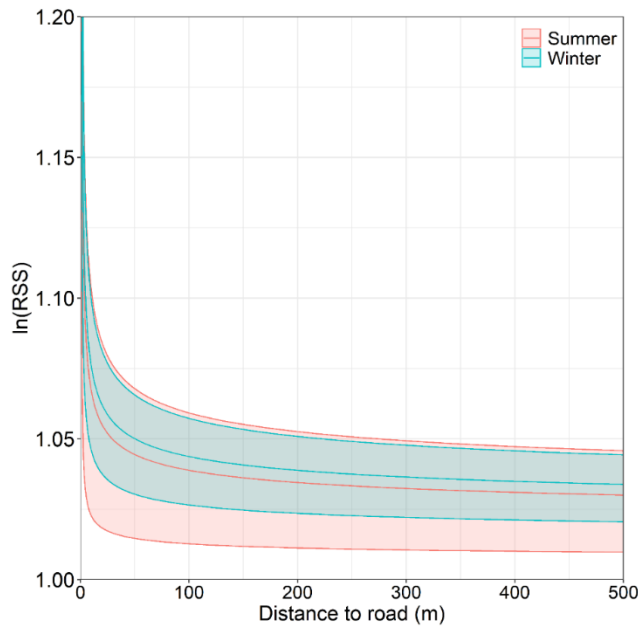


Figure 1.3 Wolf response strength to proximity to roads based on integrated step selection analyses. Seasonal wolf log-transformed relative selection strength (RSS) with 95% confidence intervals for distance to linear features (m) in summer (April 1–September 30) and winter (October 1–March 31) for Prince George South, 2018-2020.

Table 1.2 Seasonal habitat selection and movement beta coefficient estimates with lower and upper 95% confidence bounds for the global integrated step selection analysis model in summer (April 1 – September 30) and winter (October 1 – March 31) in Prince George South, 2018-2020. ‘:’ denotes an interaction between

covariates. *Bolded terms indicate significance (i.e. beta estimates do not overlap 0). ln() = log-transformed covariate. SL = step length. LF = linear feature.*

Season	Covariate	Lower	Median	Upper
Summer	Coniferous	0.074	0.152	0.255
	Deciduous	-0.059	0.145	0.297
	ln(Edge in)	-0.146	-0.127	-0.114
	ln(Edge out)	-0.152	-0.146	-0.125
	ln(LF distance)	-0.106	-0.08	-0.071
	ln(Water)	-0.081	-0.069	-0.021
	Mixed forest	-0.036	0.131	0.279
	NDVI	-0.233	1.217	1.475
	New cut	0.033	0.183	0.675
	New cut:Cut size	-0.288	-0.174	-0.052
	Pine	-0.042	0.081	0.486
	Regenerating cut	-0.334	-0.211	0.285
	Regenerating cut:Cut size	-0.226	-0.176	0.036
	LF density	-0.159	-0.086	0.034
	ln(SL)	0.325	0.381	0.435
	ln(SL):New cut	-0.109	-0.046	0.007
	ln(SL):New cut:Cut size	-0.008	0.054	0.216
	ln(SL):Regenerating cut	-0.063	-0.044	-0.004
	ln(SL):Regenerating cut:Cut size	-0.012	0.009	0.051
	ln(SL):LF density	-0.05	-0.033	-0.031
	ln(SL):ln(Distance to LF)	-0.062	-0.051	-0.049
	ln(SL):sin(hour)	-0.002	0.067	0.081
	Winter	Coniferous	-0.212	-0.14
Deciduous		-0.061	0.018	0.133
ln(Edge in)		-0.106	-0.064	-0.026
ln(Edge out)		-0.172	-0.074	-0.042
ln(LF distance)		-0.135	-0.122	-0.073
ln(Water)		-0.092	-0.057	-0.022
Mixed forest		-0.113	-0.089	0.061
NDVI		0.272	0.365	1.553
New cut		0.031	0.097	0.14
New cut:Cut size		-0.135	0.051	0.091
Pine		-0.285	-0.079	0.147
Regenerating cut		-0.131	-0.031	0.052
Regenerating cut:Cut size		-0.204	-0.08	0.042
LF density		-0.063	-0.027	0.009
ln(SL)		0.203	0.249	0.261
ln(SL):New cut		-0.113	-0.04	0.024
ln(SL):New cut:Cut size		-0.001	0.023	0.1
ln(SL):Regenerating cut		-0.037	-0.012	0.018
ln(SL):Regenerating cut:Cut size		-0.013	-0.01	-0.003
ln(SL):LF density		-0.031	-0.026	-0.022
ln(SL):ln(Distance to LF)		-0.041	-0.036	-0.028
ln(SL):sin(hour)		-0.024	0.019	0.046

Impact of salvage logging features on wolf movement

The impact of cutblocks on displacement rates varied between seasons (Table 1.2). In summer, wolf step lengths were shorter in regenerating cutblocks, but no trend existed in relation to new cutblocks or size of regenerating cutblocks. In winter, displacement rates were only associated with size of new cutblocks, with shorter step lengths as cutblock size increased.

In both seasons, wolves had faster displacement rates when closer to linear features (Fig. 1.4A). However, wolf step length decreased as the density of linear features increased (Fig. 1.4B).

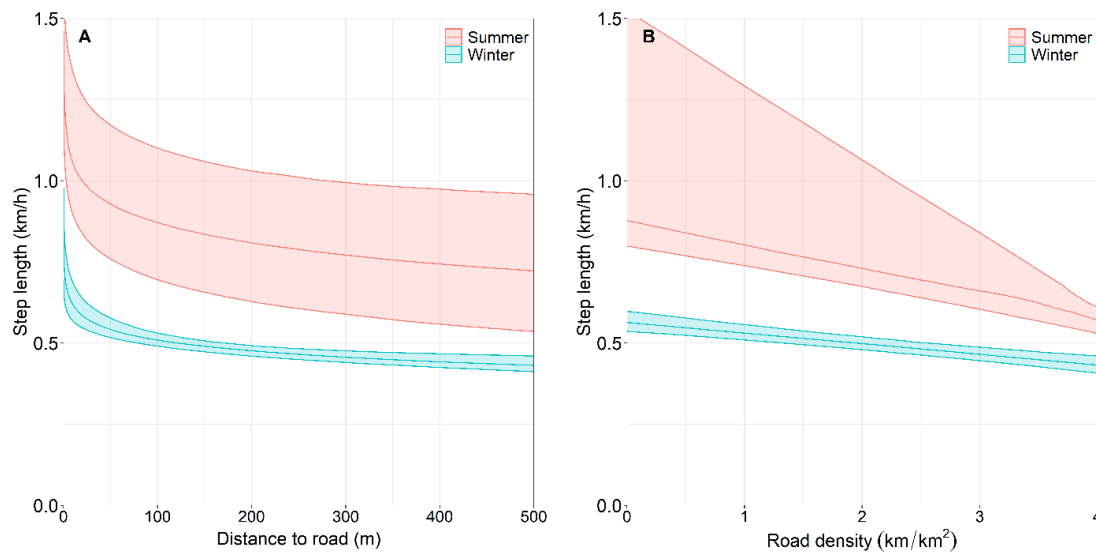


Figure 1.4 Seasonal wolf movement patterns in relation to distance to roads and road density. Seasonal mean displacement rates (km/h) with 95% confidence intervals of Prince George South wolves in comparison to A) distance to linear features (m) and B) linear feature density (km/km²) for summer (April 1–September 30) and winter (October 1–March 31), 2018-2020.

Relationship between salvage logging features and moose kill-sites

We identified 158 moose kill-sites using cluster analysis of wolf GPS locations (Appendix 1). A single top model was best supported: “Prey + Cutblocks” (Table A1.4; $r_s = 0.953$). Moose kill-sites were more likely to occur in areas with higher proportions of new and regenerating cutblocks (Fig. 1.5A-B; Table 1.3). As mean NDVI increased, the probability of a moose kill-site occurring increased (Fig. 1.5C; Table 1.3). Moose kill-sites had a lower

probability of occurring in areas with a higher proportion of deciduous-leading stands (Fig. 1.5D) and further from waterbodies (Table 1.3).

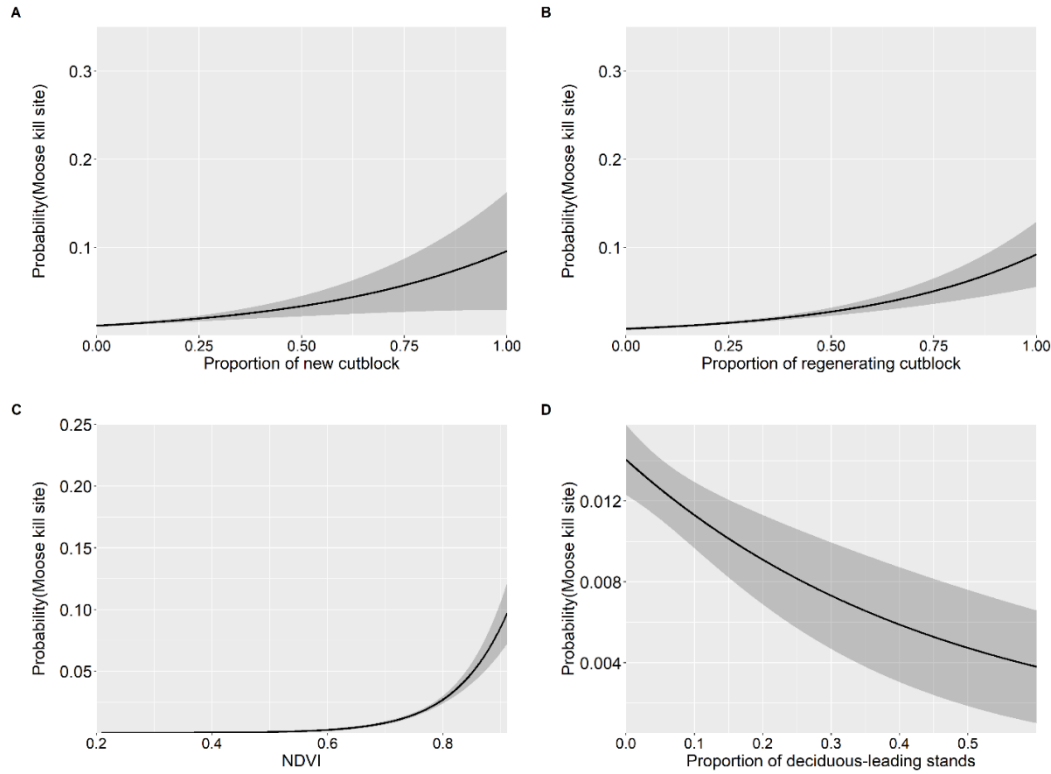


Figure 1.5 Predicted probability with 95% confidence intervals of a wolf kill-site of a moose occurring based on A) proportion of new (0-8 years old) cutblocks, B) proportion of regenerating (9-24 years old) cutblocks, and C) mean normalized difference vegetation index (NDVI), and D) proportion of deciduous-leading stands within a 883m buffer around the location, in Prince George South, 2018-2020.

Table 1.3 Beta coefficient estimates for the top logistic regression model comparing habitat features to wolf kill-sites of moose in Prince George South, 2018-2020. Bolded terms indicate significance. $\ln()$ = log-transformed covariate.

Covariate	Beta estimate	Standard error	Z value
Intercept	-13.06	1.42	-9.19
Pine	-0.28	0.92	-0.30
Deciduous	-2.20	1.28	-1.71
Mixed forest	-0.46	0.67	-0.69
Coniferous	-4.69	4.77	-0.98
ln(Water)	-0.16	0.14	-1.04
ln(Edge in)	0.065	0.096	0.49
ln(Edge out)	-0.031	0.067	-0.47
NDVI	12.17	1.86	6.53
New cut	2.25	0.85	2.66

1.4 Discussion

Large-scale logging affects predator-prey dynamics by modifying predator search efficiency, elevating predation risk for prey near disturbance features. In our study, landscape change – cutblocks and linear feature networks – impacted wolf habitat selection and movement, altering the distribution of predation events to cutblocks. Based on our results, we suggest that extensive logging potentially creates an ecological trap mediated by season and cutblock age based on patterns of moose habitat selection identified in other studies within interior BC (40, 41, 76). While this hypothesis requires further investigation, this scenario could contribute to moose population declines observed within the study area.

Wolf selection of new cutblocks, combined with an increased likelihood of moose kill-sites in areas with higher proportions of new and regenerating cutblocks, indicates that cutblocks are a risky feature for moose. In both seasons, wolves selected new cutblocks, suggesting better predation opportunities either due to higher prey availability or visibility (95, 96). Forage biomass increases post-harvest due to more solar insolation and nutrients available to plants, subsequently attracting ungulates (59, 61, 97-99). However, forage biomass and ungulate use peaks a decade post-harvest (59, 97), and while moose kill-sites were linked to higher proportions of regenerating cutblocks, there was no trend in wolf selection for regenerating blocks. Regenerating cutblocks attract moose for the increased forage biomass and cover (40, 41, 59), but increased vegetative cover would reduce prey visibility. Possibly, wolves are balancing prey availability and visibility in their selection of cutblocks, which is supported by our results: wolf movement rates were lower in regenerating cutblocks in summer, when wolf sightlines would be most obscured by vegetation. While wolves hunt with both olfactory and visual cues, areas with reduced cover (i.e. new cutblocks) are more likely to lead to a wolf successfully killing a moose due to both prey visibility and availability (100, 101), potentially leading to the observed selection of new cutblocks by wolves. However, adult female moose selection of new cutblocks – and thus, prey availability for wolves in these features – appears to vary based on season, with increased selection for new cutblocks in winter and avoidance in other seasons (40, 41, 76). Consequently, moose vulnerability in new cutblocks is likely highest in winter due to their selection of these features, in addition to the presence of deeper snow. Wolf selection for

new cutblocks throughout the year could indicate increased foraging success despite reduced moose availability in some seasons, which is supported by our kill-site analysis results. To clarify this, further studies could compare seasonal and demographic effects on spatial occurrence of wolf predation events of moose, which we were unable to do here due to limited sample sizes and data.

Consistent with previous research (49, 53, 70-72), wolves selected for habitat near linear features and increased their displacement rates there. Linear features likely increase predation risk across the landscape by allowing predators to increase their search efficiency by facilitating movement (49, 53, 74). Animals are predicted to spend less time in a foraging patch if the travel time between patches is reduced (102) and therefore, linear features could promote faster searching of more habitat patches. Further, linear features provide travel corridors into refugia or biologically important habitat for ungulates, increasing spatial overlap between prey and predators (70, 72). As a result, predation risk may increase and homogenize across the landscape due to linear features.

We suggest that wolves use linear features as travel corridors into moose habitat which could enhance their chance of successfully detecting moose; however, linear features were not an important predictor of moose kill-sites. Unless used as human-created refugia (103), ungulates generally avoid linear features due to perceived predation risk or limited forage availability relative to other habitats (76, 92, 104). The combination of wolf selection for and moose avoidance of linear features (53) likely interacts such that kill-sites are not necessarily close to linear features. Mumma and Gillingham (39) also found that adult female moose were more likely to be killed by wolves in areas of low linear feature density. Therefore, kill-sites are not a function of linear features alone and our results suggest the cumulative effects of linear features and polygonal early-seral features produce the effect on kill-sites.

Despite selection for linear features, we observed no significant trend in wolf selection for areas of high linear feature densities. Previous research has identified inconsistent responses of wolves to varying densities of linear features (105-108), which could be attributed to levels of human use – data which we lacked for PGS. While linear features may increase hunting efficiency of wolves, high linear feature densities are indicative of urban areas and increased accessibility of the landscape for human activities. If perceived as risky, areas with increased human activity would be avoided by wolves (106, 109). Alternatively, we were unable to

differentiate between varying linear feature conditions (e.g., degree of vegetation growth) in the analysis and therefore, it is possible that this lack of trend in selection is an artefact of the dataset.

We propose that the behavioural responses to logging features by wolves coupled with cutblock forage attracting moose create conditions synonymous with an ecological trap for moose, mediated by season and cutblock age, although more research is required to conclude that a trap exists. Salvage logging creates a landscape with patches of attractive foraging habitats for ungulates (cutblocks), connected by a network of linear features that enable predator movement through the system, facilitating predation. Ungulates are attracted to the increased forage offered by regenerating vegetation in cutblocks (59, 97-99), but are more vulnerable to predation due to reduced cover (100) and the ease of movement of predators through the system due to linear features (49, 53). Linear features increase spatial overlap of wolves and their prey by increasing accessibility of previously isolated habitat patches (70, 72) and allow wolves to efficiently search more of the landscape for prey (49, 53). If this potential ecological trap exists, it is likely mediated by season and cutblock age due to patterns in habitat selection by moose (i.e., increased selection for regenerating cutblocks; avoidance of new cutblocks except in winter; increased selection for cutblocks in winter) identified by previous moose research within interior BC (40, 41, 76). Further investigation is required to characterize this potential ecological trap, by further assessing habitat preference and appropriate fitness and demographic measures for moose (110).

Linear features and cutblocks function together to increase predation risk for prey, and effective management should target decoupling these disturbance features to reduce predator search efficiency. This could be accomplished by restoring linear features (e.g., felling trees, planting vegetation of >1m height (111, 112)) that link cutblocks, to reduce wolf movement rates and access into moose habitat. Linear features linking biologically important but disjunct patches of moose habitat should be prioritized and if possible, construction of linear features should proactively avoid linking critical prey habitats. Habitat enhancement (e.g., planting palatable vegetation) should occur in areas where linear feature access is limited. Deciduous-leading stands may act as refuges for moose due to reduced wolf selection and fewer associated kill sites, and replanting or retention of these stands should be prioritized. Maintaining adequate cover for prey is important, by manipulating cutblock configuration to limit sightlines and decrease distance to cover, maintaining patches of intact forest (even dead standing pine), and allowing

fast-growing shrubs to establish. However, shrub establishment may be a double-edged sword: while shrubs would disrupt predator sightlines and provide browse, they would encourage moose to use new cutblocks and potentially increase wolf-moose encounters. Overall, we emphasize the need to cohesively consider restoration and management of cutblocks and linear features in order to implement successful management programs, particularly in highly disturbed landscapes.

Chapter 2: Survival-dependent differences in forest harvest habitat selection, movement, and maternal proximity for moose calves

2.1 Background

Animals integrate information from environmental and internal cues to shape their movement behaviors and habitat selection to best maximize their fitness (113). Landscapes are dynamic systems with natural variability and disturbance, and movement allows animals to adapt and respond to these varying environmental pressures (3, 113, 114). However, current landscape change is driven by the pervasive and extensive activities of humans (4, 115, 116).

Anthropogenic disturbances rapidly and extensively impact quality, availability, and connectivity of wildlife habitat, with implications for both bottom-up (food limited) and top-down (consumer limited) regulatory processes within a system (117-119). While individuals can exhibit plasticity to these environmental changes, the drastic nature of anthropogenic landscape change often leads to animals selecting for sub-optimal habitats with negative fitness consequences (120, 121).

Individuals are predicted to optimally select habitat that confers positive fitness returns, with the assumption that habitat quality and fitness payoffs are accurately evaluated by individuals (47, 122). However, this assumption is not always true, particularly in the case of anthropogenic disturbance (120, 123). Landscape change poses a challenge to animals by altering both habitat quality and environmental cues used in habitat selection, possibly leading to animals miscalculating information and using poor quality habitat (63, 120, 123). Additionally, habitat loss and fragmentation reduce resource availability, quality, and accessibility leading to risky behaviors by animals to avoid nutritional stress, which subsequently can elevate predation risk (124, 125). In combination with altered predator distributions and hunting efficiency resulting from changing landscapes (126), these altered risks, rewards, and accompanying cues possibly lead to a decoupling of habitat selection and fitness, such that individuals use the landscape in ways that increase their mortality risk (53, 63, 127). The impacts of anthropogenic disturbance are likely exacerbated in juveniles, who are inexperienced and more vulnerable to limiting factors, such as predation (43, 128).

Identifying how anthropogenic landscape change impacts the habitat selection, movement, and survival of juveniles is important because offspring recruitment is a key parameter of population dynamics, particularly under increasing environmental severity (42, 43). While adults can buffer against environmental stressors by reducing energy invested into reproduction, juveniles cannot (129). Despite juvenile vulnerability, studies typically focus on how adult space use and survival responds to landscape change. Understanding juvenile habitat selection and movement in anthropogenically-disturbed landscapes, as well as how disturbance impacts their spatial relationship with their maternal female, illuminates the mechanisms of population decline in these regions. This is necessary when declines occur despite stable high adult survival, as in the case of moose (*Alces alces*) across vast, extensively salvage logged areas of western Canada (20, 26).

Across British Columbia (BC), Canada, large-scale mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks led to massive pine (*Pinus* spp.) die-offs followed by large-scale forest harvesting to salvage timber (33). This dual natural and anthropogenic disturbance created significantly altered landscapes: mosaics of little-remaining unharvested mature forest fragmented by massive forestry cutblocks with abundant early-seral vegetation, linked by extensive road networks facilitating human access and predator movement (78, 130-132). Moose populations declined with the MPB outbreak and significant salvage logging, with stable cow survival rates suggesting that variability in calf survival likely is linked to population declines (20, 26). Understanding how calves respond to these novel, highly disturbed landscapes is critical for identifying mechanisms driving survival variability and population dynamics. Younger calves (e.g., neonates) rely heavily on maternal habitat use and care, but as calves grow, they begin to navigate landscapes with increasing autonomy, despite their inexperience (133-135). Beyond 4 to 6 months of age, moose calves still shadow their mothers (133, 134) but their increasingly independent movement decisions, combined with variable proximity to their maternal female, could influence survival and may lead to non-ideal outcomes. How those semi-independent moose calves move and select habitat, depending on proximity to their maternal female, to deal with sudden extensive landscape change – and how this affects survival – are currently unknown.

We used integrated step selection analysis (iSSA) to compare the movement and habitat selection of 7- to 8-month-old moose calves that were recruited (i.e., survived from capture at 7-

8 months to 1 year old) and those that died (i.e., not recruited), in relation to forest harvest features (cutblocks and resource roads), natural landscape heterogeneity, and proximity to their maternal female, in two forestry-dominated landscapes of BC. We hypothesized that recruited calves would exhibit risk-averse behavior, while non-recruited calves would be risk-prone. Specifically, we predicted that recruited calves would avoid roads and cutblocks, rapidly moving out of risky disturbed habitats, and prioritizing selection for natural features with tree cover that reduced exposure and hence, predation risk. We also considered cutblocks as risky habitats as they could elevate calf vulnerability to mortality by imparting substantial energetic costs from moving through deep snow and by lacking thermal refuges. Further, we expected recruited calves to remain closer to their maternal female, to benefit from maternal care, defense, and experience. Conversely, we predicted that non-recruited calves would select for and linger in disturbed habitats which provide abundant forage but are riskier, such as new cutblocks (40, 126). Additionally, we predicted that non-recruited calves would remain further from their maternal female and make riskier decisions when spatially separated.

2.2 Methods

Study area

We collared moose in two study landscapes, Prince George South (PGS) and the Bonaparte Plateau (hereafter, Bonaparte), in interior BC, Canada (Fig. 2.1). In both study areas, salvage logging operations following the large-scale MPB outbreak resulted in the creation of extensive resource roads and early-seral cutblocks, homogenization of forest stands from replanting pine monocultures, alteration of the seral stage composition of the landscape, shifts in predator distributions, and increased human activity in previously inaccessible regions (41, 77, 78, 126). Declines in moose densities were observed in both PGS (2011/2012 to 2016/2017: 630 ± 102 moose/1000 km² in 2011/12 to 400 ± 78 moose/1000 km² 2016/17) and Bonaparte (2012/13 to 2017/18: 296 ± 18 moose/1000 km² to 254 ± 41 moose/1000 km²) over the study period following the MPB outbreak, despite cow survival rates generally remaining normal and stable (26). Predators of moose calves within these regions potentially include wolves (*Canis lupus*), cougars (*Puma concolor*), black bears (*Ursus americanus*), grizzly bears (*U. arctos*), and coyotes (*C. latrans*).

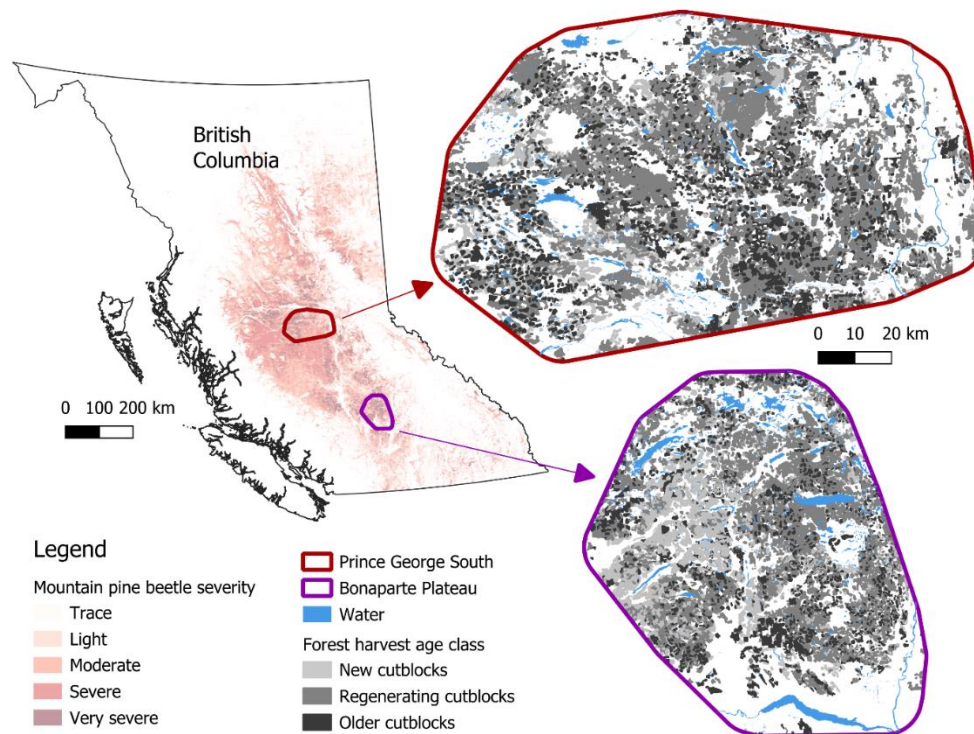


Figure 2.1 Study area maps where moose calf monitoring occurred in central British Columbia. Distribution of the mountain pine beetle (*Dendroctonus ponderosae*) outbreak based on severity across British Columbia and maps of the two study areas – Prince George South (PGS) and the Bonaparte Plateau. New (0-8 years since harvest), regenerating (9-24 years), and older (25-40 years) cutblocks, and waterbodies are shown.

Moose calf sampling

Moose calves (approximately 7-8 months old) from collared and uncollared female moose were captured during aerial surveys in December to March from 2016/2017 (Bonaparte) and 2017/2018 (PGS) to 2020/2021. Collared maternal females were captured prior to calves or at similar times, as part of a long-term provincial moose research project (26). All captures were conducted using aerial net gunning and/or chemical immobilization from a Bell 206 helicopter. Once immobilized, we fit moose with Vectronic Aerospace collars (Berlin, Germany). Calf collars were expandable and had cotton rot-off strips intended to drop the collar after approximately one year for males (as their neck size would exceed the maximum collar size) and after 2-3 years for females (only applied if collars appeared small, as collars should fit adult neck sizes). Collars provided 6 location fixes per day and produced a mortality alert if the collar was stationary for 8 hours. A mortality site visit was typically completed within 24 to 48 hours of the alert to determine cause-specific mortality based on a standardized protocol (26).

Assessing moose calf movement, habitat selection, and cow-calf distances

We used iSSA to simultaneously examine habitat selection and movement of recruited and non-recruited moose calves in relation to natural features, human disturbance, and cow-calf distance (for a subset of calves with collared mothers) in PGS and Bonaparte. In iSSA, animal space use is explained by both a resource selection function (describing habitat selection without restrictions from movement) and a movement kernel (spatial probability density function describing movement of an animal in the absence of habitat selection) (84). For each step (path between successive relocations), movement is characterized by a combination of step lengths (Euclidean distance between subsequent locations) and turn angles (angle between subsequent steps) (84, 86).

We used the package *amt* in R version 4.4.1 (85, 136) to generate ten random steps (representing available locations and providing a suitable availability sample for estimate convergence (137, 138)) for each used (observed) moose calf step (84). Available steps were drawn from step length and turn angle distributions parameterized from population-level movement data. A gamma probability density function was used to sample step length, and turn angles were drawn from a von Mises distribution (84). Used locations were included from the calf collaring date to their approximate first birthday of May 21, the mean birth date identified in the study areas based on collared female parturition movements (139), for recruited calves or the date of mortality for non-recruited calves. Capture impacts habitat selection and movement of moose for approximately five days (140), so we excluded calf locations and any individuals with mortalities during this time frame from the analyses.

For each start and end point of each used and available step, we extracted environmental covariates describing natural features and human disturbance, as well as cow-calf distances for the subset of calves with a paired maternal female. We determined the proportion of forest cover (deciduous, coniferous, and mixed) within 100-m buffers around each point, using reclassified Vegetation Resources Inventory data based on the dominant tree species (141). We combined deciduous and mixed forest proportions into a single measure of “Mixed/Deciduous” due to limited deciduous forest representation. We extracted distance to the nearest water (meters) (142), and covariates describing topography, including elevation (meters) and slope (degrees) (143). To quantify the age and spatial extent of logging, we calculated the proportion of new (0-8 years since harvest), regenerating (9-24 years), and older (25-40 years) cutblocks within a 100-m

buffer (144). These thresholds are based on identified shifts in adult female moose selection of cutblock ages in these regions (41). To represent forestry road disturbances, we determined the density of roads (km/km^2) and the distance to the nearest road (meters) for each location (145).

To assess the impacts of wildfire, we used a combination of the Historical Fire Perimeter dataset (146) and delta Normalized Burn Ratio (dNBR; estimates fire severity) rasters (147) to create a burn spatial layer. We used Google Earth Engine (148) to determine dNBR, based on the difference in values between cloud-free Landsat satellite imagery from June 1 to September 30 taken from the year before and after the fire. Within the potential fire extents delineated by the Historical Fire Perimeter dataset, we identified burned areas based on $\text{dNBR} > 0.1$ (149). Using this refined burn layer, we calculated the distance (meters) from the nearest burn of 0 – 24 years old. This burn age range corresponds with that of new and regenerating cutblocks, but not older cutblocks, because we were limited by the availability of historical Landsat data.

As maternal care likely plays a role in calf survival (135), we extracted cow-calf distances (meters; log-transformed) for the subset of calves with a paired, collared maternal female. We did not have paired females for every calf as some calves were captured from uncollared females. Our sample size was also restricted as some female collars failed after calf capture and/or location fixes between the two animals were not synchronized. Location fixes were not always captured simultaneously; thus, we considered any locations between the cow and calf captured within five minutes of each other to be paired and excluded those sets of cow-calf locations that exceeded this time threshold. It is possible that, during this time frame, maternal females and their calves moved closer to or further from each other; however, we expected this to have limited impacts on conclusions as the time window was short and unlikely to capture substantial movements. We also excluded any locations where the start and end of the step could not be paired between the calf and maternal female, to allow for analyzing the impacts of cow-calf distance on both habitat selection and movement of calves.

Following covariate extraction, we created a set of candidate iSSA models describing each of our hypotheses (Table 2.1) and fit each as a mixed-effects Poisson model using the *glmmTMB* package (150, 151). We included stratum-specific intercepts fixed at a high prior variance (10^6) to avoid shrinkage, and individual-specific random slopes for each variable (excluding step length) to account for variation between individuals (151). All candidate models included step length and log-transformed step length. We scaled (mean = 0, standard deviation =

1) all variables prior to modelling and log-transformed all distance metrics. We tested for multicollinearity prior to modeling using Pearson's correlation coefficients (r), excluding variables with $|r| > 0.7$ from the same model, and verified lack of multicollinearity following model fitting by calculating variance inflation factors. Model selection was completed separately for each study area (Bonaparte and PGS), calf fate (recruited versus not recruited), and dataset (the full dataset included calves from both collared and uncollared maternal females, or the data subset including only calves with collared females to assess cow-calf distances), using Akaike's information criterion (AIC) to determine the most supported model for each model set. For the full dataset, we completed model selection on all candidate models (Table 2.1). For the subset dataset assessing cow-calf distances, we used the most supported model from the full analysis as a base. We developed a new candidate model set, which compared the base model with the following: cow-calf distance as an additive variable or cow-calf distance interacted with components of the baseline model, specifically all variables describing habitat selection, movement, or both. To compare variable effect sizes, we calculated log-transformed relative selection strength (log-RSS) using the top model for each study area, calf fate, and dataset (93).

As we were interested in further understanding how cow-calf distances related to juvenile survival, we also regressed cow-calf distances against calf fate, sex, study area, moose age, and their interactions, with a random effect for calf ID (Table A2.1). We fit these linear mixed-effects models using the package lme4 (152) and determined the most supported model(s) using AIC. We evaluated the performance of models using 10-fold cross validation with 5 repeats, and created model predictions using the R package ggeffects (153).

2.3 Results

Moose sampling

We analyzed data from 96 calves (71 recruited, 25 not recruited) in Bonaparte and 78 calves (58 recruited, 20 not recruited) in PGS. Most calf mortalities were proximately attributed to predation in both Bonaparte (wolf = 12, bear = 1, cougar = 4, failed predation attempt = 1, health-related = 6, and vehicle collision = 1) and PGS (wolf = 14, bear = 4, failed predation attempt = 1, and health-related = 1).

Of the captured calves, 66 in Bonaparte and 40 in PGS had a collared maternal female, although only 44 (Bonaparte; 32 recruited, 12 not recruited) and 32 (PGS; 21 recruited, 11 not recruited) pairs had synchronized locations for assessing cow-calf distances. Most collared

maternal females survived through the study period, except for two in Bonaparte (1 wolf predation [calf not recruited], 1 health-related [calf recruited]) and three in PGS (all wolf predations [2 recruited calves, 1 not recruited]).

Recruited vs non-recruited moose calf habitat selection and movement

Recruited and non-recruited calves selected habitat and moved differently from one another, and between landscapes (Table 2.2, Figs. 2.2 and 2.3). For both study areas and survival outcomes, habitat selection and movement were best explained by the global model that included natural habitat heterogeneity and landscape disturbance (Table 2.1).

Table 2.1 Integrated step selection analysis candidate model structures and Akaike's Information Criterion results (ΔAIC) for recruited (survived from 7-8 months to 1 year old) and not recruited (did not survive) moose (*Alces alces*) calves in the Bonaparte and Prince George South (PGS) study areas, 2016/2017 (Bonaparte) and 2017/2018 (PGS) to 2020/2021. All models included step length (SL) and log-transformed step length (Log(SL)). Environmental covariates in each model were included as a measure from the end of the step to examine habitat selection, and from the start of the step interacted with the movement covariates (SL and Log(SL)) to examine how landscape features impacted movement.

Model	Structure	Bonaparte		PGS	
		Recruited ΔAIC	Not Recruited ΔAIC	Recruited ΔAIC	Not Recruited ΔAIC
Movement only	SL + Log(SL)	2,325.74	192.50	1,332.91	293.23
Natural Forage	Water Distance + Mixed Deciduous + Burn Distance	1,715.82	161.22	830.76	200.89
Logging Forage	New Cut + Regenerating Cut	1,450.96	113.31	868.92	151.25
Early Seral	New Cut + Regenerating Cut + Burn Distance	1,458.90	114.16	892.96	144.60
Cover	Conifer + Mixed Deciduous	1,655.04	99.39	910.53	212.60
Topography	Elevation + Slope	1,691.69	130.54	1,036.33	272.37
Natural Risk	Elevation + Slope + Conifer + Mixed Deciduous	1,087.08	37.21	664.15	192.31
Road Avoidance	Road Distance + Road Density	2,153.14	182.24	1,137.03	220.92
Cutblocks	New Cut + Regenerating Cut + Older Cut	1,295.37	93.24	770.93	137.05
Timber Harvest	New Cut + Regenerating Cut + Older Cut + Road Distance + Road Density	1,106.22	85.86	603.92	98.88
Natural Features	Water Distance + Elevation + Slope + Conifer + Mixed Deciduous + Burn Distance	952.63	33.21	588.89	172.16
Disturbances	New Cut + Regenerating Cut + Older Cut + Road Distance + Road Density + Burn Distance	1,082.63	84.26	636.42	89.14
Global	New Cut + Regenerating Cut + Older Cut + Road Distance + Road Density + Burn Distance + Water Distance + Elevation + Slope + Conifer + Mixed Deciduous	0.00	0.00	0.00	0.00

Table 2.2 Beta coefficient estimates \pm standard error for standardized covariates from the most supported integrated step selection analysis models for recruited (survived from 7-8 months to 1 year old) and not recruited (did not survive) moose (*Alces alces*) calves in Bonaparte and Prince George South (PGS) study areas, British Columbia, Canada, 2016/2017 (Bonaparte) and 2017/2018 (PGS) to 2020/2021. Terms are grouped based on whether they examine habitat selection (environmental covariates extracted from the end of the step) or movement (environmental covariates extracted from the start of the step and interacted with step length, SL, and log-transformed step length, Log(SL)). Bolded terms indicate significance (beta estimates do not overlap 0). All distance metrics were log-transformed. ‘:’ denotes an interaction between covariates.

Group	Term	Bonaparte		PGS	
		Recruited	Not Recruited	Recruited	Not Recruited
Habitat Selection	New Cut	-0.128 \pm 0.020	-0.033 \pm 0.050	-0.023 \pm 0.053	0.033 \pm 0.122
	Regenerating Cut	-0.110 \pm 0.020	-0.007 \pm 0.055	0.080 \pm 0.037	-0.020 \pm 0.088
	Older Cut	-0.139 \pm 0.025	-0.239 \pm 0.115	-0.032 \pm 0.046	-0.079 \pm 0.142
	Road Distance	0.086 \pm 0.015	0.096 \pm 0.044	0.091 \pm 0.027	0.058 \pm 0.046
	Road Density	0.036 \pm 0.016	0.064 \pm 0.048	-0.019 \pm 0.027	0.071 \pm 0.065
	Burn Distance	0.212 \pm 0.116	0.348 \pm 0.293	0.148 \pm 0.157	0.145 \pm 0.269
	Water Distance	-0.014 \pm 0.017	0.139 \pm 0.071	-0.050 \pm 0.024	-0.026 \pm 0.055
	Elevation	0.070 \pm 0.091	-0.678 \pm 0.428	0.262 \pm 0.175	0.174 \pm 0.251
	Slope	-0.080 \pm 0.014	-0.014 \pm 0.035	-0.014 \pm 0.025	-0.027 \pm 0.065
	Conifer	0.191 \pm 0.031	0.114 \pm 0.087	0.073 \pm 0.053	-0.052 \pm 0.130
	Mixed Deciduous	0.221 \pm 0.034	0.169 \pm 0.083	0.139 \pm 0.052	-0.049 \pm 0.140
Movement	SL	-0.032 \pm 0.008	-0.045 \pm 0.021	-0.047 \pm 0.009	-0.086 \pm 0.024
	Log(SL)	0.049 \pm 0.007	0.057 \pm 0.019	0.053 \pm 0.008	0.075 \pm 0.019
	SL:New Cut	0.039 \pm 0.007	0.066 \pm 0.017	-0.004 \pm 0.007	-0.126 \pm 0.022
	Log(SL):New Cut	-0.004 \pm 0.008	-0.019 \pm 0.021	0.030 \pm 0.008	0.072 \pm 0.021
	SL:Regenerating Cut	-0.023 \pm 0.008	0.078 \pm 0.023	0.034 \pm 0.008	0.035 \pm 0.020
	Log(SL):Regenerating Cut	0.026 \pm 0.008	-0.015 \pm 0.021	-0.027 \pm 0.008	-0.030 \pm 0.020
	SL:Older Cut	0.002 \pm 0.007	0.011 \pm 0.022	0.040 \pm 0.007	-0.020 \pm 0.018
	Log(SL):Older Cut	0.001 \pm 0.008	-0.023 \pm 0.020	-0.010 \pm 0.008	0.064 \pm 0.020
	SL:Road Distance	-0.015 \pm 0.009	0.029 \pm 0.031	0.001 \pm 0.009	0.038 \pm 0.025
	Log(SL):Road Distance	0.012 \pm 0.009	-0.062 \pm 0.030	-0.004 \pm 0.009	-0.021 \pm 0.023
	SL:Road Density	0.030 \pm 0.009	0.042 \pm 0.030	-0.002 \pm 0.010	0.130 \pm 0.024
Log(SL):Road Density	-0.006 \pm 0.010	-0.063 \pm 0.028	-0.009 \pm 0.009	-0.043 \pm 0.024	
SL:Burn Distance	0.027 \pm 0.009	0.093 \pm 0.022	-0.014 \pm 0.006	-0.012 \pm 0.016	

Log(SL):Burn Distance	-0.004 ± 0.007	-0.069 ± 0.022	0.011 ± 0.008	0.021 ± 0.016
SL:Water Distance	-0.046 ± 0.006	0.025 ± 0.023	-0.025 ± 0.007	0.008 ± 0.024
Log(SL):Water Distance	-0.001 ± 0.007	0.007 ± 0.021	-0.004 ± 0.008	-0.023 ± 0.020
SL:Elevation	0.023 ± 0.008	-0.014 ± 0.024	0.044 ± 0.007	0.003 ± 0.022
Log(SL):Elevation	-0.007 ± 0.007	-0.007 ± 0.022	0.004 ± 0.007	0.014 ± 0.022
SL:Slope	-0.097 ± 0.009	-0.014 ± 0.019	-0.066 ± 0.009	-0.104 ± 0.025
Log(SL):Slope	0.026 ± 0.008	-0.029 ± 0.019	0.016 ± 0.008	0.037 ± 0.021
SL:Conifer	-0.012 ± 0.015	-0.182 ± 0.046	-0.061 ± 0.016	-0.079 ± 0.038
Log(SL):Conifer	-0.015 ± 0.017	0.056 ± 0.053	0.007 ± 0.018	-0.003 ± 0.041
SL:Mixed Deciduous	-0.029 ± 0.015	-0.131 ± 0.046	-0.065 ± 0.016	-0.154 ± 0.040
Log(SL):Mixed Deciduous	0.003 ± 0.017	0.044 ± 0.053	0.032 ± 0.018	0.034 ± 0.042

Recruited calves in Bonaparte avoided higher proportions of cutblocks of all ages, whereas non-recruited calves only avoided older cutblocks (Fig. 2.2A-C). Conversely, recruited calves in PGS selected for higher proportions of regenerating cutblocks. PGS calves exhibited no trend in selection for all other cutblock age classes. Recruited calves in both study areas moved faster (i.e., longer step lengths) in areas with higher proportions of new cutblocks (Fig. 2.3A-C). Non-recruited Bonaparte calves did likewise, in addition to moving faster in regenerating cutblocks, whereas PGS calves did not. All calves in PGS moved faster in areas with higher proportions of older cutblocks.

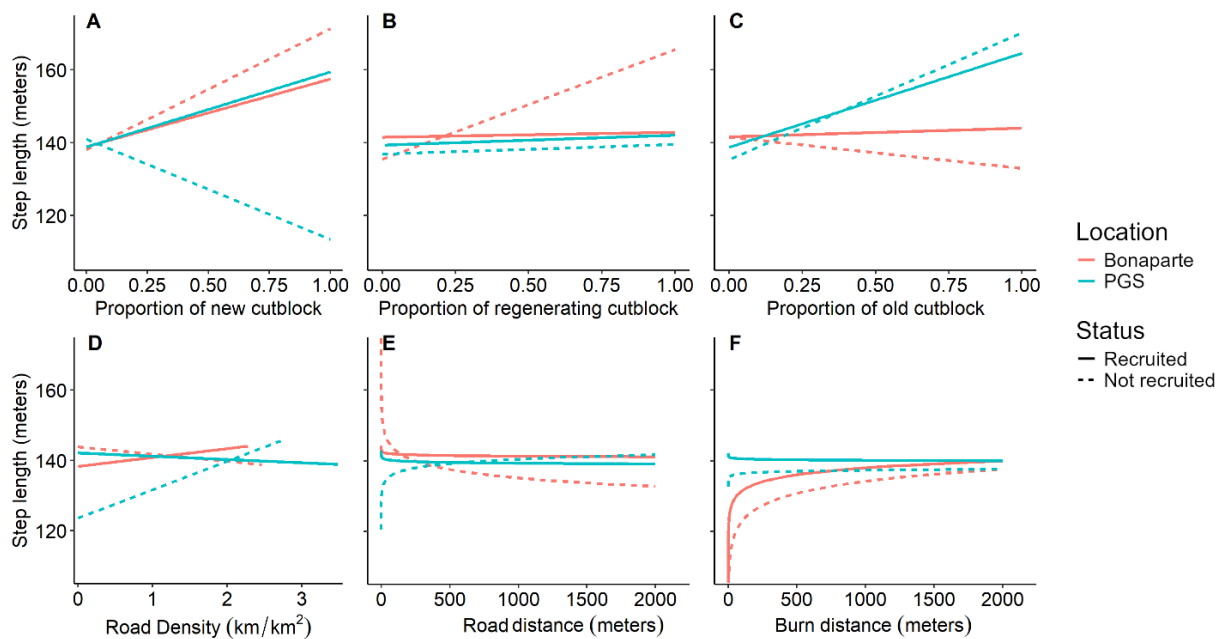


Figure 2.2. Selection of forest harvest features by study area and moose calf fate. Log-transformed relative selection strength (log-RSS) of recruited (survived from capture at 7-8 months old to 1 year) and not recruited (did not survive this period) moose (*Alces alces*) calves in Bonaparte and Prince George South (PGS) study areas, in relation to A) proportion of new (0 – 8 years since harvest), B) regenerating (9 – 24 years), and C) older (25 – 40 years) cutblocks, D) road density, E) distance to the nearest road, and F) distance to the nearest burned habitat (0-24 years since the fire).

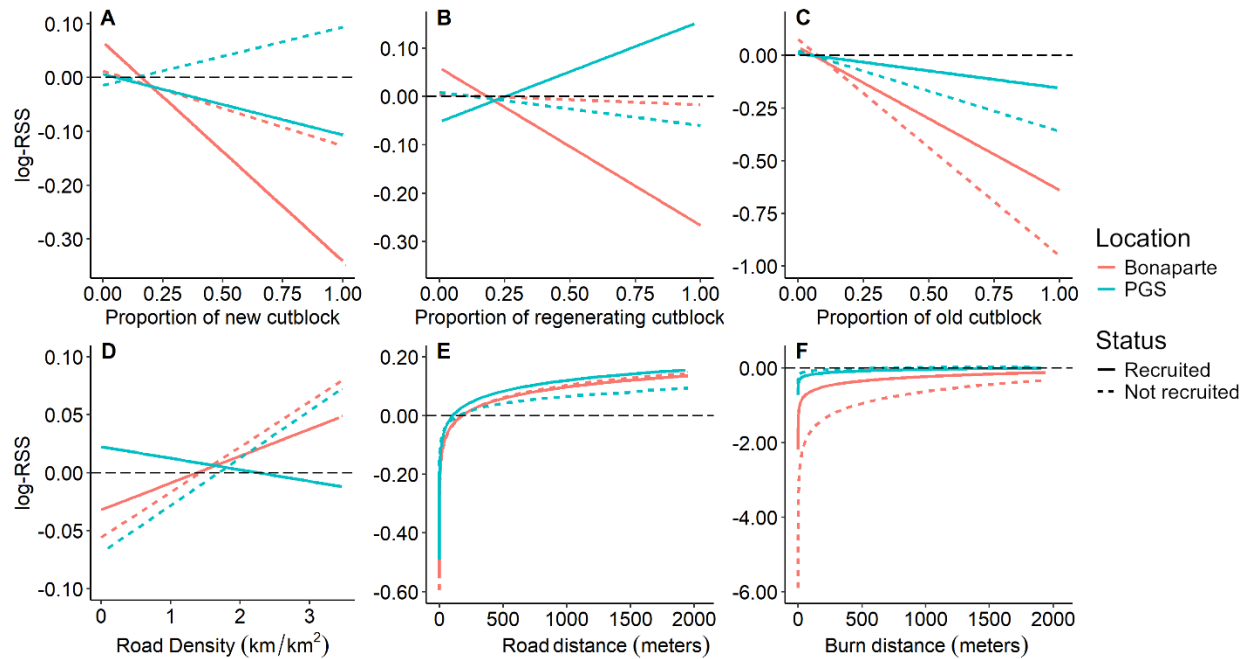


Figure 2.3. Movement rate of moose calves in relation to forest harvest features. Step length of recruited (survived from capture at 7-8 months old to 1 year) and not recruited (did not survive this period) moose (*Alces alces*) calves in Bonaparte and Prince George South (PGS) study areas, in relation to A) proportion of new (0 – 8 years since harvest), B) regenerating (9 – 24 years), and C) older (25 – 40 years) cutblocks, D) road density, E) distance to the nearest road, and F) distance to the nearest burned habitat (0-24 years since the fire).

Calves of both survival outcomes avoided proximity to roads, but most also selected for higher road densities (Fig. 2.2D-E). However, calf movement varied in response to road distance and density (Fig. 2.3D-E). Generally, calves moved faster when closer to roads, except non-recruited PGS calves did the opposite. Although statistically supported, movement rates differed little by distance to roads for recruited calves (Fig. 2.3E).

The response of calves to burned habitat varied primarily between study areas, rather than between survival outcomes (Table 2.2). In Bonaparte, calves avoided proximity to burns and exhibited longer step lengths when further from burned habitat (Figs. 2.2F and 2.3F). Conversely, PGS calves showed no trend in selection for burns but differed in their movement response to this habitat based on calf fate (Fig. 2.3).

Habitat selection and movement of calves varied in relation to natural landscape features between survival classes and landscapes, although calf responses to forests were generally consistent (Table 2.2). Non-recruited Bonaparte calves avoided higher elevations and proximity to waterbodies, whereas recruited PGS calves exhibited the opposite patterns. Both recruited

Bonaparte and non-recruited PGS calves exhibited no trend in selection for elevation and distance to waterbodies. In both study areas, step length increased for recruited calves at higher elevations and closer to waterbodies. While calves generally moved slower on steep slopes, we observed no trend in selection, except for avoidance of steeper slopes by recruited Bonaparte calves. All calves selected for higher proportions of coniferous and mixed deciduous forest, except there were no observed trends for selection of forest by non-recruited PGS calves. Additionally, as the proportion of each forest type increased, calf movement rates generally decreased.

Cow-calf spatial separation for recruited and non-recruited calves

Maternal proximity varied between months, with recruited calves generally increasing in spatial separation in May but non-recruited calves exhibiting high variability across months (Fig. 2.4A). Log-transformed cow-calf distances were best explained by interactions of calf fate with age, sex, and study area (Table A2.1). Cow-calf distances increased as the calf aged, but this increase was more rapid for non-recruited calves in Bonaparte than recruited calves (Fig. 2.4B, Table A2.2). In PGS, non-recruited calves remained spatially separate from their maternal female, whereas recruited calves gradually separated as they aged (Fig. 2.4B, Table A2.2). At one year old, recruited moose calves were predicted to be 109.9 ± 1.6 meters from their maternal female in PGS and 84.5 ± 1.5 meters in Bonaparte, whereas non-recruited calves were predicted to be spatially separated from their maternal female by 188.4 ± 2.0 meters in PGS and 223.9 ± 1.9 meters in Bonaparte. Recruited male calves had further cow-calf distances than recruited female calves (predicted distance at 1 year old, males: 182.6 ± 1.6 meters, females: 54.7 ± 1.4 meters), whereas non-recruited calves were more similar between sexes (males: 237.6 ± 1.7 , females: 186.3 ± 1.7 ; Fig. 2.4C, Table A2.2).

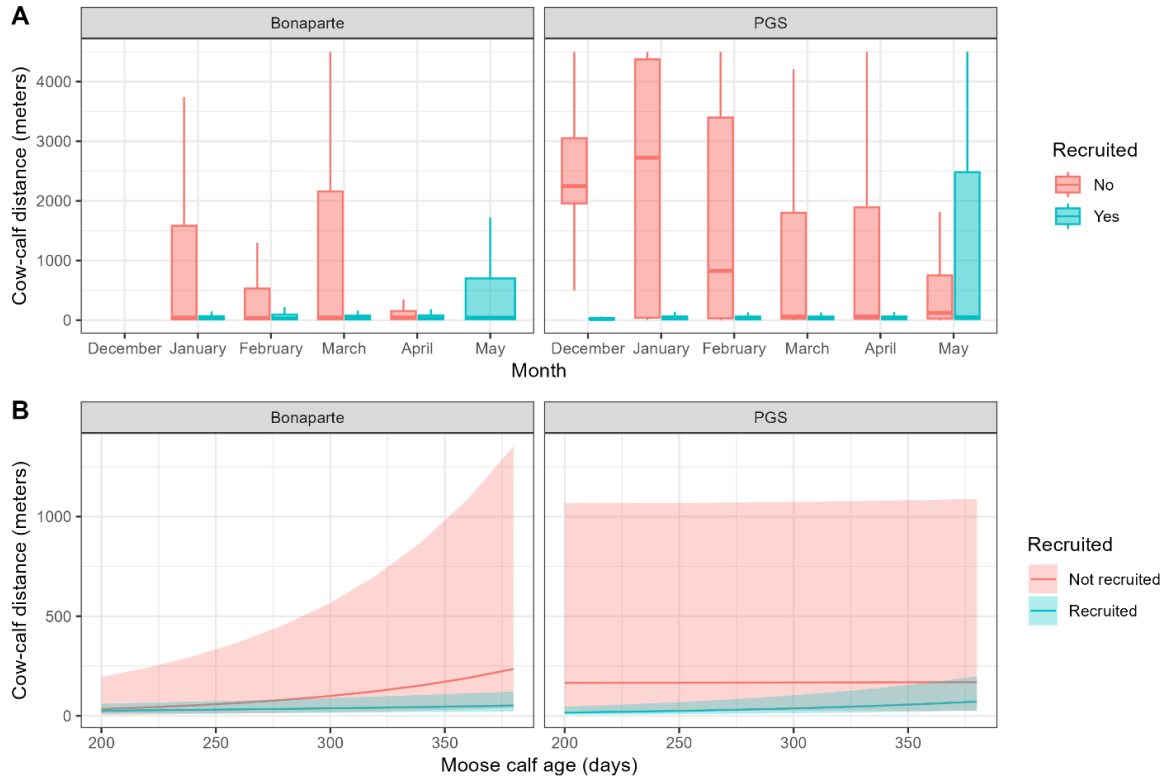


Figure 2.4 Distances of moose calves from their maternal female across months and the predicted relationship of cow-calf distances with calf ages. A) Distribution of cow-calf distances by month, and B) predicted cow-calf distances based on linear mixed-effects modeling, for recruited (i.e., survived from 7-8 months old to 1 year) or non-recruited (i.e., did not survive to 1 year old) moose (*Alces alces*) calves in Bonaparte and Prince George South (PGS) study areas. Sample sizes of individuals (recruited/non-recruited) per month are the following: December (Bonaparte: 0/0, PGS: 1/2), January (Bonaparte: 26/8, PGS: 15/9), February (Bonaparte: 32/12, PGS: 20/11), March (Bonaparte: 32/10, PGS: 21/9), April (Bonaparte: 32/9, PGS: 20/7), and May (Bonaparte: 31/0, PGS: 20/6).

Moose calf habitat selection and movement was influenced by cow-calf distance, although this effect varied between calf fates and study areas (Tables A2.3-A2.4). Only recruited Bonaparte calves were best explained by the combined effects of cow-calf distance on habitat selection and movement, whereas for non-recruited Bonaparte and recruited PGS calves, cow-calf distances only impacted movement in relation to habitat features, not their selection. For non-recruited PGS calves, the effects of cow-calf distance were only additive. All calves selected for increased proximity to their maternal female and avoided spatial separation, although avoidance was weaker for non-recruited calves in both study areas (Fig. 2.5A). Calves also moved slower when further from their maternal female, although this effect was more apparent in PGS (Fig. 2.5B). For Bonaparte and recruited PGS calves, movement rate in relation to both

natural and anthropogenic features was affected by cow-calf distance, although in many cases, this effect was weak with step length driven more by cow-calf distances (Table A2.4; Figs. A2.1-A2.2).

For recruited Bonaparte calves, cow-calf separation did impact use of habitat features, primarily forest harvest features – cutblocks and roads (Table A2.4). Avoidance of new and regenerating cutblocks weakened as cow-calf distance increased, whereas the opposite occurred for older cutblocks. As cow-calf distance increased, calves selected habitats nearer roads and with higher road densities. Of all natural features, only mixed/deciduous forest was significantly impacted by cow-calf distance, with further separation linked to increasing selection of these forest stands by calves.

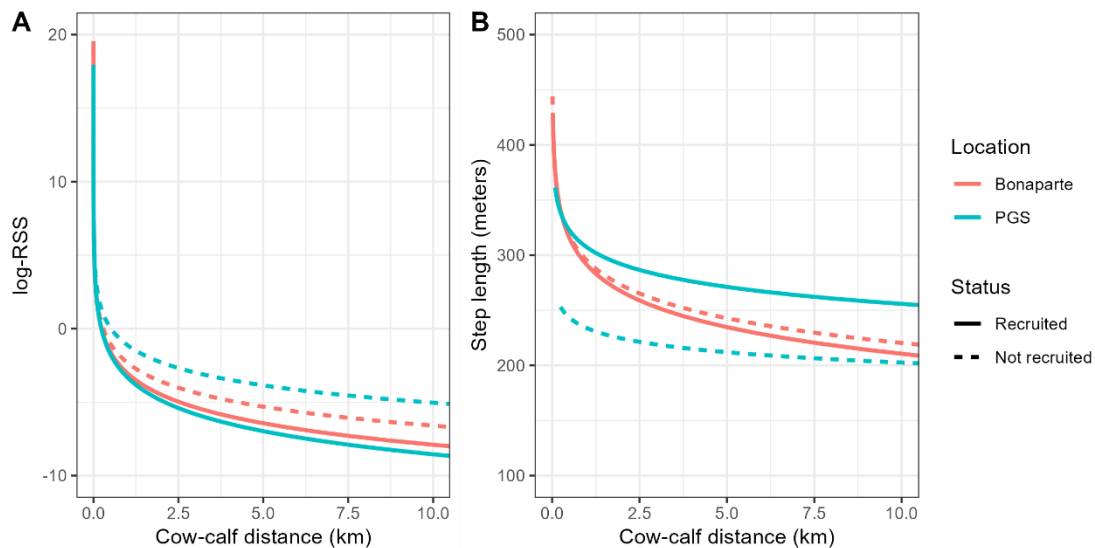


Figure 2.5 Moose calf selection and movement in relation to cow-calf distances based on study area and calf fate. A) Log-transformed relative strength (log-RSS) and B) step length, based on top integrated step selection analysis models for recruited (i.e., survived from 7-8 months old to 1 year) or non-recruited (i.e., did not survive to 1 year old) moose (*Alces alces*) calves in Bonaparte and Prince George South (PGS) study areas.

2.4 Discussion

Individual survival – and ultimately population persistence – is predicated on behaviours that acquire sufficient resources while minimizing risk (154, 155). As juveniles gain independence from their mothers, they make life-or-death decisions when selecting and moving through habitat. Although inexperienced juveniles may shadow their mothers, their own micro-decisions in complex, anthropogenically altered landscapes have significant consequences by

exposing them to risk and thence, mortality. In declining moose populations, recruited and non-recruited calves varied in their use of forestry cutblocks and remaining forest stands, possibly contributing to their survival outcomes. Recruited calves avoided all cutblocks or only selected regenerating cutblocks that balance forage and risk, moved faster through risky new cutblocks, and selected forest cover. Non-recruited calves showed little selective response to cutblocks, lingered in new or older cutblocks, and inconsistently selected for forests. All calves avoided habitat near roads, highlighting these features as risky or poor-quality habitat. Riskier space use decisions could arise from the greater independence of non-recruited calves, as they exhibited weaker avoidance of habitats further from their maternal female and spatially separated at younger ages. Further, cow-calf distances altered calf movement rates in habitats like older cutblocks, and in some cases for recruited calves, weakened avoidance of new and regenerating cutblocks and roads, while increasing selection of mixed/deciduous forest. Recruited calves could be better judges of risky habitat, but this is likely driven by them mirroring space use strategies of their mothers, evidenced by their decreased avoidance of forest harvest features when separated. Overall, movement and habitat selection choices – which appear to be shaped by an interplay of local landscape dynamics, juvenile independence, and maternal care strategies – by juveniles in human-altered systems influences their survival outcomes and likely plays a role in population dynamics.

Habitat selection, movement, and survival outcomes of moose calves

Differences in selection and movement patterns in relation to cutblocks by recruited and non-recruited calves indicate that use of these features contribute to their mortality risk. Recruited calves typically avoided cutblocks, which provide forage but elevate predation risk, thermal stress, and locomotion costs, and moved faster through new and older cutblocks, likely to minimize exposure and energetic costs. Conversely, non-recruited calves showed little selective response to cutblocks and in Bonaparte, lingered in new cutblocks where browse is more available but exposure to predators, thermal stress, and deep snow is greatest. Possibly, non-recruited calves are prioritizing forage over risk avoidance, which potentially could arise from these individuals attempting to meet nutritional demands from growth or poor body condition (which we did not assess), and/or being too inexperienced to balance this trade-off, particularly given the increased maternal separation (124, 128, 135).

Cutblock use, combined with lingering in these risky/costly environments, could increase the likelihood of calf mortality, which was primarily attributed to wolf predation based on kill site inspections. Wolves capitalize on younger cutblocks for hunting prey: wolves select new cutblocks, move slower in areas with more regenerating cutblocks, and wolf kill-sites of moose are linked to both new and regenerating cutblocks (126). Younger cutblocks are wide openings with little vegetative structure, which likely facilitates predation through prey visibility, snow depth inhibiting prey movement, ease of pursuit/capture of prey, and searchability due to associated roads (100, 126, 156, 157). Wolf kills are linked to open habitats with fewer trees (100), and predation success is higher in open habitats with greater snow depths (156, 157), which would occur in new and regenerating cutblocks. Further, cutblocks typically have abundant early successional vegetation, which attracts moose (40) – particularly inexperienced calves and those spatially separated from their maternal females – into these risky habitats. Older cutblocks, which are at a later successional stage with increasing tree dominance, offer additional vegetative cover but reduced forage availability due to canopy closure, reducing attraction by moose (41, 59). However, the forage present in younger cutblocks can be nutritionally limited (e.g., from herbicide applications (158)). Further, in years with deeper snow, this forage may be inaccessible and when searching for forage, deep snow combined with thermal stress could elevate energetic demands, reducing juvenile condition (159, 160) and increasing vulnerability to predation and other mortality causes. Increased use of new cutblocks by adult female moose over the previous 180 days elevated their risk of death from apparent starvation (39), which could similarly impact calves, which have significantly less fat stores than adults (161). Vulnerability of moose calves to mortality hazards depends on many factors, such as predation risk or health (128), but we did not account for these factors within our analysis. Teasing apart the complex interactions of forage, predation, and calf survival should be a next step to understand the mechanisms of moose population declines in forest harvested landscapes.

Contrary to predictions, recruited calves in the more southern landscape (Bonaparte) avoided regenerating cutblocks, whereas those in the northern landscape (PGS) selected these features. Adult females also exhibit similar selection patterns in relation to regenerating cutblocks, which have elevated vegetation regrowth (providing additional forage and hiding cover) in PGS compared to Bonaparte (41). Together, these results indicate that moose of multiple age classes are sensitive to vegetation regrowth post-forest harvest, and that differences

in forage between landscapes could drive variation in selection and movement patterns, as we observed. Variation in predation risk—resulting from different predator species present, their densities, and spatial distributions—may also drive these landscape differences. For adult females, use of regenerating cutblocks was not linked to survival (39), indicating that these may be less risky habitats, although wolf kill-sites of moose (both juveniles and adults) were present in both new and regenerating cutblocks (126).

Unlike cutblocks, responses of calves to roads were more consistent. All calves perceived proximity to roads as risky, but also used areas of higher road densities, possibly taking advantage of the potential protection from predators conferred by human presence. Wolves, and other predators, utilize linear features to move and hunt efficiently (53, 126). However, predators will often avoid humans and vehicles, leading to refuges for prey around well trafficked roads (162). Conversely, human hunters and vehicles do increase the riskiness of road use for moose (163). However, this risk is lower in winter and primarily impacts adults (as no calf mortalities were attributed to hunting), indicating that avoidance of proximity to roads is likely driven by predation. Thus, moose might balance these risks by avoiding using the roads themselves but taking advantage of refuge effects in areas with higher road densities.

While selection of distance to roads and their densities was generally consistent, movement patterns did differ between study areas and calf fates in relation to road densities. In Bonaparte, recruited calves moved faster at higher road densities whereas non-recruited calves moved slower, but the opposite was observed in PGS. Possibly, these results are due to the lack of accounting for differing road types (e.g., highway versus resource road), traffic levels, or statuses (e.g., decommissioning, regeneration levels, closures, snow plowing), which we were unable to integrate into the analysis due to data limitations. Further research should investigate how these factors modify roads to affect the habitat selection, movement, and survival of calf moose.

Responses of recruited and non-recruited calves varied with natural features. Recruited calves selected habitats further from burns, whereas non-recruited calves showed no patterns in selection. Often, moose are attracted to burns, especially approximately a decade following the fire when plant productivity peaks (164). However, post-fire salvage logging that occurred in wildfire burns likely altered the nutritional and risk profiles of the burns by reducing lateral cover and forage, and increasing road access. While calves in Bonaparte selected and moved

similarly in relation to conifer and deciduous forests, calves in PGS differed: recruited calves selected forests, whereas non-recruited calves showed no pattern in selection. Forest provides a combination of hiding cover, forage, and thermal shelter for moose. Non-recruited calves appear to be selecting predominantly for open habitats, likely for food availability, but these habitats would increase their risk of mortality due to lack of lateral cover creating open sightlines for predators and reduced snow interception which would increase energy expenditure.

Impacts of cow-calf distance on movement, habitat selection, and survival of calves

While calves in our study are gaining independence, their survival still depends on maternal care and their space use decisions are likely reflective of that of their mother. Although maternal care is most important for younger calves (43), it still plays a role in survival outcomes for older calves. Even though weaned older calves can (and did in this study) survive without their mother, the presence of the maternal female can improve their survival through predator defense and transmission of survival behaviors, such as risk avoidance or defensive strategies (128). While all calves in our study selected for proximity to their maternal female, non-recruited calves were more spatially separate at younger ages and exhibited weaker avoidance of further cow-calf distances, which likely reduced any survival benefits imparted by their mother's presence. Increased cow-calf separation for non-recruited calves could be driven by increased calf independence and risk-proneness, but could also result from reduced maternal investment, possibly due to poor maternal condition (165, 166) although we did not investigate this.

Although we attributed calf habitat selection and movement responses to their own decisions, these behaviors likely more so mirror those of their mother. While calves at this age have gained some experience in navigating their environments, these behaviors are primarily learned from their maternal female (167). Likely, calves are unable to fully assess the risks and benefits of habitat selection and movement decisions on their own and continue to follow similar strategies to their mother when moving independently, as evidenced by little impacts on space use when cow-calf spatial separation increased. Only recruited calves in Bonaparte exhibited variation in habitat selection in relation to maternal proximity, with calves making riskier decisions when separated, including reduced avoidance of new and regenerating cutblocks, and roads. As recruited calves, these riskier decisions did not impact their survival, but they do highlight the important role of maternal females in shaping their calf's habitat use strategies –

with potential implications for non-recruited calves that moved further from their mother and made riskier choices. However, the impact of cow-calf distance on non-recruited calf habitat selection was not well supported for the subset of calves assessed for maternal proximity. While cow-calf distance did impact movement through different habitats, this effect was much less important than the effect of cow-calf distance on movement alone.

Caveats

While our results indicate certain habitat features that may be tied to survival of older calf moose, there are some caveats that should be considered. We assessed older calves, indicating that to some degree, their and/or their mothers' habitat selection decisions have allowed them to survive to at least 7 to 8 months old. While habitat use could have delayed consequences (e.g., reduced nutrition causing later starvation), these calves have survived through the vulnerable neonate stage and until at least mid-winter. As younger calves are most vulnerable to mortality factors (43), habitat features associated with survival of older calves may not similarly impact the survival of younger calves. We chose to focus on older calves in part due to their greater independence from maternal care, meaning that their own behavioral decisions should have a greater impact on their survival outcomes. However, older calves are still influenced by decisions from their mother – as evidenced by our results – but we did not account for the effects of cow-calf distance in our main analysis, as we only had paired cow-calf data for a subset of calves. Habitat selection and movement patterns observed in non-recruited and recruited calves may reflect the temporal span of data input into models, with non-recruited calves contributing data until mortality – which could, in some cases, be primarily mid-winter locations – while recruited calves contributed data through to one year of age. Thus, seasonal effects (e.g., snow depth slowing movements) could be linked to differences in habitat use patterns observed between non-recruited and recruited calves, but we did not further divide data by season due to an increasingly limited sample size of non-recruited calves over time. Lastly, while we make interpretations based on how habitat selection and movement decisions could impact survival outcomes, we did not explicitly test for the effects of these choices on the mortality hazard for calves. While non-recruited and recruited moose calves may differ in their behavioral choices, it is possible that these differences do not contribute to mortality and further work should explore differences within a survival analysis framework.

Conclusions

Forest harvest and associated roads appear to be linked to older moose calf survival outcomes and should be managed to reduce mortality risk, particular from predators. Ensuring sufficient habitat is retained outside of cutblocks is important to allow for forest harvest avoidance and to provide refuges for older calves. The spatial arrangement of cutblocks should ensure that moose home ranges are not dominated by forest harvest, but rather contain sufficient contiguous undisturbed forest and foraging habitats. Likely, calves will continue to select for cutblocks, so managers should work to reduce predation risk in these habitats, by maintaining greater juxtaposition of hiding cover (e.g., through retention harvesting) or reducing predator sightlines (e.g., modifying cutblock configuration). When planning harvests, resource managers should ensure that mature forest stands are retained adjacent to cutblocks to provide refuges and nearby escape habitat for calves foraging in cutblocks. Promoting vegetation regrowth in cutblocks could also support older calf survival by providing additional hiding cover in combination with enhanced forage, although this may also further attract them to these features. Alternative early successional foraging habitats, such as regenerating burns, should be left undisturbed to reduce moose attraction to cutblocks. Ensuring high-quality forage remains abundantly available across the landscape could also promote increased maternal investment into calves, as females would remain in better condition. Construction of roads should generally be limited in moose habitats, especially in remote areas, and roads accessing refuges, such as forest stands, should be fully decommissioned and rehabilitated immediately following forest harvest to reduce predator movement and access (168). Older moose calf behaviors were context-dependent, with differing strategies observed between the two harvested landscapes, likely arising from varying risk, forage, and disturbance levels. Thus, management of moose and forest harvest within their habitat must be tailored to specific landscapes and their vegetation regrowth patterns to enhance calf survival outcomes. Overall, implementing these resource management strategies – while also tailoring them to specific characteristics of the landscape – could enhance survival of older calves, which would contribute to persistence of moose populations in harvested landscapes.

A multifaceted combination of juvenile habitat selection and movement behaviors, maternal proximity, and local landscape dynamics shape the survival outcomes of juvenile ungulates navigating complex ecosystems. While semi-independent juveniles do vary in their

ability to assess risks and rewards of using habitats, this variation appears to still be driven by maternal care. Our results highlight the importance of the maternal-offspring bond in shaping juvenile survival and space use strategies, even for older juveniles, in human altered landscapes.

Chapter 3: Risk-prone maternal resource selection linked to survival of older moose calves across disturbed landscapes

3.1 Introduction

Understanding the impacts of maternal habitat selection on juvenile recruitment is important for conservation of ungulate populations in disturbed landscapes. For species with extensive parental care, offspring survival is often shaped by maternal habitat use (45, 169). Habitat selection impacts the resources and risks that a mother and offspring experience, impacting the fitness of both. While females should select habitat that increases offspring fitness, these decisions can contradict what is best for the mother (45, 170). In these cases, mothers are expected to select for resources that maximize their net fitness, balancing energy expenditure into current offspring with their own survival and future reproduction, even if this comes at a cost to the offspring (43, 121, 129).

Females make trade-offs between safety and resources, impacting reproductive investment and offspring survival (170-172). Because maternal condition affects recruitment (165, 173), selection of resource-rich habitat is commonly linked to calf survival (169). Healthier females produce larger, faster-growing offspring, with increased survival probability (166, 169). Prior to parturition, nutritionally-rich habitats let mothers build energy stores for winter and gestation, increasing reproductive investment (173, 174). Following parturition, increased energy intake allows females to produce sufficient high-quality milk for offspring and offset the high costs of lactation (175). During and after weaning, offspring directly benefit from the resources within their habitats (176). Nutritionally-rich habitats help juveniles survive winter and improve their condition to escape predators (165). Poor maternal condition reduces energy allocation to offspring during gestation and lactation, leading to reduced offspring survival (177). Effects of malnutrition are both immediate and long-lasting, such that pre- and post-reproduction nutrition has lifelong impacts on offspring fitness (178).

However, resource-rich habitat often co-occurs with elevated predation risk (121, 179). Predators select for increased prey density which should occur in forage-producing habitats (121,

179). Prey selecting resource-rich, risky habitats encounter predators more often leading to mortality, and juveniles are the most vulnerable age class to predation (43). Additionally, increased risk suppresses prey reproduction due to chronic physiological stress and/or reduced energy acquisition from anti-predator behaviors (180, 181), leading to smaller offspring in poorer condition, contributing to reduced recruitment success (182, 183).

In balancing energetic needs with predator avoidance (172), individuals in poorer condition will use risk-prone strategies to obtain energy, regardless of risk to the offspring (45, 124, 171). Juveniles are highly vulnerable to limiting factors like predation and nutritional constraints (43, 128) and as such, maternal habitat selection could have population-scale outcomes. This may be particularly pertinent when drastic landscape changes affect predation outcomes (129), such as across western North America, where moose (*Alces alces*) populations declined concurrently with widespread anthropogenic disturbance (24).

In British Columbia (BC), Canada, moose population declines corresponded with increased timber harvest following large-scale mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks commencing in the 1990s (78). The extensive logging and linear infrastructure was hypothesized to increase moose mortality rates through elevated vulnerability to hunters and predators (32, 184). However, adult female survival rates were generally reflective of stable populations, indicating low calf survival may produce observed population changes (68). Female moose in BC prioritize forage acquisition over risk avoidance, which we hypothesized may impact calf recruitment (40).

We asked, how does seasonal maternal habitat selection vary between female moose that successfully recruited older (8 months old) calves to one year of age (i.e., ‘successful’) versus females that were unsuccessful? We examined seasonal resource selection by successful and unsuccessful adult female moose with a paired collared calf in two disturbed landscapes. Additionally, we compared maternal condition – body fat and winter tick (*Dermacentor albipictus*) load – and previous rearing success, between successful and unsuccessful mothers to assess how maternal quality impacts recruitment success.

We hypothesized that mothers would select for foraging habitat during seasons with high energy requirements (e.g., lactation) and that variation in habitat selection between successful and unsuccessful females reflects maternal quality, with unsuccessful females having lower body fat, higher winter tick load, and lower success recruiting a previous calf. We predicted

unsuccessful mothers would follow a risk-prone strategy through all seasons, with prioritization for habitat with higher foraging potential but increased vulnerability to predators, such as open disturbed areas (burns and cutblocks), waterbodies, forestry roads, and higher plant productivity. Conversely, successful mothers were expected to use a risk-averse foraging strategy, reducing predation risk by selecting habitats with less food but more cover (e.g., forests) and avoiding anthropogenic disturbances that facilitate predation (126).

3.2 Methods

Study area

Our study spanned two landscapes of interior BC, including the interior Douglas fir, sub-boreal pine-spruce, montane spruce, and sub-boreal spruce biogeoclimatic zones: Prince George South (PGS) and the Bonaparte Plateau (hereafter, Bonaparte) (Fig. 3.1; Appendix 3). PGS and Bonaparte experienced large-scale MPB outbreaks starting in the 1990s, leading to widespread pine (*Pinus* spp.) mortality and salvage logging (78). Consequently, both regions have abundant cutblocks and pervasive linear infrastructure networks. Declining moose populations were observed in both Bonaparte ($296 \pm 18/1000 \text{ km}^2$ in 2012/2013 to $254 \pm 41/1000 \text{ km}^2$ in 2017/18) and PGS ($630 \pm 102/1000 \text{ km}^2$ in 2011/12 to $400 \pm 78/1000 \text{ km}^2$ in 2016/17) (68).

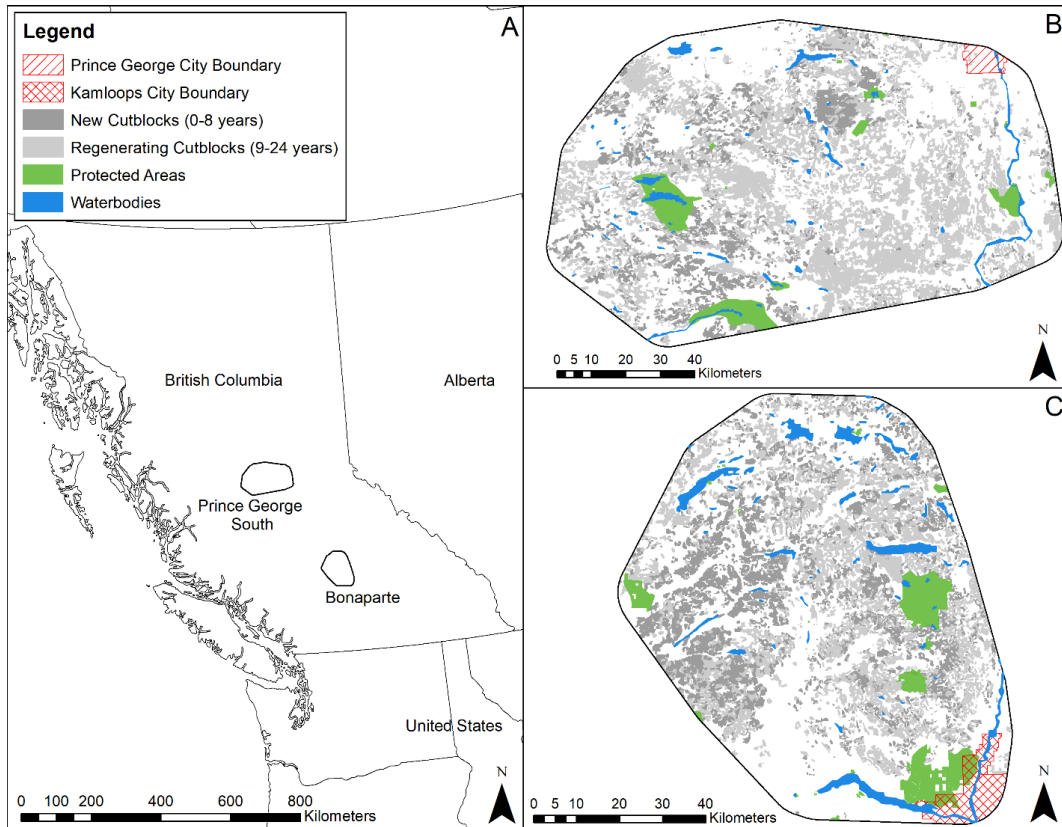


Figure 3.1 Study area maps where adult female moose and calf collaring and research occurred. Maps showing (a) the study areas within British Columbia, with close-up views of (b) Prince George South and (c) the Bonaparte Plateau, showing new (0-8 years) and regenerating (9-24 years) cutblocks, protected areas, waterbodies, and municipal boundaries of Prince George and Kamloops.

Moose captures and surveys

Pairs of adult female and ca. 8 month-old calves were captured randomly from aerial searches between December and March (Appendix 3). All captures followed the Canadian Council on Animal Care guidelines, in accordance with BC Ministry of Environment Standards for Live Animal Capture and Handling guidelines. Animal care and experiment protocols received approval under the British Columbia Wildlife Act (permit: CB17-277227). Both adult females and calves were fitted with GPS collars, and adult females were measured for maximum rump fat and winter tick load (Appendix 3).

For a subsample of females captured prior to the calf, we completed mid-winter aerial surveys (December – January) to visually assess whether females were accompanied by a previous calf in the year prior to calf capture, indicating prior rearing success. Calf presence was marked as unknown if the mother was not clearly visible or could not be located.

Resource selection functions

We assessed successful and unsuccessful mother moose habitat selection using seasonal third-order resource selection functions (RSF) within a used-available framework (185). “Successful” mothers had their calf survive from capture to approximately one year old, whereas “unsuccessful” mothers did not. Calf birth date was estimated based on mother parturition movements or if unknown, the mean calving date for both regions (May 21) (68). We divided RSFs into biological seasons: summer (July 1 – September 14 prior to parturition), rut (September 15 – October 15 prior to parturition), early gestation (October 16 – January 31), late gestation (February 1 – April 30), neonatal (May 1 – June 30), weaning (July 1 – September 14), autumn (September 15 – October 15), early winter (October 16 – January 31), and late winter (February 1 – May 21 or calf mortality) (Appendix 3).

We defined ‘availability’ for each adult moose as their annual home range, using 95% kernel density estimates with a least-squares cross-validation smoothing parameter (186). Ten random locations per used location were generated within each female’s home range. At each location, we extracted proportion of new (0-8 years since disturbance) and regenerating (9-24 years) cutblocks and burns, road distance and density, proportion of forest (deciduous, coniferous, pine, and mixed forest), distance to water, plant productivity, distance to forest edge, elevation, slope, and aspect (Appendix 3).

We modeled seasonal RSFs using the exponential form, comparing used (1) to available (0) locations using the structure:

$$[1] w(x) = \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_nx_n)$$

Where $w(x)$ is probability of selection, and β is the selection coefficient of covariate x (185). We modeled RSFs with binomial generalized linear mixed models using the ‘lme4’ package in R (136, 152). Environmental variables were included as fixed variables (Table 3.1), with mother ID as a random intercept to account for individual variability. We scaled covariates for each season and used variance inflation factors (VIFs) to assess multicollinearity. If VIFs > 5, we ran separate models for collinear variables, interpreting results from the most supported model.

Following an information-theoretic approach, we weighed evidence for competing hypotheses describing successful and unsuccessful moose seasonal habitat selection, represented by *a priori* candidate models (Table 3.1). We used Akaike’s Information Criterion corrected for

small sample sizes (AIC_c) to separately rank models for recruitment successes, study areas, and seasons (187). We evaluated model predictive ability using k -fold cross validation (94).

Table 3.1 Candidate models examining seasonal habitat selection of successful (calf survival from 8-months to 1 year old) and unsuccessful (calf mortality before 1 year old) mother moose in Prince George South and Bonaparte.

Model	Structure
Cover	Log(Edge) + Coniferous + Deciduous + Pine + Mixed Forest
Disturbance Avoidance	Log(Road Distance) + Road Density + New Cut + Regenerating Cut + Pine + Log(New Burn) + Log(Regenerating Burn)
Topography	Elevation + Slope + E-W Aspect + N-S Aspect
Risk-Avoidant Foraging	Log(Edge) + Coniferous + Mixed Forest + Pine + Deciduous + NDVI + Elevation + Slope + Log(Road Distance) + Road Density
Resources	Log(Water) + NDVI + E-W Aspect + N-S Aspect + Deciduous
Disturbance Resources	Log(New Burn) + Log(Regenerating Burn) + New Cut + Regenerating Cut
Cutblock Resources	New Cut + Regenerating Cut
Risk Prone Foraging	Log(Edge) + Log(Water) + NDVI + Log(New Burn) + Log(Regenerating Burn) + New Cut + Regenerating Cut + Log(Road Distance) + Road Density + E-W Aspect + N-S Aspect
Global	New Cut + Regenerating Cut + Log(Road Distance) + Road Density + Log(New Burn) + Log(Regenerating Burn) + NDVI + Elevation + Slope + E-W Aspect + N-S Aspect + Log(Edge) + Log(Water) + Deciduous + Pine + Coniferous + Mixed Forest

Notes: $\text{Log}()$ = log-transformed covariate.

Maternal condition and previous rearing success

We compared current and lagged body fat (measured by ingesta free body fat) and winter tick load, as well as previous calf survival to mid-winter, between a subset of successful and unsuccessful mothers using logistic generalized linear models (Appendix 3). Current measurements were taken during the winter of calf capture, whereas lagged measurements were from the previous winter. Separate models were run for each variable, due to differing sample sizes (Table A3.5 – A3.7). We pooled data from both regions due to limited sample sizes, including “region” as a covariate. Model goodness of fit was assessed using cross validation.

3.3 Results

Moose collaring

In PGS, we collared 38 moose calves from 29 adult females between December 15 and February 24, 2018-2021 (calf sample size by birth year 2017: 12, 2018: 6, 2019: 14, 2020: 6) (Table A3.1). Of these calves, 25 were recruited, while 13 were not. All PGS mortalities were

attributed to predation (wolf: 12, bear: 1), with calf age at mortality ranging from 239 to 364 days old (mean \pm SE: 322 \pm 11 days).

In Bonaparte, we collared 65 calves from 48 mothers between January 7-30, 2017-2021 (calf sample size by birth year 2016: 19, 2017: 19, 2018: 9, 2019: 9, 2020: 9) (Table A3.1). Of these calves, 46 were recruited and 19 were not. Bonaparte calf mortalities were attributed to predation (wolf: 7, cougar: 4, bear: 1) or health-related reasons (apparent starvation: 5, failed predation: 1, infection: 1), with calf mortalities at 270 to 347 days old (mean \pm SE: 321 \pm 5 days).

Resource selection by successful and unsuccessful mothers

Across all landscapes and seasons, resource selection by successful and unsuccessful mothers was best explained by a combination of risk avoidance and energy acquisition (“Global” model; Tables A3.2-3.3). However, selection for forage and security habitats varied among seasons, regions, and recruitment successes (Table 3.2). All supported models had high prediction success (Table A3.4).

Table 3.2 Seasonal beta coefficient estimates ($\beta \pm$ standard error) from the most supported resource selection function models for successful (calf survival from 7-8 months to 1 year of age) and unsuccessful (calf mortality prior to 1 year old) female moose (*Alces alces*) in summer (July 1 – September 14 prior to parturition), rut (September 15 – October 15 prior to parturition), early gestation (October 16 – January 31), late gestation (February 1 – April 30), neonatal (May 1 – June 30), weaning (July 1 – September 14), autumn (September 15 – October 15), early winter (October 16 – January 31), and late winter (February 1 – May 21 or date of calf mortality) in the Prince George South (PGS; 2016-2020) and Bonaparte Plateau (2015-2020) study areas, British Columbia, 2016-2020. All distance metrics were log-transformed.

Location	Success	Covariate	Summer	Rut	Early Gestation	Late Gestation	Neonatal	Weaning	Autumn	Early Winter	Late Winter
PGS	Successful	New Cut	0.07 ±	0.44 ±	0.31 ±	0.15 ±	0.32 ±	0.34 ±	0.33 ±	0.26 ±	0.054 ±
			0.043	0.072	0.031	0.031	0.030	0.027	0.042	0.021	0.020
		Regenerating Cut	-0.11 ±	-0.51 ±	0.27 ±	0.37 ±	0.23 ±	0.17 ±	-0.32 ±	0.15 ±	0.198 ±
			0.060	0.125	0.045	0.042	0.045	0.043	0.078	0.032	0.023
		Distance to Road	-0.12 ±	-0.17 ±	0.10 ±	-0.05 ±	0.24 ±	0.00 ±	0.14 ±	-0.28 ±	0.017 ±
			0.059	0.113	0.045	0.043	0.051	0.046	0.078	0.026	0.022
		Road Density	-0.22 ±	-0.77 ±	-0.16 ±	-0.31 ±	0.08 ±	-0.21 ±	-0.32 ±	-0.29 ±	-0.013 ±
			0.071	0.152	0.048	0.047	0.051	0.052	0.089	0.031	0.021
		Distance to New Burn	-0.397 ±	-0.194 ±	0.003 ±	-0.370 ±	-0.342 ±	-0.196 ±	-0.127 ±	-0.087 ±	0.017 ±
			0.046	0.072	0.036	0.036	0.040	0.035	0.047	0.027	0.025
		Distance to Regenerating Burn	-0.392 ±	-0.513 ±	-0.070 ±	0.652 ±	0.186 ±	-0.044 ±	-0.047 ±	0.167 ±	0.206 ±
			0.048	0.089	0.044	0.066	0.056	0.041	0.057	0.033	0.028
		NDVI	0.326 ±	0.397 ±	-0.087 ±	0.075 ±	0.075 ±	0.490 ±	0.202 ±	0.158 ±	0.211 ±
			0.054	0.093	0.033	0.029	0.033	0.043	0.047	0.029	0.018
		Elevation	0.199 ±	-0.529 ±	-0.123 ±	-0.567 ±	0.131 ±	0.208 ±	-0.066 ±	0.230 ±	-0.354 ±
			0.051	0.093	0.044	0.055	0.060	0.056	0.052	0.035	0.027
		Slope	-0.083 ±	-0.006 ±	-0.005 ±	0.147 ±	-0.002 ±	-0.003 ±	0.043 ±	0.069 ±	0.111 ±
0.044	0.065		0.031	0.024	0.033	0.029	0.043	0.020	0.014		
E-W Aspect	-0.065 ±	-0.003 ±	-0.102 ±	0.005 ±	0.128 ±	0.035 ±	-0.003 ±	-0.004 ±	0.040 ±		
	0.037	0.061	0.029	0.026	0.031	0.027	0.043	0.020	0.015		
N-S Aspect	0.042 ±	0.245 ±	0.033 ±	0.274 ±	0.050 ±	0.019 ±	-0.026 ±	-0.009 ±	0.025 ±		
	0.038	0.064	0.029	0.026	0.031	0.028	0.043	0.020	0.015		
Edge Out Distance	-0.079 ±	-0.139 ±	0.054 ±	-0.245 ±	-0.163 ±	-0.200 ±	-0.199 ±	0.248 ±	-0.081 ±		
	0.058	0.098	0.046	0.042	0.044	0.042	0.069	0.033	0.024		
Distance to Water	-0.302 ±	-0.231 ±	0.192 ±	0.077 ±	-0.510 ±	-0.341 ±	-0.157 ±	0.090 ±	0.046 ±		
	0.035	0.061	0.039	0.032	0.027	0.025	0.042	0.025	0.019		

PGS	Unsuccessful	Deciduous	0.111 ± 0.041	0.257 ± 0.049	0.073 ± 0.029	0.122 ± 0.024	0.006 ± 0.036	-0.045 ± 0.031	-0.069 ± 0.046	0.098 ± 0.021	-0.025 ± 0.017	
		Pine	0.254 ± 0.047	-0.092 ± 0.099	-0.018 ± 0.033	-0.265 ± 0.040	0.204 ± 0.033	-0.119 ± 0.032	-0.078 ± 0.051	0.050 ± 0.021	-0.108 ± 0.020	
		Coniferous	0.252 ± 0.051	0.269 ± 0.082		0.103 ± 0.033						0.068 ± 0.019
		Mixed Forest			0.184 ± 0.030		0.197 ± 0.033	-0.161 ± 0.032	0.139 ± 0.044	-0.031 ± 0.023		
		New Cut	0.09 ± 0.048	-0.17 ± 0.096	0.02 ± 0.040	-0.11 ± 0.045	-0.06 ± 0.057	-0.10 ± 0.051	-0.03 ± 0.075	0.06 ± 0.036		-0.079 ± 0.054
		Regenerating Cut	0.28 ± 0.060	0.29 ± 0.098	0.52 ± 0.049	0.43 ± 0.044	0.51 ± 0.056	0.13 ± 0.054	0.40 ± 0.090	0.57 ± 0.045		0.120 ± 0.049
		Distance to Road	0.19 ± 0.059	0.59 ± 0.106	0.10 ± 0.045	-0.22 ± 0.040	0.06 ± 0.056	-0.01 ± 0.052	0.18 ± 0.090	-0.07 ± 0.036		-0.012 ± 0.053
		Road Density	0.03 ± 0.056	0.13 ± 0.098	0.14 ± 0.044	-0.01 ± 0.041	0.19 ± 0.054	-0.01 ± 0.052	-0.17 ± 0.092	-0.12 ± 0.037		-0.464 ± 0.060
		Distance to New Burn	-0.322 ± 0.069	-0.369 ± 0.098	-0.312 ± 0.045	0.055 ± 0.059	-0.179 ± 0.061	-0.108 ± 0.060	-0.503 ± 0.086	-0.311 ± 0.046		0.138 ± 0.069
		Distance to Regenerating Burn	-0.520 ± 0.050	-0.289 ± 0.082	0.326 ± 0.056	0.371 ± 0.063	-0.167 ± 0.049	-0.424 ± 0.042	-0.304 ± 0.073	0.083 ± 0.046		0.464 ± 0.102
		NDVI	0.577 ± 0.063	0.029 ± 0.083	-0.159 ± 0.032	0.124 ± 0.035	0.221 ± 0.046	0.386 ± 0.056	0.455 ± 0.078	-0.210 ± 0.038		0.041 ± 0.045
		Elevation	0.363 ± 0.044	0.397 ± 0.066	0.039 ± 0.036	0.115 ± 0.035	0.469 ± 0.045	0.519 ± 0.040	0.409 ± 0.068	0.221 ± 0.035		-0.381 ± 0.058
		Slope	-0.021 ± 0.042	-0.218 ± 0.072	-0.052 ± 0.037	0.095 ± 0.031	-0.169 ± 0.046	-0.122 ± 0.040	-0.213 ± 0.069	-0.155 ± 0.035		-0.137 ± 0.041
		E-W Aspect	-0.016 ± 0.037	0.093 ± 0.058	0.016 ± 0.030	0.114 ± 0.029	0.015 ± 0.038	0.063 ± 0.034	0.152 ± 0.055	0.022 ± 0.028		0.115 ± 0.032
		N-S Aspect	0.015 ± 0.038	-0.008 ± 0.058	0.080 ± 0.030	0.129 ± 0.030	0.042 ± 0.038	0.144 ± 0.035	0.068 ± 0.055	0.165 ± 0.029		-0.010 ± 0.032
		Edge Out Distance	-0.216 ± 0.059	-0.263 ± 0.098	0.149 ± 0.049	-0.050 ± 0.047	-0.268 ± 0.057	-0.174 ± 0.053	-0.084 ± 0.088	0.034 ± 0.045		-0.250 ± 0.050
		Distance to Water	-0.112 ± 0.041	-0.038 ± 0.068	0.011 ± 0.036	0.379 ± 0.054	-0.368 ± 0.037	-0.246 ± 0.035	-0.190 ± 0.058	0.136 ± 0.037		-0.080 ± 0.037
		Deciduous	0.251 ± 0.038	0.473 ± 0.058	0.446 ± 0.031	-0.404 ± 0.066	0.316 ± 0.038	0.195 ± 0.034	0.540 ± 0.050	0.446 ± 0.026		0.132 ± 0.036

Bonaparte	Successful	Pine	0.105 ± 0.039	0.080 ± 0.072	0.218 ± 0.036	0.093 ± 0.030	0.325 ± 0.037	-0.099 ± 0.040	-0.009 ± 0.061	-0.064 ± 0.033	-0.165 ± 0.048	
		Coniferous		0.145 ± 0.080	0.269 ± 0.039							
		Mixed Forest	0.148 ± 0.041			0.189 ± 0.030	0.114 ± 0.045	0.136 ± 0.038	0.083 ± 0.063	0.245 ± 0.029	0.441 ± 0.033	
		New Cut	0.155 ± 0.026	0.027 ± 0.043	-0.022 ± 0.021	-0.194 ± 0.022	0.143 ± 0.025	0.169 ± 0.024	-0.044 ± 0.039	0.124 ± 0.019	0.054 ± 0.020	
		Regenerating Cut	0.066 ± 0.027	0.023 ± 0.045	0.163 ± 0.021	-0.083 ± 0.022	0.085 ± 0.028	0.100 ± 0.025	-0.083 ± 0.041	0.230 ± 0.021	0.198 ± 0.024	
		Distance to Road	0.265 ± 0.034	0.260 ± 0.055	-0.060 ± 0.024	-0.015 ± 0.024	0.291 ± 0.033	0.141 ± 0.030	0.308 ± 0.049	-0.057 ± 0.019	0.017 ± 0.022	
		Road Density	-0.055 ± 0.034	-0.094 ± 0.055	-0.125 ± 0.025	-0.083 ± 0.024	0.024 ± 0.032	-0.120 ± 0.030	0.083 ± 0.046	-0.280 ± 0.021	-0.013 ± 0.022	
		Distance to New Burn	0.015 ± 0.025	-0.010 ± 0.038	0.031 ± 0.019	0.156 ± 0.021	-0.184 ± 0.017	-0.144 ± 0.018	-0.040 ± 0.032	-0.063 ± 0.014	0.017 ± 0.025	
		Distance to Regenerating Burn	0.066 ± 0.038	-0.064 ± 0.052	-0.144 ± 0.023	0.027 ± 0.023	-0.084 ± 0.023	-0.070 ± 0.022	-0.342 ± 0.037	-0.193 ± 0.019	0.206 ± 0.028	
		NDVI	0.366 ± 0.023	0.080 ± 0.042	-0.221 ± 0.017	-0.086 ± 0.016	0.023 ± 0.020	0.474 ± 0.022	0.178 ± 0.035	-0.089 ± 0.016	0.211 ± 0.018	
		Elevation	0.561 ± 0.030	0.99 ± 0.054	0.434 ± 0.022	-0.514 ± 0.023	0.113 ± 0.023	0.275 ± 0.023	0.707 ± 0.041	0.285 ± 0.019	-0.354 ± 0.027	
		Slope	-0.241 ± 0.024	-0.064 ± 0.033	0.003 ± 0.016	-0.021 ± 0.016	-0.354 ± 0.026	-0.212 ± 0.021	0.046 ± 0.028	-0.074 ± 0.016	0.111 ± 0.014	
		E-W Aspect	-0.241 ± 0.024	-0.064 ± 0.033	0.003 ± 0.016	-0.021 ± 0.016	-0.354 ± 0.026	-0.212 ± 0.021	0.046 ± 0.028	-0.074 ± 0.016	0.111 ± 0.014	
		N-S Aspect	0.043 ± 0.019	-0.024 ± 0.029	0.047 ± 0.015	0.004 ± 0.015	-0.007 ± 0.019	0.021 ± 0.017	0.063 ± 0.027	0.014 ± 0.014	0.025 ± 0.015	
		Edge Out Distance	-0.125 ± 0.027	-0.314 ± 0.044	-0.027 ± 0.021	0.002 ± 0.021	-0.121 ± 0.026	-0.125 ± 0.024	-0.177 ± 0.040	-0.034 ± 0.020	-0.081 ± 0.024	
		Distance to Water	-0.082 ± 0.019	-0.035 ± 0.033	-0.008 ± 0.017	0.001 ± 0.016	-0.312 ± 0.017	-0.112 ± 0.018	-0.072 ± 0.030	0.005 ± 0.017	0.046 ± 0.019	
		Deciduous	-0.381 ± 0.038	-0.011 ± 0.042	0.265 ± 0.018	0.226 ± 0.017	0.078 ± 0.024	-0.125 ± 0.024	0.076 ± 0.034	0.182 ± 0.016	-0.025 ± 0.017	
		Pine	-0.123 ± 0.034	-0.112 ± 0.054	0.104 ± 0.028	0.157 ± 0.029	0.187 ± 0.034	-0.161 ± 0.031	-0.183 ± 0.051	0.049 ± 0.024	-0.108 ± 0.020	

Bonaparte	Unsuccessful	Mixed Forest	0.0004 ± 0.033	0.045 ± 0.052	0.167 ± 0.027	0.136 ± 0.026	0.102 ± 0.032	-0.015 ± 0.029	0.012 ± 0.048	0.092 ± 0.023	
		Coniferous	-0.045 ± 0.038	-0.192 ± 0.062	0.121 ± 0.032	0.085 ± 0.032	0.220 ± 0.037	-0.157 ± 0.034	-0.289 ± 0.057	-0.040 ± 0.027	0.068 ± 0.019
		New Cut	0.064 ± 0.079	-0.085 ± 0.124	0.079 ± 0.053	-0.186 ± 0.059	0.482 ± 0.059	0.255 ± 0.055	-0.263 ± 0.102	0.005 ± 0.042	-0.079 ± 0.054
		Regenerating Cut	0.246 ± 0.078	0.231 ± 0.118	0.255 ± 0.052	0.137 ± 0.051	0.323 ± 0.062	0.226 ± 0.055	0.076 ± 0.087	0.274 ± 0.039	0.120 ± 0.049
		Distance to Road	-0.092 ± 0.085	0.044 ± 0.131	0.019 ± 0.056	0.308 ± 0.058	0.144 ± 0.076	0.388 ± 0.072	0.441 ± 0.113	-0.260 ± 0.034	-0.012 ± 0.053
		Road Density	-0.526 ± 0.094	-0.183 ± 0.128	0.117 ± 0.055	0.215 ± 0.051	-0.104 ± 0.073	-0.094 ± 0.067	0.022 ± 0.103	-0.403 ± 0.041	-0.462 ± 0.060
		Distance to New Burn	0.169 ± 0.068	0.919 ± 0.144	0.392 ± 0.064	0.172 ± 0.045	0.375 ± 0.070	0.341 ± 0.057	0.477 ± 0.099	0.007 ± 0.030	0.138 ± 0.069
		Distance to Regenerating Burn	1.443 ± 0.129	1.659 ± 0.209	0.056 ± 0.062	1.091 ± 0.085	1.026 ± 0.104	0.905 ± 0.090	0.862 ± 0.136	0.007 ± 0.031	0.464 ± 0.102
		NDVI	0.227 ± 0.054	-0.235 ± 0.097	-0.105 ± 0.041	-0.032 ± 0.038	-0.033 ± 0.049	0.207 ± 0.049	0.370 ± 0.096	-0.026 ± 0.035	0.041 ± 0.045
		Elevation	0.526 ± 0.065	0.358 ± 0.100	0.706 ± 0.049	-0.007 ± 0.048	0.476 ± 0.056	0.065 ± 0.054	0.298 ± 0.079	0.126 ± 0.035	-0.381 ± 0.058
		Slope	-0.433 ± 0.061	-0.192 ± 0.084	-0.173 ± 0.040	-0.049 ± 0.034	-0.493 ± 0.058	-0.256 ± 0.045	-0.045 ± 0.061	-0.008 ± 0.028	-0.137 ± 0.041
		E-W Aspect	-0.433 ± 0.061	-0.192 ± 0.084	-0.173 ± 0.040	-0.049 ± 0.034	-0.493 ± 0.058	-0.256 ± 0.045	-0.045 ± 0.061	-0.008 ± 0.028	-0.137 ± 0.041
		N-S Aspect	-0.039 ± 0.046	0.231 ± 0.073	0.060 ± 0.035	-0.194 ± 0.033	-0.079 ± 0.040	-0.019 ± 0.037	0.287 ± 0.060	0.123 ± 0.027	-0.010 ± 0.032
		Edge Out Distance	-0.317 ± 0.066	-0.519 ± 0.108	-0.208 ± 0.050	-0.455 ± 0.049	-0.566 ± 0.057	-0.388 ± 0.050	-0.410 ± 0.086	-0.142 ± 0.039	-0.250 ± 0.050
		Distance to Water	-0.173 ± 0.047	-0.112 ± 0.077	0.037 ± 0.047	-0.116 ± 0.039	-0.551 ± 0.041	-0.087 ± 0.044	0.048 ± 0.082	0.188 ± 0.044	-0.080 ± 0.037
		Deciduous	-0.046 ± 0.056	0.248 ± 0.096	0.310 ± 0.039	0.016 ± 0.046	0.221 ± 0.047	0.032 ± 0.042	0.192 ± 0.066	0.226 ± 0.033	0.132 ± 0.036
		Pine	-0.263 ± 0.104	0.158 ± 0.182	-0.040 ± 0.068	0.183 ± 0.076	0.316 ± 0.072	0.064 ± 0.067	-0.139 ± 0.117	0.159 ± 0.054	-0.165 ± 0.048
		Mixed Forest	-0.182 ± 0.089	0.376 ± 0.156	0.237 ± 0.063	0.154 ± 0.072	0.314 ± 0.069	0.015 ± 0.064	-0.147 ± 0.118	0.405 ± 0.051	0.441 ± 0.033

Coniferous	-0.243 ±	0.220 ±	-0.061 ±	0.325 ±	0.189 ±	-0.362 ±	-0.581 ±	0.105 ±
	0.101	0.192	0.073	0.081	0.078	0.075	0.134	0.061

Selection for cutblocks varied between study areas, seasons, recruitment successes, and cutblock age classes (Figs. 3.2-3.3; Table 3.2). In PGS, successful females selected for higher proportions of new cutblocks, while selection by unsuccessful females varied seasonally (Fig. 3.2). Bonaparte females selected for new cutblocks during neonatal and weaning periods but varied otherwise (Fig. 3.3). In both regions, unsuccessful females selected for regenerating cutblocks, while responses by successful females varied.

All females avoided roads following parturition (Table 3.2), but selection varied prior to the neonatal period and during winter. High road densities were typically avoided but selected during the neonatal period by PGS females and in autumn (successful) or during gestation (unsuccessful) by Bonaparte females.

Moose mothers responded differently to burns between study areas, recruitment successes, and seasons (Table 3.2). PGS females typically selected for proximity to new burns (Fig. 3.2). Regenerating burns were selected by successful PGS females from summer to early gestation, while unsuccessful PGS females selected these habitats in most seasons. In Bonaparte, successful females selected for new and regenerating burns from the neonatal period through early winter, whereas unsuccessful females avoided burns in most seasons (Fig. 3.3).

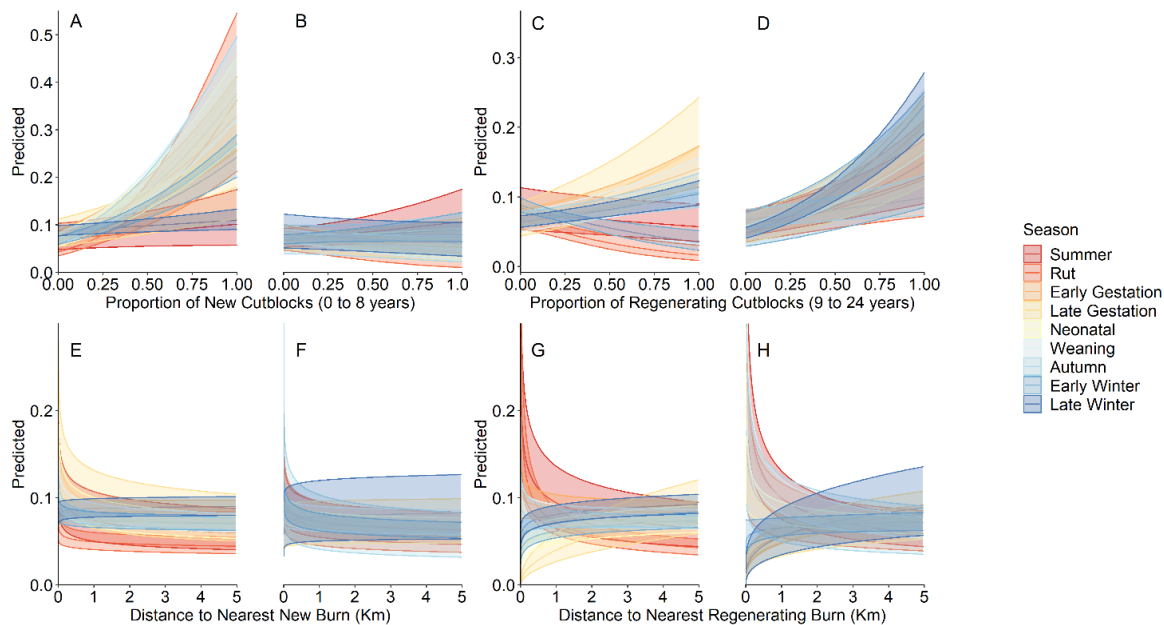


Figure 3.2 Seasonal selection of cutblocks and burns by maternal female moose in Prince George South. Seasonal predicted selection probability for: (a) and (b) proportion of new cutblocks (0-8 years); (c) and (d) proportion of regenerating cutblocks (9-24 years); (e) and (f) distance to the nearest new burn (0-8 years); and (g)

and (h) distance to the nearest regenerating burn (9-24 years) for successful (a, c, e, and g; calf survived from 8 months to 1 year) and unsuccessful (b, d, f, and h; calf mortality between 8 months to 1 year) female moose in Prince George South, 2015-2020.

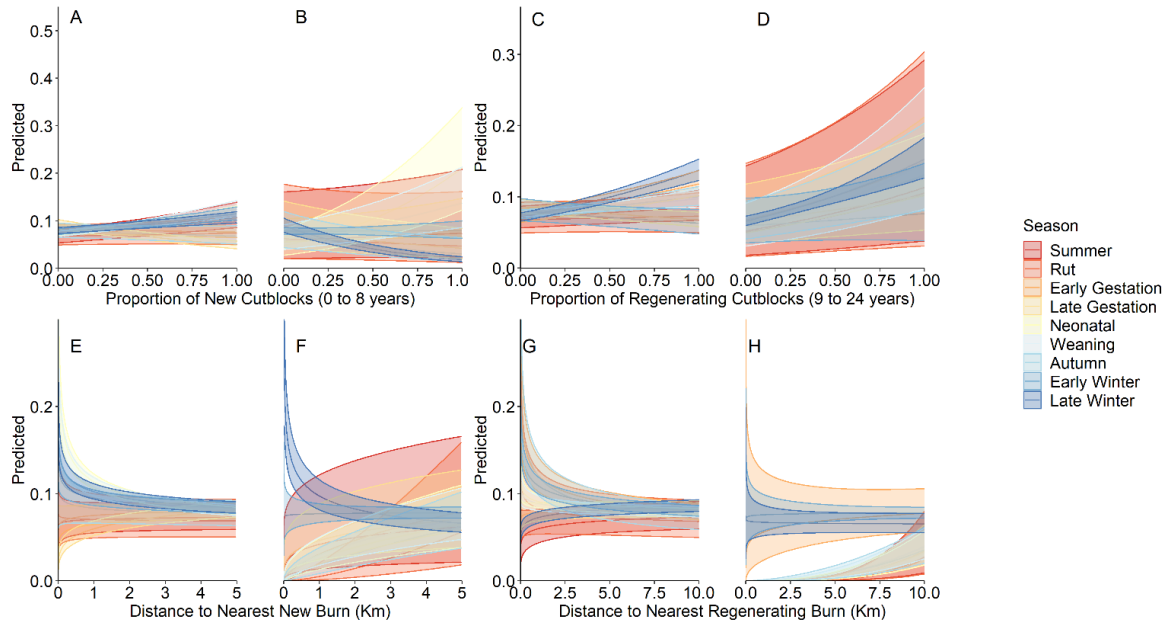


Figure 3.3 Seasonal selection of cutblocks and burns by maternal female moose in Bonaparte. Seasonal predicted selection probability for: (a) and (b) proportion of new cutblocks (0-8 years); (c) and (d) proportion of regenerating cutblocks (9-24 years); (e) and (f) distance to the nearest new burn (0-8 years); and (g) and (h) distance to the nearest regenerating burn (9-24 years) for successful (a, c, e, and g; calf survived from 8 months to 1 year) and unsuccessful (b, d, f, and h; calf mortality between 8 months to 1 year) female moose in Bonaparte, 2016-2020.

Within regions, successful and unsuccessful moose exhibited similar NDVI selection patterns. PGS females selected for higher NDVI, but Bonaparte responses varied seasonally. There was a trend for avoidance of high NDVI in early gestation by all mothers.

Female moose selected for higher elevations (except in late gestation and late winter) and shallower slopes, with varying responses to aspect. Successful females selected western-facing habitats during neonatal and weaning periods, while unsuccessful females selected these habitats in rut, late gestation, and late winter. Northern-facing slopes were selected by Bonaparte and PGS females in most seasons (Table 3.2).

Edge habitat and waterbodies were usually selected by mothers, except in gestation and early winter for PGS females. Unsuccessful Bonaparte females avoided waterbodies through winter.

Females typically selected for all forest types, but responses to pine varied (Table 3.2). Higher proportions of forest were consistently selected from early gestation to the neonatal season, although PGS and unsuccessful Bonaparte females exhibited some seasonal variability. Forest avoidance occurred during weaning and autumn for all successful mothers.

Condition and Previous Calf Survival of Successful and Unsuccessful Mothers

We assessed current and lagged body fat of 48 and 21 adult female moose, respectively (Table A3.5). Mothers with higher body fat in the previous year were less likely to recruit a calf (Fig. 3.4, $\beta = -0.87 \pm 0.65$), but current body fat was not significantly related to recruitment success ($\beta = -0.21 \pm 0.23$) (Table A3.8).

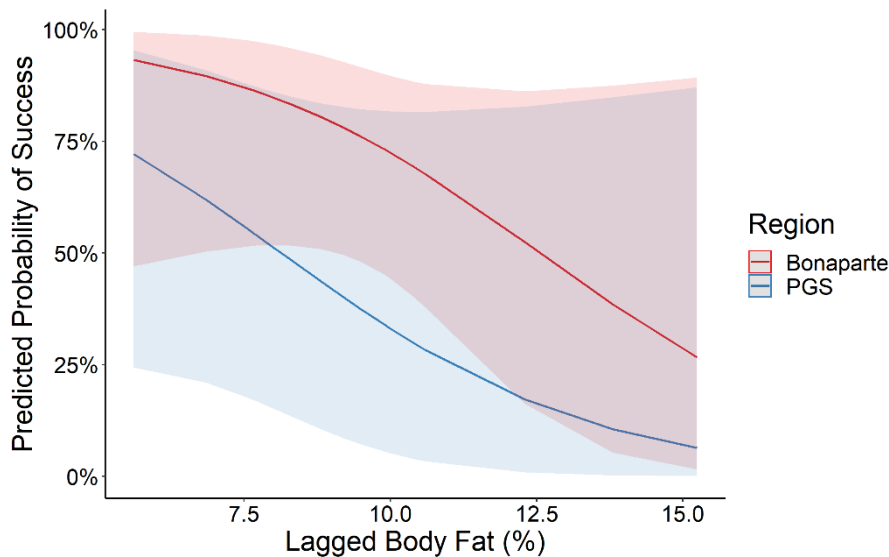


Figure 3.4 Maternal success in recruiting offspring based on lagged body fat and study area. Predicted probability of female moose successfully recruiting an 8-month-old calf to one year, compared to the mother's lagged body fat (%) in Prince George South (PGS) and Bonaparte, 2018-2021.

Current and lagged winter tick load was assessed for 58 and 22 adult females, respectively (Table A3.6). Mothers with fewer ticks in the current year were more likely to recruit a calf (Table A3.8, $\beta = -0.75 \pm 0.40$), but tick load in the previous year was not significantly related to recruitment success ($\beta = 0.09 \pm 0.49$).

We completed mid-winter surveys on 38 females (PGS: 17, Bonaparte: 21) (Table A3.7). Mothers with a calf present mid-winter had a higher probability of success the following year ($\beta = 1.19 \pm 0.89$) (Table A3.8).

3.4 Discussion

To successfully recruit offspring, females must optimally balance risk avoidance and forage potential when selecting habitats (45, 188). Contrary to our hypothesis, successful mothers did not avoid risk, instead often prioritizing habitats with higher forage potential despite reduced security cover. This is despite the fact that predation was the primary calf mortality cause in both landscapes and predation risk intensifies in disturbed early-seral landscapes embedded with roads (126). Conversely, mothers adopting a risk-averse strategy, selecting cover with less potential forage, were unsuccessful. They also had higher tick infestations which require additional food intake to offset deficits from blood loss (189).

Contrary to predictions, successful mothers were not consistently in better body condition. We attribute this to previous success in rearing offspring to mid-winter: successful mothers were more consistently successful, but raising young takes additional energy. Foraging habitats and maternal quality play significant roles in successful older calf recruitment. Acquiring forage was more important than avoiding predation risk for recruitment success: risky habitat selection pays-off for mothers, highlighting the need for high quality foraging habitats in proximity to security cover for moose.

Seasonal habitat selection patterns supported our hypothesis that females select forage-rich habitats during seasons with intensive energy requirements, using less risky habitats in other seasons. In winter, less forage is available, but moose metabolisms are lower, food intake decreases, and vulnerability to predators increases (190-193). Thus, in winter, moose likely prioritize safety over forage, avoiding open disturbed areas with reduced security cover and greater snow depths. When energy requirements increased following gestation, particularly during neonatal and weaning periods, mothers switched to selection for foraging habitats with higher plant productivity proximal to waterbodies and polygonal disturbances (burns and cutblocks). While gestation is energetically expensive, its costs are minimal compared to lactation (175) and selecting for forage helps offset these costs. Females deplete body fat through winter due to gestation and reduced forage, and must replenish these reserves for lactation, surviving the upcoming winter, and future reproduction (175, 194).

Contradicting our second hypothesis, successful females selected for riskier habitats with increased potential forage availability and/or quality, while unsuccessful females avoided these features. Variation in habitat selection between successful and unsuccessful mothers was

observed primarily for polygonal and anthropogenic disturbances (burns and new cutblocks) providing early-seral forage but increased risk from reduced tree cover (59, 61, 99, 126, 195). Also, roads associated with cutblocks facilitate predator hunting (53, 126). Possibly, polygonal features have the most significant differences in risk versus reward for moose compared to other landscape features, hence why differences in selection between successful and unsuccessful mothers were more notable.

Successful PGS females selected for new cutblocks, whereas unsuccessful females typically exhibited avoidance. We expected that new cutblocks would increase moose vulnerability due to lack of cover and wolf selection of new cutblocks and associated roads (74, 126). However, moose could optimally balance risk avoidance and forage potential to facilitate calf survival by utilizing new cutblocks spatially complemented by adjacent forest cover and avoiding roads. Selection for edges and forest by successful PGS moose in most seasons despite use of new cutblocks supports this hypothesis. Conversely, unsuccessful PGS females avoided new cutblocks and prioritized regenerating cutblocks likely for security cover due to a risk-averse strategy, possibly impacting diet quality. Following timber harvest, young cutblocks increase rapidly in forage biomass before gradually declining in forage availability as canopy cover increases (97, 196). While both new and regenerating cutblocks generally provide additional forage compared to forests, new cutblocks may offer higher foraging potential due to rapid vegetative growth and availability of preferred forage species prior to suppression via browsing pressures (196-198).

If new cutblocks supplemented successful females' diets, avoidance by unsuccessful females could lead to nutritional deficits that contribute to recruitment failure, particularly considering their higher winter tick infestations. However, current body fat estimates did not differ between successful and unsuccessful females – possibly, chronic stress from elevated risk in new cutblocks (126) negated dietary benefits for successful females. Also, increased solar radiation in new cutblocks promotes production of plant secondary compounds, reducing forage digestibility and causing energetic stress from protein limitation (198-200). Successful females could overcome these nutritional limitations by selecting shaded edges of cutblocks, optimally balancing nutritional quality with forage availability and predation risk.

Selection patterns by successful and unsuccessful Bonaparte mothers were similar for cutblocks but differed for burns. Successful females selected for new and regenerating burns

from the neonatal period onward, while unsuccessful females exhibited avoidance. Burns provide high early-seral vegetation biomass with regrowth following similar trajectories to cutblocks (195). Moose density increases often occur post-fire, from increased immigration and reproductive success (201, 202). Possibly, supplemental forage in burns bolstered the condition of successful females, promoting calf survival. Also, unlike cutblocks, burns are not always linked by roads, and tree blowdown impedes predator movement and provides horizontal cover. Burns and cutblocks appear to function differently for both moose and predators (59), leading to different expected calf recruitment outcomes.

Mothers avoided roads and high road densities in both regions, suggesting they are perceived as risky. Linear features improve predator search efficiency between prey refugia (53, 126), combined with increased risk from human hunters. However, PGS moose did select higher road densities and avoided habitat near roads during the neonatal period, possibly due to predator avoidance (100, 162). Conversely, Bonaparte mothers avoided roads and higher road densities during neonatal and weaning periods, indicating these habitats were perceived as risky when calves are most vulnerable. Possibly, Bonaparte females use other refugia less available in PGS, such as higher elevations (100, 188, 203).

Successful and unsuccessful Bonaparte mothers exhibited similar trends in selection for forests. During gestation, deeper snow confines moose to forests, which provide shelter and cover (204, 205). Forests serve as refugia during the neonatal period, when offspring are the most vulnerable to predation (188). PGS females also selected forests during the neonatal season, suggesting that all moose mothers prioritized neonate safety (188).

Successful mothers increasingly avoided forests as calves aged and vulnerability decreased. By fall, mothers have decreased body reserves compared to females without calves, caused by the high energetic requirements of gestation and lactation, combined with reduced foraging during calving (165, 188, 189, 206). Forests provide security cover for neonates but less forage than open habitats (188). Switching from prioritization of cover to nutrition allows females to build energy reserves to help survive winter (188, 194). This is supported by Bonaparte females, particularly successful mothers, also prioritizing plant productivity and lower forest proportions following parturition. However, unsuccessful PGS females continued selecting for forests (except pine), possibly due to higher risk aversion.

While maternal habitat selection varied with risk sensitivity, we did observe consistent selection patterns for habitats like edges among landscapes, indicating that all mothers perceived certain spatial features as good or bad habitat. Observed similarities may result from researching older calf survival, as the main habitat-related effects influencing calf survival could have already played out in calves that died prior to 8 months of age. All mothers had successfully reared a calf to 8 months old, indicating that their habitat selection strategies were viable for calf survival up to this point. While consistent selection patterns may indicate habitats that facilitate younger calf survival, we did not compare these results to females with earlier reproductive failures.

Overall, risky habitat selection with forage prioritization appears to pay off for recruiting older moose calves. Successful mothers exhibited risk-prone behavior with selection for polygonal disturbances with early-seral vegetation forage, likely bolstering energy allocation to offspring. Risky habitat selection likely helped successful moose offset body fat losses caused by energy invested into a previous calf. Conversely, unsuccessful females selected habitat with more security cover but poorer forage. Given higher winter tick infestations on unsuccessful females, this risk-averse strategy possibly contributed to reduced energy allocation to their calves. Additionally, if unsuccessful females select habitats with higher tick densities, this could lead to increased tick loads on their calves and potential mortality (207, 208). Lack of a significant difference in current body fat estimates between successful and unsuccessful mothers supports this hypothesis, as tick infestation has stronger impacts on calves (29).

Dramatic changes to landscape management may be needed to conserve moose populations. Spatial complementation of high-quality foraging habitats and security cover is important for calf recruitment past 8 months. Less risky landscapes interspersed with foraging habitats would promote survival of calves from both risk-averse and risk-sensitive mothers. Burns and cutblocks should be managed to maximize forage potential while minimizing predation risk. If post-fire logging occurs, managers should ensure that sufficient forage and security cover is retained. Building of roads into burned areas should be minimized. Any developed roads linking polygonal disturbances should be deactivated and restored (e.g., replanted) following harvest, to impede predator movement (61, 209). Cutblocks should be designed to maximize edge habitat to augment forage, while minimizing risk with interspersed mature forest for cover. If cutblocks are replanted, deciduous vegetation should be included to

provide forage for moose and stand tending practices (e.g., herbicide) that reduce deciduous vegetation should be avoided. Landscape management must support recruitment success of female ungulates with varying habitat selection strategies to reduce population declines and meet conservation objectives.

Chapter 4: Silviculture shapes the spatial distribution of wildlife in managed landscapes

4.1 Introduction

Forestry is a prominent driver of change across landscapes globally (210, 211). Forest harvest (i.e., removal of mature trees for wood processing) alters vegetation communities, microclimate, and edaphic conditions, impacting wildlife and their interactions, and causing cascading effects upon ecosystem dynamics (59, 66). Any landscape disturbance could alter ecosystem dynamics, but the unprecedented scale of modern forestry poses a critical threat to biodiversity (212). Understanding how forestry practices impact wildlife habitat and species relationships is important for resource managers in mitigating the adverse effects of landscape change while promoting sustainable forest harvest.

Silviculture, the management of tree establishment and growth to achieve landscape objectives through treatments such as site preparation, reforestation, and stand tending (fertilization, brush management, and tree spacing), is a key factor influencing ecological outcomes in harvested forests. While these treatments often aim to maximize merchantable timber production, they can be implemented in a sustainable manner to mitigate ecological impacts and maintain forest ecosystem resilience (213). While the effects of commercial forest harvest (specifically the quantity and distributions of tree removal, and years since harvest) and creation of associated roads on wildlife are well documented across regions and taxa (59), the impacts of silvicultural treatments are poorly understood (214).

For predators and ungulates, understanding the impacts of silviculture is crucial to guide forest and wildlife management decisions. Predator-prey relationships are often disrupted by extensive disturbances that alter, fragment, or reduce habitat (60, 162, 215). Forest harvest fragments habitat by creating open clearings and forestry road networks. Cutblocks create early seral forage for ungulates by removing the forest canopy but increase their predation risk through open sightlines created by reduced lateral cover, and increased connectivity by linear features, which allow predators to search more efficiently for prey (41, 126, 215). However, silvicultural treatments affect vegetation regrowth and thus habitat conditions, potentially impacting use of forest harvest features by predators and ungulates (216, 217). Silviculture treatments that move

forest stands more rapidly towards conifer dominance, like planting seedlings and brushing (removal of competing vegetation), reduce forage abundance for ungulates (214, 216). Other treatments, such as herbicide applications, may reduce forage quality (158, 218). Decreased forage availability and/or quality could decrease ungulate occurrence which in turn, reduces the attractiveness of these treated cutblocks to predators (216, 217). Further, silviculture that alters forest structure (e.g., spacing) could impact forage availability or predator hunting efficiency. Together, forest harvest and silviculture, in combination with roads, could alter outcomes of predation, especially when forest disturbance is significant.

Across western Canada, a mountain pine beetle (*Dendroctonus ponderosae*) outbreak started in the late 1990s, impacting millions of hectares of forest and leading to extensive harvest of beetle-infested forests intended to salvage economic value and reduce wildfire risk (33, 130). These drastic landscape changes coincided with ungulate population declines (20, 31). Landscape-mediated changes to predator-prey dynamics were identified as a potential contributing factor for declines (32). In these regions, forest harvest does influence grey wolf (*Canis lupus*) and moose (*Alces alces*) habitat use, but with inconsistent selection responses potentially arising from varying silviculture treatments altering habitat suitability (40, 41, 126). Additionally, there is a lack of information on how species in this system – particularly predators – respond to forest harvest patterns or silviculture treatments. Improving our understanding of how forest harvest and silviculture influences predators and ungulates in harvested systems will better enable wildlife and landscape management, helping to mitigate adverse responses of wildlife to anthropogenic disturbances.

Using two camera trap arrays deployed across a gradient of forest harvest in interior British Columbia, we investigated the impacts of forest harvest, silvicultural treatments, and roads, on the spatial distributions and relationships of predators – wolves, coyotes (*C. latrans*), black bears (*Ursus americanus*), grizzly bears (*U. arctos*), cougar (*Puma concolor*), lynx (*Lynx canadensis*), bobcat (*L. rufus*), and wolverine (*Gulo gulo*) – and ungulates – moose, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (*Cervus canadensis*). We expected that ungulate occurrence would be driven by silviculture treatments that reduce forage by enhancing tree growth or remove deciduous shrubs and herbaceous plants, such as brushing or replanting. Even under elevated predation risk, we expected increased ungulate occurrence in relation to features that increased early seral forage, like unbrushed or fertilized cutblocks.

Conversely, we expected predators to use habitats that facilitate hunting opportunities, such as unbrushed or prepared cutblocks, and roads (126), and that prey presence would strengthen these associations.

4.2 Methods

Camera sampling design

To monitor wildlife response to forest harvest and silviculture, we deployed an array of Reconyx™ HyperFire 2 Covert IR remote cameras (Reconyx, Holmen, WI) across a gradient of forestry disturbances in each array (Fig. 4.1; Appendix 4). Fifty camera sites per array were selected using stratified random sampling, with each landscape divided into 1x1-km grid cells and stratified based on quantiles of proportions of new (0 – 8 years since harvest), regenerating (9 – 24 years), and older (25 – 40 years) cutblock age classes. We did not stratify by silviculture, which possibly affected results, but did inspect distributions of silviculture covariates to ensure adequate distributions. We located camera sites >2 km apart to ensure independent wildlife detections and reduce spatial autocorrelation.

At each site, we deployed one camera at a height of approximately 1.5 meters on the nearest tree adjacent to a wildlife game trail, facing north (when possible) to minimize glare and false triggers from the sun. To maximize detection probability, we applied commercial scent lure (O'Gorman's™ Long Distance Call), which is commonly used in camera trapping studies, in front of the camera as a long-lasting attractant (219-221). Predators are elusive and lure ensures adequate detections for modelling, with limited effect on ungulates (219, 221). Lure moves animals in front of the camera over short distances, but landscape features explain most variation in animal movement (221). We programmed cameras to capture 1 photo per trigger, with a high sensitivity and the quiet period set to no delay. We set a timelapse photo to be taken at 12:00 pm each day, to ensure cameras operated daily. Following camera retrieval, we manually reviewed images using Timelapse Image Analyzer 2.0 (222). We treated any detections exceeding a 30-minute threshold as independent events (223).

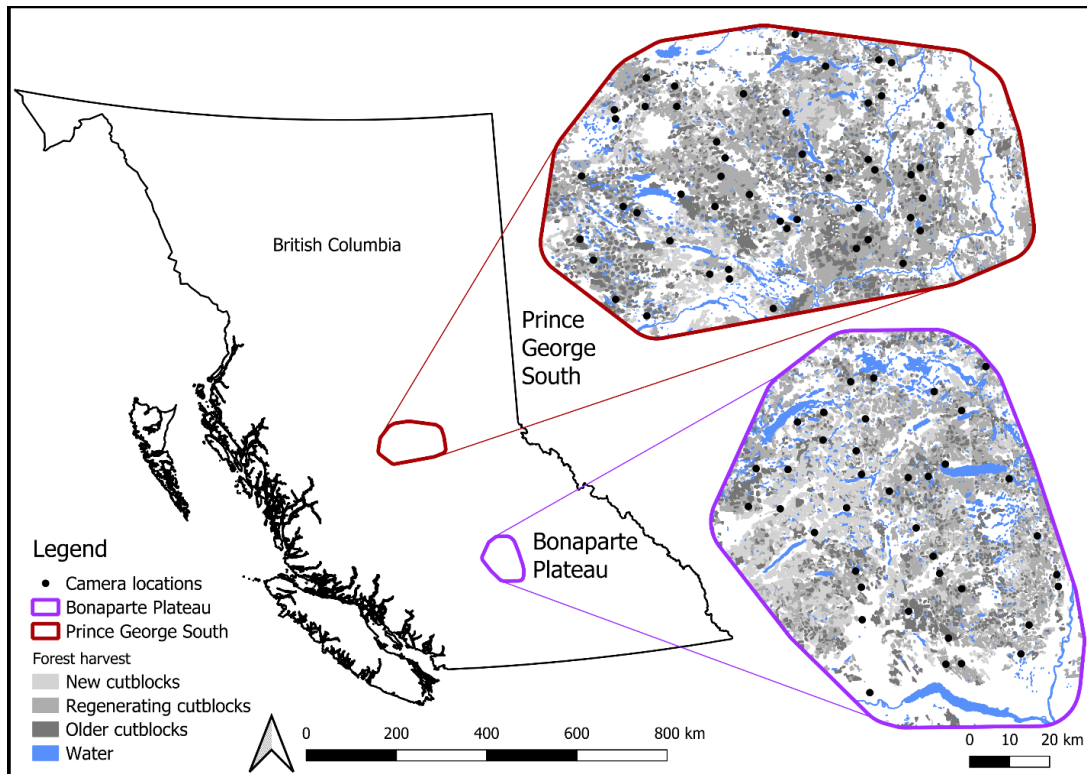


Figure 4.1 Wildlife camera arrays, Prince George South (PGS; red) and Bonaparte Plateau (purple), in British Columbia, Canada. Camera sites (black points) were deployed in PGS in May 2021 – 2022 and the Bonaparte Plateau in May 2022 – 2023. New (0 – 8 years), regenerating (9 – 24 years), and older cutblocks (25 – 40 years) are in grey, and water in blue. Areas outside of cutblocks generally represent unharvested forests, cutblocks >40 years, agriculture, and private land

Quantifying forest harvest, silviculture, natural land cover, and predator/prey occurrence

We quantified metrics describing forest harvest patterns (cutblock age classes and edge densities), silvicultural treatments (silvicultural systems, site preparation, planting, brushing, spacing, and fertilization), and natural landcover (forest type and age, water, and burns) at multiple spatial scales (224). Around each camera site, we created circular buffers every 500 meters (radii: 500 to 2500 meters) and extracted landscape variables from within these buffers.

We quantified forest harvest and silviculture using Reporting Silviculture Updates and Land Status Tracking System (RESULTS) data (144). Wildlife occurrence often depends on cutblock age class due successional vegetation regeneration (59) so we extracted proportions of new (0 – 8 years since harvest), regenerating (9 – 24 years), and older (25 – 40 years) cutblocks. We based age thresholds on those identified for moose by Mumma, Gillingham (41), which

correspond with delineations in Fisher and Wilkinson (59). We also quantified the proportion of all age classes combined, as cutblock presence alone could influence wildlife occurrence. Forest harvest creates edges between different vegetation regeneration stages that wildlife may use (126, 225, 226). Thus, for each age class, we extracted edge densities (meters/hectare). For all other cutblocks metrics (see below), we also split each classification by age class (when possible based on variable distributions).

Next, we quantified proportions of silvicultural systems (treatment programs designed for specific forest stand objectives): clearcuts, clearcuts with reserves, and selection systems. Clearcuts remove entire stands in one cut, whereas clearcuts with reserves retain certain trees across the block to meet objectives other than regeneration. Both leave wide forest openings, but reserves provide additional heterogeneity for wildlife. Selection systems retain heterogeneous forest, only harvesting single or small groups of trees repeatedly, but provide less early seral vegetation than clearcuts. Other systems, like seed tree (trees supplying seeds are unharvested), shelterwood (harvests stands in stages, leaving larger trees as shelter for regenerating trees), and patch cut (<1 hectare stands harvested in one cut), are limited in our study areas; thus, we excluded these systems as covariates. Silvicultural systems create even-aged (uniform regeneration; clearcuts, clearcuts with reserves, seed tree, shelterwood, and patch cut) or uneven-aged stands (multiple age classes; selection). Because regeneration heterogeneity could impact wildlife, we extracted proportions of even- and uneven-aged systems. Our arrays predominantly have clearcut variants, so the even-aged system variable primarily tests whether presence of reserves impacts wildlife.

Stand tending, including site preparation, planting, brushing, spacing, and fertilization, removes species competing with regenerating trees and/or promotes tree growth. Site preparation readies cutblocks for planting by improving environmental conditions for seedlings through mechanical (e.g., excavators) or other methods (e.g., herbicide, burning, fire). Herbicides in BC are typically glyphosate, which lasts in plants up to 10 years and may impact ungulate nutrition (158). Prepared sites have lower tree seedling mortality and faster growth, but potentially less ungulate forage (227). We extracted proportions of each site preparation status (prepared or unprepared) and type (none, mechanical, or other). We merged non-mechanical site preparations into one category due to limited distributions. Following, cuts are either planted or naturally

regenerate. We classified cuts by planting status and extracted the proportions of each. Planted sites often have reduced ungulate forage compared unplanted (216, 228).

Fertilization, brushing, and spacing impact vegetation present in a cutblock. Fertilizers are typically slow-release inorganic fertilizers that improve stand growth and development (229), but also enhance shrub and herb abundance (230). Brushing (manual, mechanical, or chemical) occurs after planting and helps seedlings establish by removing competing vegetation. Spacing removes undesirable trees and/or is implemented to meet stand density objectives. Spacing can improve ungulate forage abundance (231), but may also improve predator search efficiency. We extracted proportions of brushed (yes or no; mechanical, chemical [herbicide], manual, or none), spaced (yes or no), and fertilized (yes or no) cutblocks.

Resource roads are extensive in both arrays and facilitate predator travel (126). We quantified road density (km/km^2) using Digital Road Atlas data (145). We did not differentiate between road types or traffic levels due to data limitations. Roads in the study areas are predominantly one- or two-lane dirt roads with some large maintained mainline access roads and high densities of roads in cutblocks in varying levels of deactivation or natural regeneration.

We determined natural land cover (proportion of unharvested conifer or deciduous forest, and mean forest age) (141), unharvested burn (proportion of burns <40 years) (146, 232, 233), distance to water (142) and mean elevation (143). We defined unharvested conifer as forest stands dominated by $\geq 65\%$ coniferous species, and deciduous forest as a combination of deciduous-leading forests ($\geq 65\%$ deciduous species) and mixed forest (< 65% coniferous and deciduous trees), grouped due to limited availability of deciduous-leading forests and similarity of resources offered by both habitats.

Lastly, we extracted predator and prey relative occurrence indices for each site based on camera detections. Relative occurrence indices were calculated as the total number of independent detections for each species at each site, divided by the total functional camera days. We calculated indices for each species, cattle, and summed indices for groupings (ursids, canids, felids, ungulates, deer [mule deer and white-tailed deer], prey [excluding cattle], prey [including cattle], and predators). We tested the 'prey' variable with and without cattle, as predators may respond differently to livestock. We included all prey terms for wolf, black bear, grizzly bear, cougar, and coyote; deer terms for lynx and bobcat; all predator terms for mule deer and white-tailed deer; and all predator terms (excluding felids) for moose. For some predators, ungulates

play a small role in their diet, but we included these terms to account for opportunistic predation and/or scavenging behaviors. Bears are omnivores but are opportunistic predators of ungulates, both juveniles and adults (234). Lynx and bobcat prey upon small mammals and birds but will eat deer (235-238). Coyotes select small prey but will hunt deer and moose, primarily juveniles but also adults (239, 240). We did not include small mammals as a variable due to detectability, despite their importance in certain predator diets.

Statistical analysis

Following an information theoretic approach (241), we constructed candidate models describing our hypotheses on how forest harvest, silviculture, roads, predator/prey occurrence, and their combinations, influence species occurrence (Table A4.1). In each model, we controlled for environmental variability using the variables: conifer forest, deciduous forest, forest age, distance to water, and elevation. Prior to model construction, we checked variables for collinearity using Pearson's correlation coefficients ($|r| > 0.7$) and excluded them from the same model. We incorporated data from both arrays (when possible) into the same analysis and included a random effect for camera site nested within array. For species detected in one array only, we included a random effect for site. For species with limited detections, we restricted models to one variable or one variable interacting with predator/prey occurrence variables.

We fit binomial generalized linear mixed-effects models for each species using *glmmTMB* (150). Our response variable was weekly species occurrence at each site (0 = absence, 1 = presence). We treated zeros as ecological signals, not imperfect detections (60, 242). For each species, we first ran univariate models for landscape covariates at each buffer size to determine the most supported scale for each variable for inclusion into candidate models (243), based on minimizing Akaike's Information Criterion corrected for small sample sizes (AICc). We scaled continuous variables (mean = 0, standard deviation = 1) to facilitate coefficient comparisons. We used AICc to assess model support, with $\Delta\text{AICc} < 2$ indicating substantial support (241). Using the most supported model(s) for each species, we completed model validation using 10-fold cross validation, repeated 5 times (244), and used the R package *ggeffects* (153) to produce model predictions. All statistical analyses were completed using R version 4.3.3. (136).

4.3 Results

Camera deployment and species detections

We deployed 50 cameras in the PGS array, which operated May 22, 2021 to May 14, 2022. Bear damage to equipment and camera failure limited our Bonaparte array to 39 cameras, which operated May 15, 2022 to May 19, 2023. We detected moose, mule deer, white-tailed deer, coyote, grey wolf, lynx, and black bear in both arrays (Fig. A4.1). Grizzly bears were only detected in PGS; bobcats were only observed in Bonaparte. We only analyzed grizzly bears and bobcats with univariate models due to limited detections. With limited cougar detections, especially in PGS, we modeled their occurrence using Bonaparte data only, as a univariate relationship or one term interacted with prey occurrence. While we detected elk and wolverine in PGS, there were insufficient detections for modeling.

Predator occurrence in response to silviculture and prey occurrence

Canids

Wolf occurrence was associated with silvicultural systems by age class, cutblock fertilization, road density, and interactions between prey (prey including cattle or moose only) and roads or fertilized cutblocks (Table 4.1; Fig. A4.2). Wolf occurrence increased with denser roads (Fig. A4.2), more regenerating/older clearcuts with reserves, and less regenerating clearcuts, new clearcuts with reserves, and/or fertilized cutblocks (Table 4.2). Wolf occurrence increased at higher moose or prey (including cattle) occurrence frequency: moreover, when prey occurred more frequently, wolf occurrence increased with denser roads (Fig. 4.2A). Fertilization altered wolf response to cutblocks when moose occurred frequently, with wolf occurrence increasing rapidly only at very low proportions of fertilized cutblocks (Fig. 4.2B) but exhibiting gradual increases with unfertilized cutblocks (Fig. 4.2C). Higher elevations and deciduous forest were positively associated with wolf occurrence (Table 4.2), but no pattern was observed for new clearcuts, older clearcuts, and selection cuts.

Coyote occurrence was linked to cutblock brushing and deer (Table 4.1; Fig. A4.3). Coyote occurrence decreased with more unbrushed cutblocks, and less manually brushed cutblocks (Table 4.2). As deer occurrence frequency increased, coyote occurrence decreased with higher proportions of chemically brushed cutblocks (Fig. 4.2D) but increased more rapidly with higher proportions of manually brushed cutblocks (Fig. 4.2E) or lower proportions of unbrushed

cutblocks (Fig. 4.2D). Additionally, coyotes were associated with younger trees and less conifer forest (Table 4.2; Fig. A4.3).

Table 4.1 Model selection results for predator and ungulate occurrence in relation to habitat features, based on wildlife camera trap data from Prince George South and the Bonaparte Plateau. Akaike's Information Criterion corrected for small sample sizes (AICc) results for the top five models (ranked by $\Delta AICc$) explaining wolf (*Canis lupus*), black bear (*Ursus americanus*), grizzly bear (*U. arctos*), cougar (*Puma concolor*), coyote (*C. latrans*), lynx (*Lynx canadensis*), bobcat (*L. rufus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) occurrence in Prince George South and the Bonaparte Plateau, 2021 to 2023.

Species	Model	AICc	Delta AICc	AICc weight	Log-likelihood
Black bear	Site preparation by cutblock age X Prey (including cattle) + Roads X Prey (including cattle)	2791.401	0	0.305	-1372.7
	Site preparation by cutblock age X Prey (including cattle) + Roads	2793.028	1.628	0.135	-1374.51
	Site preparation by cutblock age X Deer + Roads	2793.997	2.596	0.083	-1375
	Site preparation by cutblock age X Deer + Roads X Deer	2794.012	2.611	0.083	-1374.01
	Site preparation by cutblock age X Prey (including cattle) + Roads	2794.201	2.8	0.075	-1375.1
Bobcat	Uneven-aged system	195.203	0	0.228	-95.602
	Forest age	196.040	0.837	0.15	-96.02
	Clearcuts with reserves	196.610	1.407	0.113	-96.305
	Conifer forest	197.576	2.373	0.07	-96.788
	Regenerating unprepared cutblock	197.668	2.465	0.067	-96.834
Cougar	Older brushed cutblocks X Moose	228.385	0	0.957	-110.193
	Manually brushed cutblocks X Moose	237.829	9.443	0.009	-114.914
	Edge density	238.967	10.581	0.005	-117.483
	Edge density X Moose	239.466	11.08	0.004	-115.733
	Older brushed cutblocks + Moose	240.653	12.268	0.002	-117.327
Coyote	Brushing type X Deer + Roads X Deer	2844.753	0	0.443	-1403.38
	Brushing type X Deer + Roads	2845.904	1.151	0.249	-1404.95
	Brushing type X Mule deer + Roads X Mule deer	2847.150	2.397	0.133	-1404.58
	Brushing type X Mule deer + Roads	2847.306	2.553	0.123	-1405.65
	Brushing type	2850.579	5.826	0.024	-1412.29
Grey wolf	Silviculture system by cutblock age + Roads X Prey (including cattle)	852.763	0	0.272	-409.382
	Fertilization X Moose + Roads	854.347	1.583	0.123	-413.173
	Silviculture system by cutblock age + Roads X Prey (excluding cattle)	854.355	1.592	0.123	-410.178

	Fertilization X Moose + Roads X Moose	855.064	2.301	0.086	-412.532
	Silviculture system by cutblock age X Moose + Roads	855.221	2.457	0.08	-405.61
Grizzly bear	Regenerating/older clearcuts with reserves	159.322	0	0.338	-77.661
	Manually brushed cutblocks	160.858	1.536	0.157	-78.429
	Chemically brushed cutblocks	161.993	2.671	0.089	-78.996
	Cutblocks with site preparation	162.473	3.151	0.07	-79.237
	Regenerating brushed cutblocks	162.660	3.338	0.064	-79.33
Lynx	Site preparation by cutblock age X Mule deer + Roads	1011.521	0	0.428	-483.761
	Site preparation by cutblock age X Deer + Roads	1013.026	1.505	0.202	-484.513
	Site preparation by cutblock age X Mule deer + Roads X Mule deer	1013.514	1.993	0.158	-483.757
	Site preparation by cutblock age X Deer + Roads X Deer	1014.540	3.019	0.095	-484.27
	Site preparation by cutblock age + Roads X Deer	1015.296	3.774	0.065	-490.648
Moose	Cutblock age X Wolf + Roads	2272.461	0	0.729	-1120.23
	Cutblock age X Wolf + Roads X Wolf	2274.448	1.987	0.27	-1120.22
	Age system age X Wolf + Roads	2286.591	14.13	0.001	-1125.3
	Age system age X Wolf + Roads X Wolf	2287.590	15.129	0	-1124.8
	Age system age X Coyote + Roads	2291.368	18.907	0	-1127.68
Mule deer	Site preparation by cutblock age X Predator + Roads	3204.798	0	0.628	-1580.4
	Site preparation by cutblock age X Predator + Roads X Predator	3205.922	1.124	0.358	-1579.96
	Spacing + Roads X Predator	3214.255	9.456	0.006	-1594.13
	Planting by cutblock age X Wolf + Roads	3215.349	10.551	0.003	-1585.68
	Spacing X Predator + Roads X Predator	3216.180	11.382	0.002	-1593.09
White-tailed deer	Silviculture system X Predator + Roads	617.101	0	0.186	-292.551
	Age system by cutblock age X Bear + Roads	617.196	0.094	0.177	-290.598
	Silviculture system X Predator + Roads X Predator	617.234	0.133	0.174	-291.617
	Age system by cutblock age X Bear + Roads X Bear	617.265	0.163	0.171	-289.632
	Silviculture system X Bear + Roads	619.640	2.538	0.052	-293.82

Table 4.2 Odds ratios for variables explaining predator and ungulate occurrence based on wildlife camera trap data in Prince George South and the Bonaparte Plateau. Odds ratios (with lower and upper confidence levels) for all coefficients explaining wolf (*Canis lupus*), black bear (*Ursus americanus*), grizzly bear (*U. arctos*), cougar (*Puma concolor*), coyote (*C. latrans*), lynx (*Lynx canadensis*), bobcat (*L. rufus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) occurrence in Prince George South and the Bonaparte Plateau, 2021 to 2023.

	Black bear	Grizzly bear	Bobcat	Cougar	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
Intercept	0.258 (0.143, 0.465)	0.004 (0.001, 0.012)	0.007 (0.004, 0.012)	0.006 (0.003, 0.011)	0.011 (0.002, 0.055)	0.093 (0.073, 0.119)	0.008 (0.002, 0.036)	0.055 (0.028, 0.108)	0.126 (0.030, 0.529)	0.005 (0.002, 0.008)
Predator/Prey occurrence				0.668 (0.362, 1.232)	2.371 (1.702, 3.302)	0.848 (0.671, 1.071)	4.843 (2.447, 9.584)	0.737 (0.588, 0.923)	1.151 (1.005, 1.319)	1.160 (0.752, 1.787)
New cut								0.519 (0.416, 0.648)		
Regenerating cut								1.059 (0.849, 1.319)		
Older cut								0.676 (0.547, 0.836)		
New cut:Predator/Prey								0.450 (0.327, 0.619)		
Regenerating cut:Predator/Prey								1.471 (1.275, 1.697)		
Older cut:Predator/Prey								0.772 (0.671, 0.888)		
Uneven-aged (Selection) system			1.753 (1.373, 2.239)		0.949 (0.643, 1.401)					0.205 (0.094, 0.447)

	Black bear	Grizzly bear	Bobcat	Cougar	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
Clearcut										0.725 (0.435, 1.208)
Clearcut with reserves										0.658 (0.415, 1.041)
New clearcut					1.159 (0.888, 1.512)					
Regenerating clearcut					0.546 (0.355, 0.841)					
Older clearcut					0.929 (0.627, 1.378)					
New clearcut with reserves					0.536 (0.381, 0.756)					
Regenerating/older clearcut with reserves		0.173 (0.060, 0.497)			1.381 (1.049, 1.818)					
Clearcut:Predator/Prey										2.299 (1.479, 3.573)
Uneven-aged (Selection) system:Predator/Prey										0.408 (0.210, 0.794)
Clearcut with reserves:Predator/Prey										0.458 (0.296, 0.708)
New prepared cutblock	0.979 (0.847, 1.131)						0.621 (0.173, 2.230)		0.964 (0.839, 1.109)	

	Black bear	Grizzly bear	Bobcat	Cougar	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
Regenerating prepared cutblock	1.034 (0.849, 1.258)						0.767 (0.495, 1.187)		0.829 (0.714, 0.963)	
Older prepared cutblock	1.083 (0.904, 1.298)						1.756 (1.266, 2.436)		0.697 (0.595, 0.816)	
New unprepared cutblock	0.766 (0.640, 0.917)						0.827 (0.580, 1.181)		0.978 (0.867, 1.103)	
Regenerating unprepared cutblock	1.330 (1.060, 1.668)						1.576 (1.173, 2.119)		1.009 (0.846, 1.202)	
Older unprepared cutblock	0.891 (0.755, 1.051)						0.923 (0.649, 1.314)		0.902 (0.805, 1.009)	
New prepared cutblock:Predator/Prey	0.773 (0.662, 0.904)						1.064 (0.292, 3.875)		0.860 (0.707, 1.046)	
Regenerating prepared cutblock:Predator/Prey	1.117 (0.934, 1.336)						2.643 (1.277, 5.470)		0.710 (0.588, 0.857)	
Older prepared cutblock:Predator/Prey	1.119 (0.940, 1.334)						0.878 (0.559, 1.380)			
New unprepared cutblock:Predator/Prey	1.107 (1.010, 1.213)						0.882 (0.536, 1.451)		1.436 (1.273, 1.621)	
Regenerating unprepared cutblock:Predator/Prey	0.914 (0.749, 1.117)						0.968 (0.604, 1.554)		0.831 (0.718, 0.962)	
Older unprepared cutblock:Predator/Prey	0.847 (0.703, 1.021)						2.449 (1.409, 4.255)		0.581 (0.446, 0.758)	

	Black bear	Grizzly bear	Bobcat	Cougar	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
Older prepared cutblock:Predator/Prey									1.205 (1.041, 1.395)	
Cutblock without brushing						0.657 (0.541, 0.798)				
Older cutblock with brushing				1.277 (0.670, 2.436)						
Cutblock with mechanical brushing						1.058 (0.967, 1.158)				
Cutblock with chemical brushing						0.872 (0.665, 1.142)				
Cutblock with manual brushing						1.260 (1.128, 1.407)				
Older cutblock with brushing:Predator/Prey				0.352 (0.164, 0.758)						
Cutblock without brushing:Predator/Prey						1.145 (1.004, 1.307)				
Cutblock with mechanical brushing:Predator/Prey						1.265 (0.898, 1.782)				
Cutblock with chemical brushing:Predator/Prey						0.700 (0.501, 0.978)				
Cutblock with manual brushing:Predator/Prey						1.195 (1.074, 1.328)				

	Black bear	Grizzly bear	Bobcat	Cougar	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
Road density	0.843 (0.739, 0.962)				1.411 (1.140, 1.746)	1.010 (0.888, 1.149)	0.184 (0.039, 0.864)	0.810 (0.665, 0.988)	0.927 (0.818, 1.050)	0.768 (0.548, 1.076)
Road density:Predator/Prey	0.796 (0.630, 1.005)				1.324 (1.060, 1.654)	0.861 (0.727, 1.020)				
Deciduous forest	1.305 (1.125, 1.515)				1.366 (1.082, 1.725)	0.962 (0.854, 1.084)	0.893 (0.609, 1.311)	1.250 (1.079, 1.448)	0.861 (0.765, 0.968)	1.410 (1.124, 1.770)
Conifer forest	1.237 (0.948, 1.613)				0.957 (0.633, 1.446)	0.754 (0.613, 0.926)	2.649 (1.840, 3.812)	0.789 (0.610, 1.021)	0.780 (0.656, 0.927)	0.963 (0.585, 1.584)
Forest age	1.148 (1.027, 1.284)				1.039 (0.782, 1.380)	0.821 (0.727, 0.927)	0.940 (0.771, 1.146)	1.183 (1.042, 1.343)	0.907 (0.815, 1.010)	0.614 (0.419, 0.898)
Burn	1.223 (1.024, 1.460)				1.140 (0.837, 1.553)	1.050 (0.886, 1.243)	0.563 (0.315, 1.007)	1.003 (0.834, 1.208)	1.030 (0.899, 1.179)	2.039 (1.434, 2.900)
Elevation	1.015 (0.858, 1.201)				2.616 (1.638, 4.178)	1.009 (0.797, 1.276)	1.841 (1.340, 2.529)	1.249 (1.026, 1.522)	0.659 (0.557, 0.779)	1.485 (0.972, 2.271)
Distance to water	1.133 (1.008, 1.274)				1.310 (1.009, 1.701)	1.017 (0.892, 1.158)	0.941 (0.760, 1.164)	0.979 (0.848, 1.131)	1.056 (0.949, 1.176)	0.961 (0.683, 1.352)

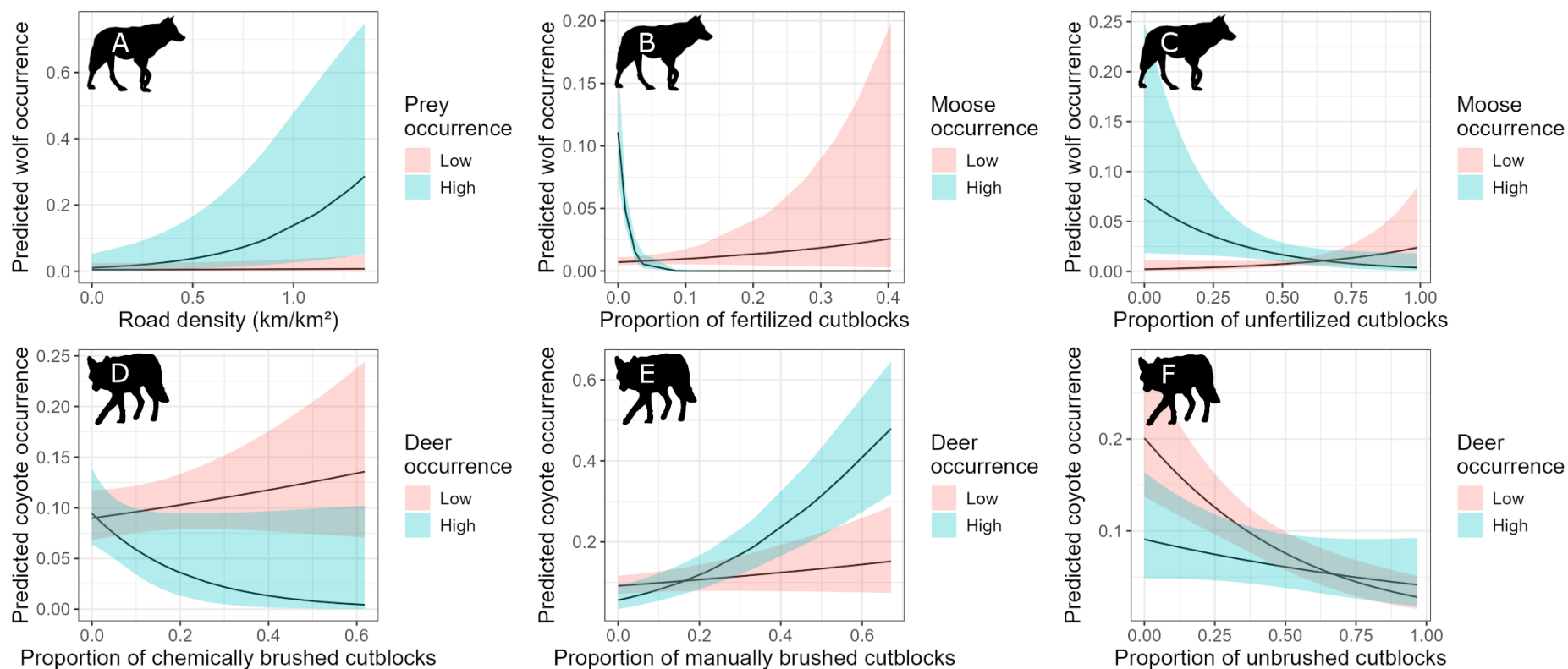


Figure 4.2 Predicted occurrence of canids in relation to forest harvest, silvicultural treatments, and prey occurrence based on camera trap data. Predicted occurrence of grey wolves (*Canis lupus*; A – C) and coyotes (*C. latrans*; D – F) in relation to road density (km/km²; A) and silviculture metrics (B – F) as an interaction with prey (including cattle; A), moose (*Alces alces*; B and C), or deer (*Odocoileus virginianus* and *O. hemionus*; D – F) occurrence frequency, based on supported models explaining species occurrence using wildlife cameras deployed in Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023). Prey occurrences are low (blue) and high (red), based on the 5th and 95th percentiles of relative abundance indices, respectively (prey including cattle occurrence: low = 0.006, high = 0.148; moose occurrence: low = 0, high = 0.047; deer occurrence: low = 0, high = 0.137)

Ursids

Black bear occurrence was linked to site preparation based on harvest age, road density, and prey (including cattle) (Table 4.1; Fig. A4.4). Black bear occurrence was linked to more frequent prey occurrence, less new prepared cutblocks, lower road densities (Fig. A4.4), and more regenerating prepared cutblocks (Table 4.2). Black bear occurrence increased with more new prepared cutblocks when prey occurred infrequently but decreased when prey occurrence frequency increased (Fig. 4.3A). Black bears decreased more rapidly in areas with more new unprepared cuts when prey occurred frequently (Fig. 4.3B). Additionally, black bear occurrence increased with older forests, deciduous forest, burnt habitat, and distance to water (Table 4.2; Fig. A4.4).

Increased grizzly bear occurrence was linked to lower proportions of regenerating/older clearcuts with reserves (Tables 4.1 and 4.2; Fig. 4.3C). The model 'Manually brushed cutblocks' was also supported (Table 4.1), but the variable showed no trend (Fig. A4.5).

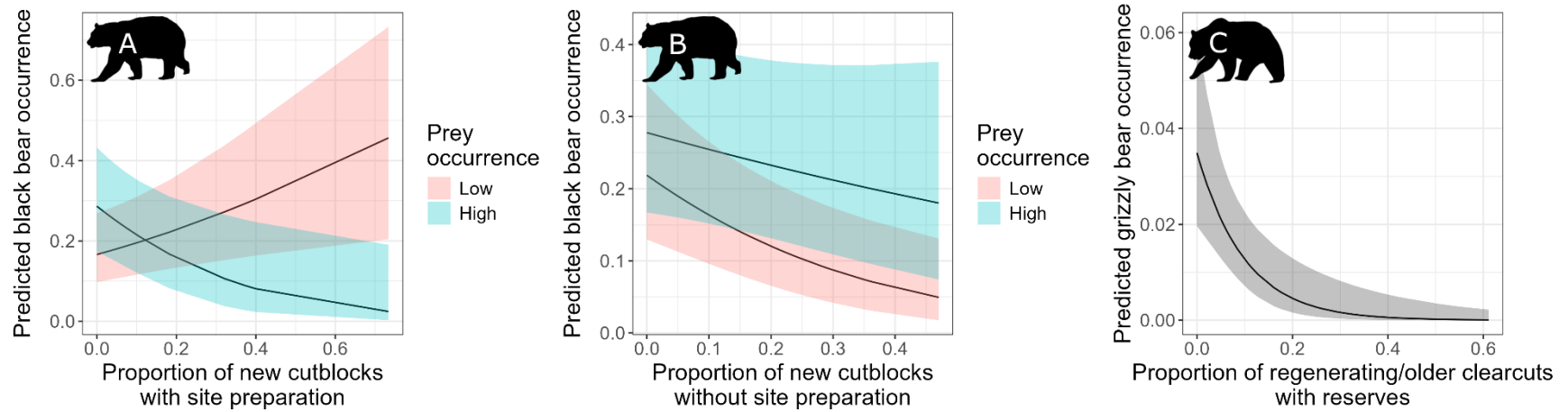


Figure 4.3 Predicted occurrence of ursids in relation to forest harvest, silvicultural treatments, and prey occurrence based on camera trap data. Predicted occurrence of black bears (*Ursus americanus*; A – B) and grizzly bears (*U. arctos*; C) in relation to silviculture metrics, with an interaction with prey occurrence frequency (including cattle; A and B only), based on wildlife camera data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023). Model predictions for grizzly bears are from Prince George South only. Prey occurrences are low (blue) and high (red) based on the 5th and 95th percentiles of relative abundance indices, respectively (prey including cattle occurrence: low = 0.006, high = 0.148)

Felids

Lynx occurrence varied based on whether site preparation was applied to each cutblock age class, as a function of deer or mule deer occurrence frequency (Tables 4.1 and 4.2; Fig. A4.6). Lynx occurrence was highest with frequent mule deer or deer occurrences (Fig. A4.6). Frequent prey occurrences were linked to rapid increases in lynx occurrence in areas with more regenerating prepared (Fig. 4.4A) or older unprepared cutblocks (Fig. 4.4B). No pattern was evident for prey modifying the relationship between lynx occurrence and other cutblock age classes, with or without site preparation (Table 4.2). However, lynx occurrence increased with higher proportions of older prepared and regenerating unprepared cutblocks (Table 4.2). Lynx occurrence decreased with lower road densities (Fig. A4.6). While a model including the interaction between road density and mule deer was supported, there was no trend in covariate (Table 4.1; Fig. A4.6). Additionally, lynx occurrence was positively associated higher elevations and conifer forest.

Cougar occurrence was best explained by the interaction between older brushed cutblocks and moose occurrence (Table 4.1). Cougar occurrence increased in areas with higher proportions of older brushed cuts when moose occurred infrequently but decreased with high moose occurrence frequency (Table 4.2; Fig. 4.4C).

Three variables were associated with bobcat occurrence: uneven-aged systems, forest age, and clearcuts with reserves (Table 4.1). Bobcat occurrence increased with higher proportions of uneven-aged systems (Table 4.2; Fig. 4.4D), older forests, and lower proportions of clearcuts with reserves (Fig. A4.7).

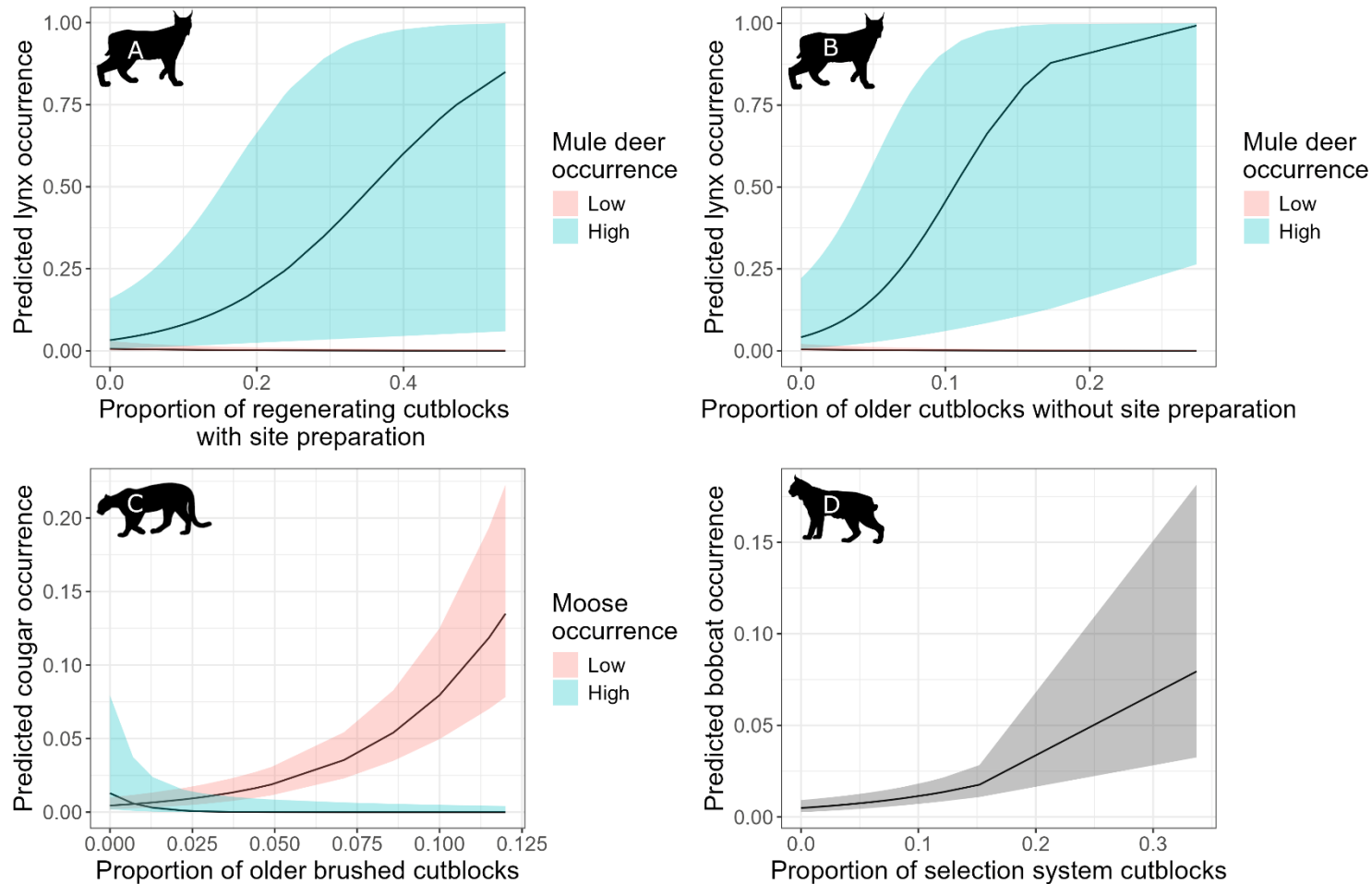


Figure 4.4 Predicted occurrence of felids in relation to forest harvest, silvicultural treatments, and prey occurrence based on camera trap data. Predicted occurrence of lynx (*Lynx canadensis*; A – B), cougar (*Puma concolor*; C), and bobcat (*L. rufus*; D) in relation to silviculture metrics, with an interaction with mule deer (*Odocoileus hemionus*; A and B) or moose (*Alces alces*; C), based on wildlife camera data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023). Model predictions for cougar and bobcat are from Bonaparte only. Prey occurrences are split into low (blue) and high (red) based on the 5th and 95th percentiles of relative abundance indices, respectively (mule deer occurrence: low = 0, high = 0.134)

Ungulate occurrence in response to silviculture and predator occurrence

Moose occurrence was best explained by cutblock age class interacting with wolf occurrence frequency (Table 4.1). Moose decreased with more new and older cutblocks, and less regenerating cutblocks (Table 4.2). When wolves occurred frequently, moose occurrence decreased (Table 4.2). Wolves modified moose relationships with cutblock age classes (Fig. 4.5A – C). Moose occurrence declined more rapidly in relation to higher proportions of new and older cutblocks when wolves frequently occurred (Fig. 4.5A and C). Conversely, moose occurrence increased with higher proportions of regenerating cutblocks when wolf occurrence frequency was high, but the opposite occurred when wolves occurred infrequently (Fig. 4.5B). Lower road density was linked to moose occurrence in one model, but not the other (Table 4.2). Although the interaction between road density and wolf occurrence frequency was included in one supported model, the coefficient showed no trend (Table 4.1; Fig. A4.8). Moose occurred at higher elevations, older forests, and deciduous forests (Table 4.2).

Mule deer occurrence was linked to site preparation based on cutblock age, roads, and their interaction with predator occurrence (Table 4.1). Mule deer decreased with regenerating and older prepared cutblocks but showed no trend for other site preparation age classes (Table 4.2). A slight positive relationship between mule deer and predator occurrence existed in one supported model, but not the other (Fig. A4.9). Higher predator occurrence modified mule deer occurrence in relation to proportions of site preparation by cutblock age classes but not road densities (Table 4.2; Fig. 4.5D – F). When predator occurrence frequency was low, mule deer occurrence decreased in areas with higher proportions of older prepared and new unprepared cutblocks (Fig. 4.5D and E). Conversely, mule deer occurrence was higher with more new unprepared cutblocks at higher predator occurrence levels (Fig. 4.5E). Mule deer occurrence decreased more rapidly in relation to higher proportions of older unprepared cutblocks when predators occurred frequently but increased when predator occurrence levels were low (Fig. 4.5F). Mule deer decreased with higher elevations, older forests, and conifer or deciduous forest (Table 4.2).

White-tailed deer occurrence was best explained by models including the interaction between silviculture system or cutblock age system with predator occurrence (all predators or bears only), and in some models, road density interacting with predator occurrence (Table 4.1). White-tailed deer decreased with selection cutblocks and new even-aged cutblocks, but we found no trend for clearcuts, clearcuts with reserves, or road density (Table 4.2). Predator and bear

occurrence frequency modified the relationship of white-tailed deer with silviculture systems and age systems, respectively (Table 4.1; Fig. A4.10). At high predator occurrence frequencies, white-tailed deer increased rapidly at higher proportions of clearcuts, lower proportions of clearcuts with reserves, and less selection cuts (Fig. 4.5G – I). More frequent bear occurrences were linked to higher white-tailed deer occurrence at lower proportions of new and regenerating even-aged cutblocks, and higher proportions of older even-aged cutblocks (Fig. A4.10). White-tailed deer occurrence increased with more deciduous forest or burnt habitat, and in some cases, younger forests (Table 4.2).

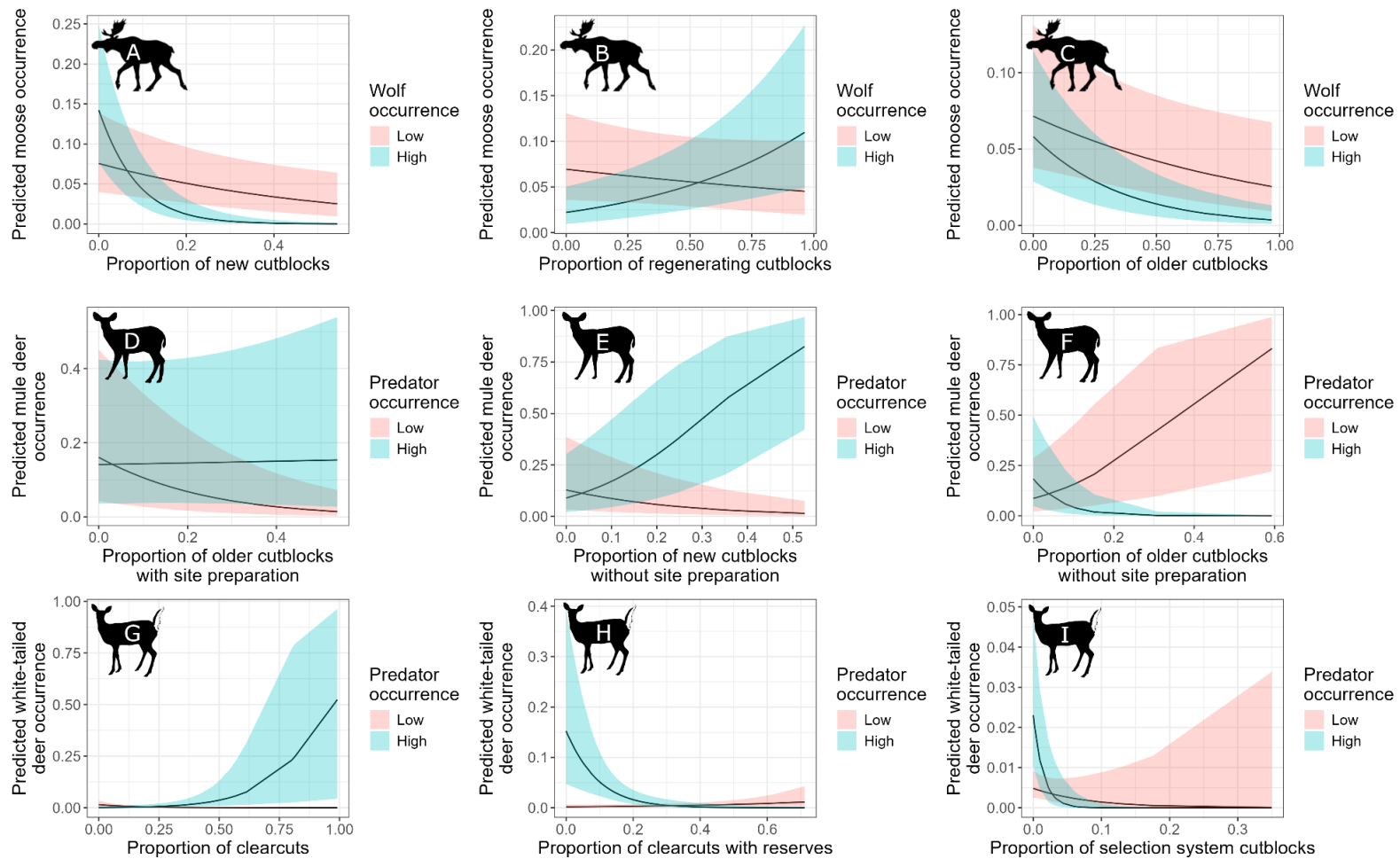


Figure 4.5 Predicted ungulate occurrence in relation to forest harvest, silvicultural treatments, and predator occurrence based on camera trap data.

Predicted occurrence of moose (*Alces alces*; A – C), mule deer (*Odocoileus hemionus*; D – F), and white-tailed deer (*O. virginianus*; G – I) in relation to silviculture, interacting with wolf (*Canis lupus*; A – C) or predator (D – I) occurrence frequency, based on wildlife camera data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023). Predator occurrences are low (blue) and high (red) based on the 5th and 95th percentiles of relative abundance indices, respectively (wolf occurrence: low = 0, high = 0.013; predator occurrence: low = 0.011, high = 0.169)

Seasonal responses of black bears, coyote, mule deer, and moose

To further explore the relationships of wildlife to silviculture, we conducted a post-hoc analysis examining seasonal occurrence of black bears, coyotes, mule deer, and moose – which all had sufficient detections for subsetting the data. We followed similar methods, but divided data into winter (November-April; excluding black bears), early summer (May-June; calving and ungulate neonates present), and late summer (July-October; juveniles gaining independence).

Seasonal predator occurrence

Black bear occurrence in early summer was associated with silviculture system by harvest age, roads, and prey; in late summer, we linked black bear occurrence to the interaction between site preparation by cutblock age and prey occurrence (Table A4.2). In early summer, black bears increased with selection system cutblocks, prey (including cattle) occurrence frequency, less new clearcuts, and in one supported model, lower road densities (Table A4.3). In late summer, black bears were increasingly associated with higher proportions of new prepared cutblocks at higher mule deer occurrence frequencies. During late summer, black bear occurrence decreased with higher road densities.

Coyote occurrence was driven by cutblock brushing in early summer and winter, and site preparation based on harvest age in late summer (Table A4.2). As manually brushed cutblocks increased, so did coyote occurrence during early summer and winter, but decreased proportions of unbrushed cutblocks were associated with increased coyote occurrence in winter (Table A4.3). In late summer, coyote occurrence increased with older clearcuts, selection cutblocks, and regenerating/older clearcuts with reserves (Table A4.2 and A4.3). Coyotes were linked to denser roads, mule deer occurrence, deciduous forest (late summer), older forests (late summer and winter), and less conifer forest (winter) (Table A4.3).

Seasonal ungulate occurrence

Moose seasonal occurrence was associated with age system (early summer), site preparation type (late summer), cutblock fertilization (winter), and the interaction of predator occurrence and silviculture or roads (Table A4.2). In early summer, moose were linked to lower proportions of uneven-aged systems and burns, and increased predator occurrence frequencies (Table A4.3). In late summer, moose occurrence increased more rapidly around cutblocks with non-mechanical or no site preparation when coyote occurred frequently. Moose occurred frequently near water and with infrequent coyote occurrences in late summer. In winter, moose

occurrence increased more rapidly in areas with more fertilized cutblocks when wolf occurred frequently (Table A4.3). During winter, moose occurrence increased with higher wolf occurrence frequencies and deciduous forest.

We linked mule deer seasonal occurrence to the interaction of predator occurrence with edge density by cutblock age (early summer), site preparation by cutblock age (late summer), or silviculture system (winter), and the additive effects of roads (Table A4.2). In early summer, mule deer occurred more with higher edge densities of older cutblocks when canids occurred frequently (Table A4.3). Additionally, mule deer decreased with higher regenerating cutblock edge densities, denser roads, conifer forest, and lower elevations. In late summer, mule deer occurrence decreased with regenerating and older prepared cutblocks, deciduous forest, and older forests. As predators increased, mule deer occurred less frequently with regenerating prepared cutblocks and older unprepared cutblocks but increased with new unprepared cutblocks. During winter, mule deer occurrence increased around clearcuts with reserves when predators occurred infrequently but increased around selection cutblocks when predator occurrence was frequent. Winter mule deer occurrence was negatively associated with elevation and distance to water.

4.4 Discussion

Predator and ungulate occurrence and their spatial relationships were linked to silvicultural treatments, not just patterns of forest harvest. A combination of forest harvest patterns, silvicultural treatments, and predator/prey occurrence frequency best explained species distributions across extensively harvested landscapes. Additionally, all species examined for seasonal occurrence exhibited varied habitat associations throughout the year, indicating that the impacts of silviculture treatments are often seasonally dependent. Our results highlight the importance of considering the complex effects of silviculture upon predator-prey dynamics in wildlife studies and when planning forest management strategies, to maintain ecological integrity and resilience of wildlife populations.

The role of silviculture in wildlife occurrence and predator-prey relationships

Although forest successional patterns influence wildlife distributions (59), silvicultural treatments also shape species occurrences. Across all predator and ungulates in our study, only moose were best explained by cutblock age classes. In contrast, occurrence of all other species (and moose seasonally) was better described by various silvicultural treatments, including

silviculture system, site preparation, planting, brushing, spacing and fertilization, although often in combination with harvest age.

Possibly, the importance of harvest age to moose, and lessened impact on other species, reflect our cutblock age thresholds. These thresholds are based on adult female moose habitat selection in our study areas (41), likely explaining the close relationship between moose occurrence and harvest age. Our results reflected those in Mumma, Gillingham (41), with lower moose occurrence in new and older cutblocks, but higher occurrence in regenerating cutblocks (when wolves occur frequently). These patterns reflect successional shifts in vegetation composition and regrowth, which impacts forage and predation risk (40, 41, 126). Wolves in PGS select new cutblocks and moose kill-sites were linked to both new and regenerating cutblocks (41, 126). This would explain reduced moose occurrence in new cutblocks when wolves occur frequently – although the opposite was observed for regenerating cutblocks, indicating that moose may perceive these habitats as less risky, perhaps due to increased lateral cover. Our cutblock age thresholds also capture broad successional trends in post-harvest vegetation regeneration which impact wildlife utilization across multiple taxa (59). Silvicultural treatments modify these stages by enhancing tree growth and removing competing vegetation, causing varied responses among other species that are influenced by both harvest age and silviculture. Variation in forest regeneration created by different silvicultural treatments could explain some variability observed in moose habitat selection (40, 41), as seasonal moose occurrence was explained by site preparation, silviculture system, and fertilization.

Both the successional stages captured by harvest age classes and their modification through silviculture are important for predators and ungulates. We found that silvicultural systems impacted bobcat, grey wolf, grizzly bear, and white-tailed deer occurrences; site preparation impacted black bear, lynx, and mule deer; brushing impacted cougar and coyote; and fertilization impacted wolf. These silvicultural treatments play an important role in shaping species occurrence, often in combination with harvest age classes and predator/prey occurrence.

Silvicultural systems guide forest stand treatments, broadly shaping vegetation regeneration and stand structures present in successional stages (228, 245). Uneven-aged selection systems create canopy openings facilitating patchy understory vegetation growth, potentially benefiting species like bobcat that require hiding cover and understory vegetation for prey (246). For species associated with abundant early seral vegetation, heterogenous

regeneration patterns in selection cutblocks may not be ideal. Moose in early summer and white-tailed deer were negatively associated with selection cutblocks, consistent with their association with younger forest and nutritional requirements in this season due to lactation (40, 176, 247). However, for white-tailed deer, we only observed increased occurrence in clearcuts when predators frequently occurred: possibly, clearcuts offer improved predator detection and escape routes, in addition to potential forage, for white-tailed deer. Even-aged systems create larger forest openings with reduced cover, with heterogeneity modified by configuration and retention of unharvested forest that may affect species occurrences (248), like wolves. Regenerating/older clearcuts with reserves provide both abundant forage and cover for ungulates, which could create ideal hunting opportunities for wolves. Conversely, regenerating clearcuts without reserves might have inadequate habitat complexity to support ungulates (248), leading to decreased wolf occurrence unless prey are present. Due to limited prevalence of other silviculture systems in our arrays, we primarily tested the effects of clearcuts, clearcuts with reserves, and selection systems. Future studies should assess how alternative systems that retain additional habitat complexity (e.g., shelterwood, patch cut) impact predator-prey dynamics.

Silvicultural treatments further modify regeneration trajectories and vegetation communities (228, 249, 250). A main objective of silviculture is to achieve a free growing status – an established forest stand meeting stocking requirements and ensuring the tree species of interest dominates future growth without being outcompeted or requiring further interventions – by creating favorable tree growing environments, often by removing or inhibiting growth of competing plant species. We linked species occurrences and predator-prey relationships to silvicultural treatments that enhance tree regeneration and reduce competing vegetation, including site preparation (black bear, lynx, and mule deer), brushing (cougar and coyote), and fertilization (wolf).

Site preparation creates ideal microsites for tree regeneration but, depending on disturbance severity and site attributes, impacts structural and species diversity (245, 249). Surprisingly, black bear occurrence increased in new cutblocks with site preparation when prey occurred infrequently but decreased in those without site preparation – despite the negative impacts of site preparation on berry production (249). However, when prey occur infrequently, new prepared cutblocks may provide alternative foods, like graminoids, that are part of black bear diets (249, 251). Mule deer were impacted by site preparation, with increases in occurrence

around older prepared cutblocks but decreases in occurrence in relation to older unprepared cutblocks, in areas with frequent predator occurrences. Possibly, lynx are opportunistically preying on mule deer (236), as lynx increased in occurrence when mule deer occurred frequently in older unprepared cutblocks.

Vegetation management treatments intended to enhance tree growth rates by providing nutrients or removing competition, such as brushing and fertilization, impacted species occurrences. When deer occurred frequently, coyote occurrence decreased more rapidly in chemically brushed cuts but increased in manually brushed cutblocks. Herbicides reduce understorey forage biomass for deer (218), whereas manually brushing likely has a lessened effect on available browse. When deer occur infrequently, coyotes may use chemically-brushed cutblocks for hunting smaller prey that are unaffected or increase in abundance in these habitats (250). Unexpectedly, coyotes were negatively associated with unbrushed cutblocks, indicating that vegetation disturbances are beneficial for this species (252). Cougar occurrence increased rapidly in relation to older brushed cutblocks when moose occurred infrequently, suggesting a different use for this habitat, such as hunting alternative prey. Cutblock fertilization affected wolf relationships with moose, with wolf occurrence increasing more drastically in fertilized cutblocks, compared to unfertilized cutblocks, when moose occurred frequently. Fertilized cutblocks could increase browse for moose or alternatively, inhibit growth of shade-intolerant species due to faster forest canopy regeneration (253).

Unexpectedly, other silvicultural treatments, such as planting and spacing, were not among the most supported models for all species. Tree planting impacts species compositions, creates uniform tree spacing and densities, and improves forest establishment (254). Spacing would influence habitat structure and tree growth, due to impacts on competition, canopy closure, light availability, and understory vegetation growth (254, 255). Despite our results, these silvicultural treatments could still affect wildlife and should be explored further.

Industrial roads and wildlife occurrences

Industrial roads have well documented impacts on wildlife, with predators typically utilizing these linear features for travel and hunting, and ungulates exhibiting varied responses due to predator avoidance or human refuge effects (53, 126, 162). Our results support these general patterns of use: wolves and coyotes were associated with higher road densities, whereas ungulates were not or showed no patterns.

Wolves use disturbance features to travel and hunt prey (49, 126), which is supported by our findings that wolf occurrence increased with road densities when prey were available. Coyotes were linked to increasing road densities, and likely use these features similarly. Not all predators shared this association, though. Black bears decreased with denser road, possibly due to human avoidance as hunting is common in both regions. However, only one supported model indicates avoidance of road densities. Black bears do use linear features for travel and forage on vegetation along road shoulders (53, 251), which may result in the unclear trend. Lynx occurrence decreased at higher road densities, supporting studies showing human avoidance by lynx (256).

Ungulates either were negatively associated with roads (moose) or exhibited no patterns (mule and white-tailed deer). Moose likely avoid roads due to wolves (126). Lack of observed response for other species may indicate a mix of road avoidance due to predators (although interactions between predator occurrence and road density were poorly supported) and selection for roads as travel corridors or forage subsidies.

Caveats

Our study has limitations that may influence results on the associations of wildlife with forest harvest and silviculture. A main caveat is that stand tending treatments are not always applied across the entire cutblock but are still recorded as treated in RESULTS data. If treatments were only applied to part of the cutblock, measurements of that treatment would be overinflated, creating bias in our results. However, we were unable to assess the effects of silvicultural treatment distributions within cutblocks. We did not explore the effects of repeated silviculture treatments (e.g., multiple herbicide applications), which could affect the strength of response of species to treatments. Additionally, while silviculture decisions likely interact with each other to influence wildlife occurrences, we were unable to test for these effects due to limited sample sizes, but these interactions should be explored in future studies.

Management implications and recommendations

Considering the effects of silviculture is important to guide ungulate and predator management in harvested landscapes. We observed cases where species exhibited opposing relationships to cutblocks based on varying silvicultural applications. In these cases, not accounting for silviculture would mask wildlife relationships with cutblocks, producing misleading results that researchers might misinterpret as lack of response. Despite this, many

studies only quantify the effects of harvest area or age on wildlife. We provide evidence indicating that integrating silvicultural approaches benefits wildlife, because of all species, only moose occurrence was best explained by cutblock age class. When studying relationships between wildlife and forest harvest, researchers should account for silviculture to provide additional insights for wildlife management.

Resource managers are encouraged to consider ecological effects of silviculture on predators and ungulates, and their relationships. Our results support a growing body of work indicating that silviculture impacts predator-prey dynamics (216, 217), possibly contributing to population declines of species inhabiting extensively harvested landscapes. Because species respond in complex ways to silviculture, we recommend that resource managers implement diverse treatments across a variety of harvest ages, such that a mosaic of habitats is maintained at landscape- and home range-scales. In regions with declining populations, like moose in BC (20), resource managers should ensure that silvicultural treatments that negatively affect habitat suitability, predation risk, and/or prey availability for that species, are applied conservatively. Silvicultural treatments benefiting ungulates, which are less preferred by their predators (e.g., fertilized cutblocks which were linked to moose winter occurrence but decreased wolf occurrence), could be implemented for declining ungulate populations to increase spatial separation from predators. Ecological objectives should be increasingly incorporated into silvicultural programs, as treatments can enhance wildlife habitat and support their populations. However, licensees are incentivized to quickly achieve free-to-grow status for cutblocks due to regulatory requirements and/or financial motivations, potentially impacting treatment feasibility. In such cases, we recommend resource managers implement alternative treatments that meet resource objectives while ensuring beneficial ecological impacts, such as implementing variable retention harvesting, promoting natural regeneration, or employing fertilization treatments that enhance forage while limiting predator attraction, to benefit ungulate populations. Integrating ecological objectives into silvicultural programs will ensure sustainable forestry practices that support both timber production and biodiversity goals.

Chapter 5: Forest harvest and natural stressors compound to reduce juvenile ungulate survival

5.1 Introduction

Resource extraction is a primary driver of changing landscapes worldwide, with profound and often adverse consequences for biodiversity (257). Anthropogenic disturbances rapidly alter and fragment habitat, modifying animals' fitness outcomes by affecting resources and risk factors (60). Juveniles – whose survival is often critical in population persistence – may be particularly sensitive to anthropogenic disturbance (42). Unlike adults, who generally exhibit stable survival rates in response to disturbances, juveniles face a more precarious existence (42, 43). Juveniles face numerous challenges to survive and are more vulnerable than adults to intrinsic and extrinsic risk factors, leading to wide variation in survival (44, 128). In human-altered landscapes, these stressors may intensify, further impacting juvenile survival and in some cases, leading to population declines (42).

For species increasingly affected by these human disturbances, such as moose *Alces alces*, understanding the impacts of resource extraction on juvenile survival is crucial for effective population management and conserving functional ecosystems. Moose, a species of great importance to Indigenous food sovereignty, are experiencing population declines that often both coincide with high human disturbance and are tied to low juvenile survival (20, 24, 134). Forest harvest is one of the main disturbances affecting moose habitats (214). Creation of forest harvest features, such as early-seral cutblocks and forestry roads, modifies the availability, quality, and distribution of resources, in addition to altering predator-prey dynamics and hunting harvest (40, 41, 126, 258). Cutblocks provide clear sightlines for predators and hunters, while concentrating moose in remaining resource patches and altering forage availability and quality (126, 158, 258). Roads facilitate predator travel efficiency and access to remote areas by hunters, improving their hunting efficiency (126, 259).

While moose benefit from forest harvest creating early successional habitats with high forage biomass, population declines can also coincide with logging (214). One such example is found in western Canada, where moose populations decreased concurrently with rapid and

extensive salvage logging following mountain pine beetle *Dendroctonus ponderosae* outbreak (20, 139). In this region, moose show variable responses to forest harvest (40, 41), and recent cutblocks and roads are linked to adult female mortality risk from wolves, hunters, and apparent starvation (39). Stable adult female survival potentially implicated juveniles in population declines (139), but little is known about how juvenile moose survival is affected by forest harvest or how other risk factors, such as parasitism, predation, forage, and weather, compound with forest harvest to influence juvenile vulnerability.

Given the critical role of juvenile survival in ungulate population dynamics (42), understanding the complex natural and anthropogenic mechanisms driving their vulnerability in anthropogenically-altered landscapes is essential. Using survival analysis, we explored the interactions between forest harvest and health (weight and winter ticks *Dermacentor albipictus*), predation risk, forage availability, long-term forest harvest use, and weather (daily and previous winter temperature) on juvenile moose survival from 7-8 months old to recruitment at 18 months old in multiple altered landscapes in British Columbia, Canada. Specifically, we ask: (i) Does use of cutblocks and roads increase juvenile mortality risk? And (ii) Is this risk modified by juvenile body condition, long-term use, forage availability, weather, or predation risk from grey wolves *Canis lupus* and/or black bears *Ursus americanus*? We expected use of forest harvest features would increase juvenile mortality risk due to increased search efficiency of predators and hunters on roads and cutblocks. We predicted that as predator occurrence increased in these habitats, so would juvenile hazard. As animals in poor condition often exhibit risk-prone behaviors and vulnerability to predation, we predicted that winter tick infestations, lower body weights, higher forage availability, long-term forest harvest use, and thermal stress would elevate juvenile mortality risk when using areas with more forest harvest features.

5.2 Methods

Study areas

Moose populations declined across British Columbia (20, 31). We selected two different study areas representative of this trend: Prince George South (PGS; 11,060 km²) and the Bonaparte Plateau (6,776 km²; Fig. 5.1; Appendix 5). Moose population declines were observed in both, coinciding with significant salvage logging and linear infrastructure following mountain pine beetle outbreaks (20, 31, 33, 41). While current trends indicate stable and/or increasing

populations (139), understanding potential mechanisms for declines is key for future management.

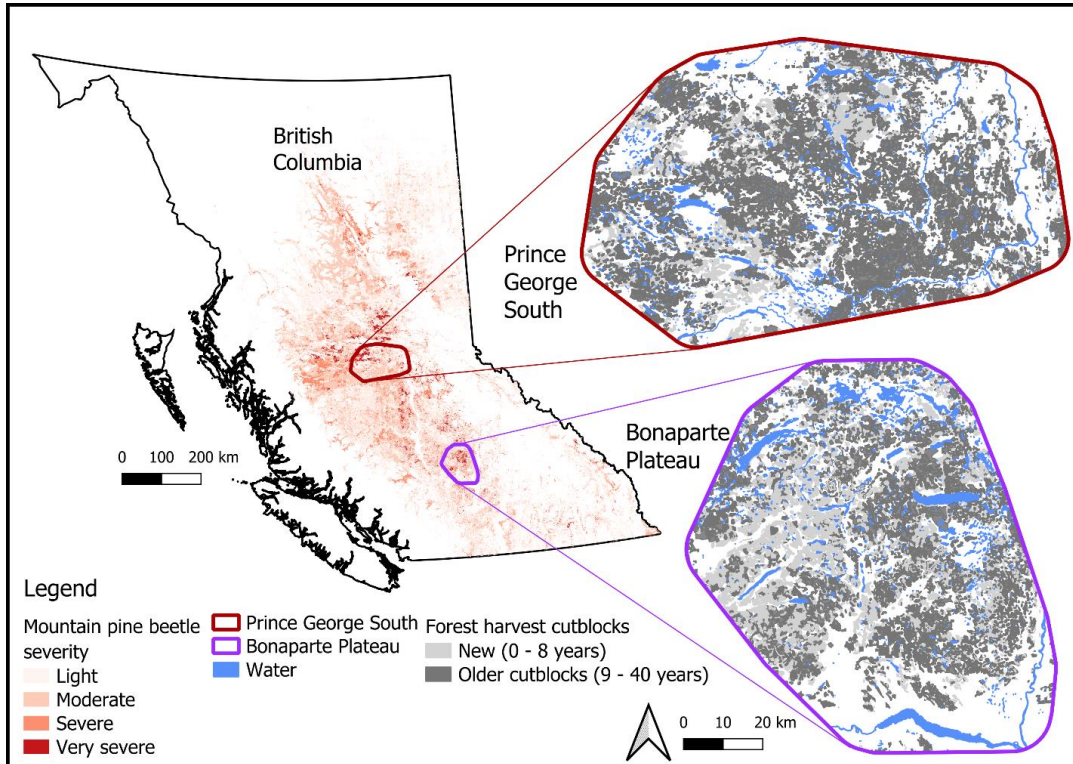


Figure 5.1 Distribution of mountain pine beetle infestation and forest harvest across the study areas, Prince George South and Bonaparte Plateau, in British Columbia, Canada.

Juvenile moose monitoring and mortality investigations

We captured juvenile moose following Canadian Council on Animal Care guidelines and BC *Wildlife Act* permit CB17-277227. All captures were conducted between December and March 2016/2017-2020/2021 (Bonaparte) or 2017/2018-2020/2021 (PGS), when animals were 7-8 months old (mean birth date: May 21) (Appendix 5 for capture details). We weighed calves in kilograms using a helicopter-lifted sling or estimated weight using morphological measurements. We quantified winter ticks by totaling counts from 10x10 cm rump and shoulder plots with transects spaced every 2 cm (260). We fit calves with expandable Vectronic Aerospace VERTEX Survey Iridium collars (Berlin, Germany), which transmitted six locations per day and sent alerts if no movement was detected for 8 hours.

Mortality sites were assessed, typically within 24 to 48 hours of alerts, to determine proximate cause of death (the event immediately responsible for death) following a standardized protocol (32, 139). During investigation, the mortality site was searched for predator sign (e.g.,

scat). Carcass remains were examined for trauma, pre-existing health issues, and abnormalities. When available, we collected samples to further inform the ultimate cause of death (conditions predisposing the animal to die), including long bone(s) for bone marrow fat analysis. High marrow fat content does not necessarily indicate good condition, as marrow fat is utilized last, but low percentages indicate malnutrition (261). Marrow was extracted from a 10-cm section, dried at 60°C until weight stabilization, and the final dry-to-wet weight ratio indicated apparent starvation (262).

Based on investigations, we classified mortalities as predation (wolf, cougar, or bear), health-related (parasitism, nutrient deficiencies, disease, etc.), or human-caused (vehicle strike, hunting). We focused on proximate mortality causes, rather than ultimate as it is often difficult to discern. Mortalities within five days following capture were removed from analyses, as capture can influence behavior and survival (140).

Survival rates and cause-specific mortality

Using generalized Kaplan-Meier estimators calculated on the complementary log-log scale using the package *survival* (263, 264), we estimated overall survival rates with 95% confidence intervals of juvenile moose from capture to recruitment into the population at 18 months old, estimated as November 1 in the year following their birth. We chose 18 months as this indicated survival through the first rut when juveniles could breed (265). Moose were right-censored if they survived to recruitment or on the collar failure date. We used log-rank tests to compare estimates between groupings that may influence survival rates, including sex and study area (266). If groups did not differ significantly, we pooled data in further analyses. To assess cause-specific mortality rates, we calculated cumulative incidence functions accounting for competing risks using the *cmprsk* package and smoothed cause-specific hazard curves using the *bshazard* package (267-269). We used linear regressions to compare bone marrow fat content and winter tick loads to mortality causes, and winter ticks to body weight. All analyses were conducted in R version 4.4.1 (136).

Survival analysis

We assessed how predation risk, forest harvest, health (body weight and winter tick load), forage availability, long-term forest harvest use, and weather influenced juvenile moose daily mortality risk using the Andersen-Gill formulation of the Cox proportional hazards model – a

continuous time-to-event counting process method that accommodates time-dependent covariates (270, 271) – expressed as:

$$[1] \quad h(t|x_i) = h_0(t)e^{x_i\beta}$$

Where $h_0(t)$ represents the baseline hazard function at time t , x_i represents covariate i which potentially modifies the mortality hazard, and β represents the risk regression coefficient (272). Hazard ratios (HR) are calculated by exponentiating beta coefficients from the survival model, with $HR > 1$ indicating increasing risk and $HR < 1$ indicating decreasing risk, as the corresponding risk covariate increases.

Juveniles had staggered entry into the analysis, entering at time of capture and exiting at death (event = 1) or right-censoring (event = 0) at recruitment or the collar failure date. We did not separately model mortality causes due to limited sample sizes.

We constructed a set of *a priori* candidate models representing our hypotheses on how risk factors impact juvenile moose survival and fit models using the function ‘coxph’ in the package *survival* (263). All models included a cluster term for individual ID and a categorical term for sex. We used winter tick load and age-adjusted weight (i.e., weight/age at capture) to represent body condition. We tested the effects of forest harvest – new (0-8 years since harvest) and older (9-40 years) cutblocks, and road density (km/km²) – as well as forage availability and predation risk, by extracting spatial data around daily moose locations, and weather by extracting daily and winter temperatures (Appendix 5 for details). Using the full model, we assessed the proportional hazards assumption (263), accounting for violations using time stratifications. We used Akaike’s Information Criterion corrected for small sample sizes (AIC_c) for model selection, with $\Delta AIC_c < 2$ indicating substantial support (187). We report the concordance index as a measure of predictive accuracy.

5.3 Results

Juvenile moose survival monitoring

We captured 100 calves (female: 48, male: 52) in Bonaparte and 80 calves (female: 44, male: 37) in PGS (Table A5.1). Calf weight (mean ± s.d.) was 176.4 ± 22.1 kg in Bonaparte and 195 ± 16.5 kg in PGS. Winter tick load (mean ± s.d.) on calves was 9 ± 14 in Bonaparte and 12 ± 11 in PGS.

Of 180 juveniles, 111 survived to recruitment. Juvenile survivorship was 0.59 (95% CI = 0.51, 0.67) (Fig. 5.2, Table A5.2). Juveniles in Bonaparte ($\hat{S} = 0.63$, 95% CI = 0.52, 0.72) and PGS ($\hat{S} = 0.55$, 95% CI = 0.42, 0.66) had similar survival rates ($\chi^2 = 0.1$, $p = 0.8$; Fig. 5.2). Females ($\hat{S} = 0.71$, 95% CI = 0.59, 0.80) had higher survival than males ($\hat{S} = 0.47$, 95% CI = 0.36, 0.57; $\chi^2 = 9.9$, $p = 0.002$).

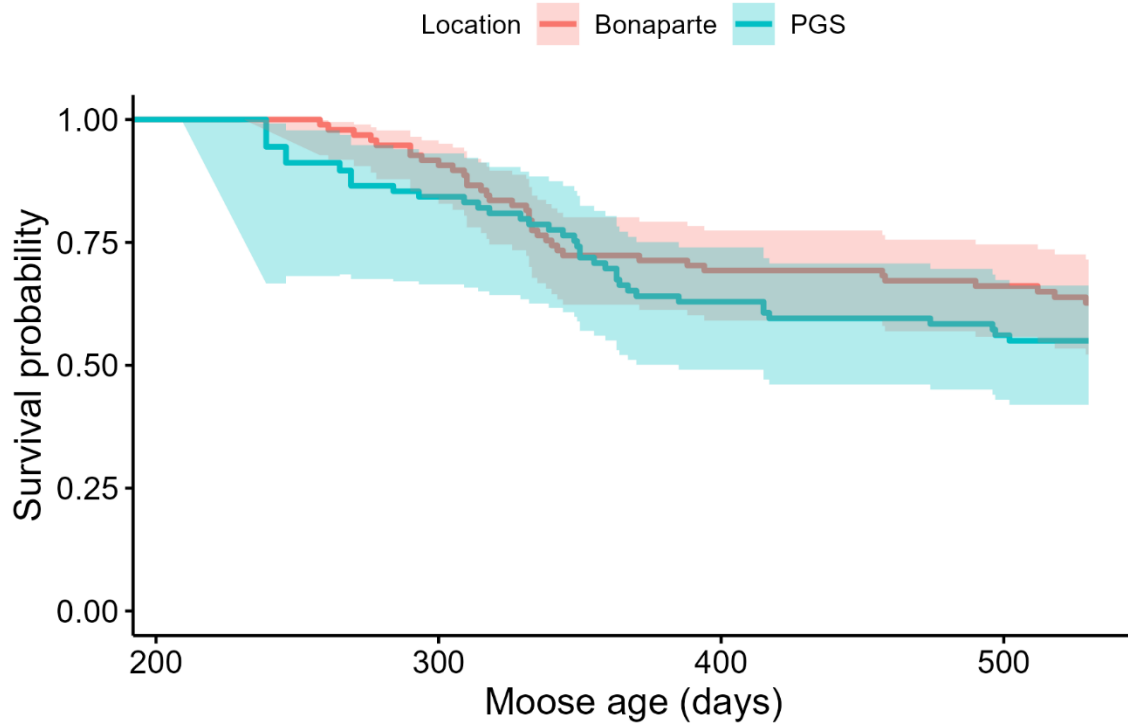


Figure 5.2 Juvenile moose survival probability from capture (7-8 months old) to 18 months old in Bonaparte and Prince George South (PGS), 2016-2021.

Wolf predation was the main cause of juvenile mortality ($n = 38$). Other causes included bear predation (black bear $n = 8$, grizzly bear $n = 2$), human-related (licensed $n = 6$, unlicensed [legal Indigenous harvest or illegal poaching] = 3, vehicle strike $n = 1$), health-related ($n = 7$), and cougar predation ($n = 4$) (Table A5.1; Fig. 5.3). Most mortalities were from predation (CIF = 0.289, 95% CI = 0.225-0.357) rather than other causes (CIF = 0.098, 95% CI = 0.059-0.147) (Fig. 5.3). Wolf predation had the highest probability of occurring (Fig. 5.3A; CIF = 0.211, 95% CI = 0.155-0.274), with the first occurrence at a moose age of 239 days. Hazard from wolves peaked in late winter, while hazard from other causes increased later in spring (Fig. 5.3B). Human-related mortality causes had a cumulative incidence of 0.059 (95% CI = 0.030-0.101). Human-related mortalities began by the age of 332 days (vehicle strike) but hunting events

occurred later, during fall (unlicensed hunting = 458 days, licensed = 490 days). Moose mortalities from bear predation had a cumulative incidence of 0.06 (95% CI = 0.03-0.10), beginning in spring at an age of 335 days (CIF = 0.006, 95% CI = 0.0005-0.03), with hazard increasing over summer. Health (CIF = 0.039, 95% CI = 0.017-0.075) and cougar predation (CIF = 0.022, 95% CI = 0.007-0.052) contributed the least to mortalities. Health-related mortalities first occurred at an age of 284 days, whereas cougar predation occurred at 270 days.

Mean bone marrow fat content was $28.5 \pm 26.8\%$ (range: 0 – 94.7, n = 53). Human-caused mortalities had the highest bone marrow fat content ($\beta \pm SE = 71.27 \pm 13.67$), whereas health-related mortalities had the lowest (Fig. 5.4A), compared to wolf ($\beta \pm SE = 16.29 \pm 9.26$), bear ($\beta \pm SE = 26.21 \pm 11.00$), and cougar ($\beta \pm SE = 22.56 \pm 13.69$). Juveniles with more winter ticks had lower body weights at capture ($\beta \pm SE = -0.18 \pm 0.07$) but not lower bone marrow fat content at death ($\beta \pm SE = -0.13 \pm 0.09$). Health-related mortalities had most winter ticks ($\beta \pm SE = 32.31 \pm 4.48$) compared to human-caused ($\beta \pm SE = 3.23 \pm 3.79$), wolf ($\beta \pm SE = 3.50 \pm 2.16$), bear ($\beta \pm SE = 4.43 \pm 3.79$), and cougar mortalities ($\beta \pm SE = 0.78 \pm 5.85$) (Fig. 5.4B). Weight was lowest for health-related mortalities ($\beta \pm SE = -13.40 \pm 5.4$), compared to human-caused ($\beta \pm SE = -4.87 \pm 4.61$), wolf ($\beta \pm SE = 0.21 \pm 2.62$), bear ($\beta \pm SE = -5.23 \pm 4.61$), and cougar mortalities ($\beta \pm SE = -1.83 \pm 7.10$) (Fig. 5.4C).

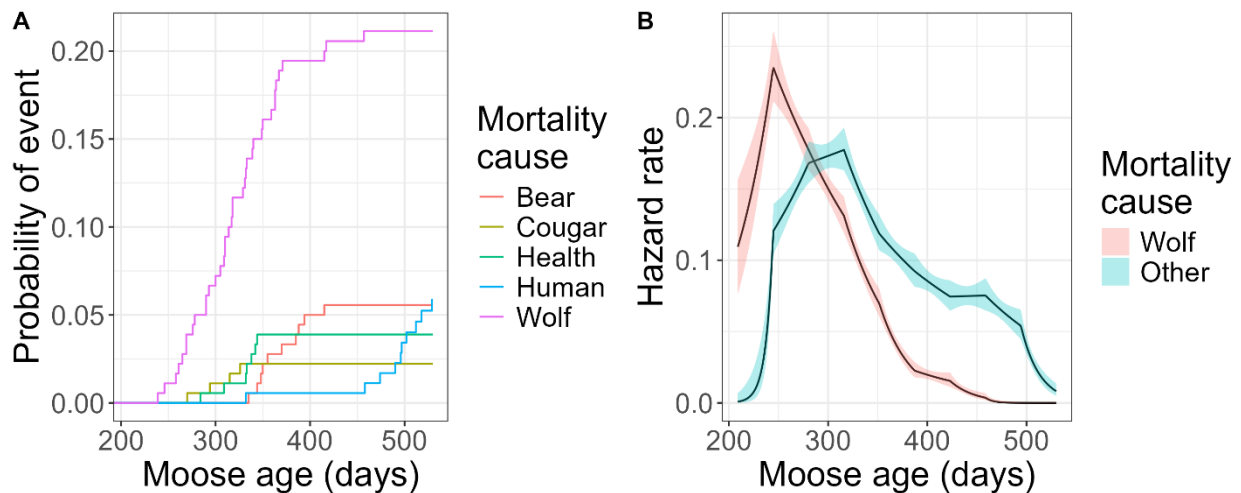


Figure 5.3 Probability of event and hazard rate for moose calves based on different mortality causes. A) Cause-specific mortality probability of juvenile moose between capture (7-8 months old) to 18 months old, created using cumulative incidence functions. B) Hazard rate from wolves or other mortality causes (including human-caused, health, cougar, or bear) for juvenile moose.

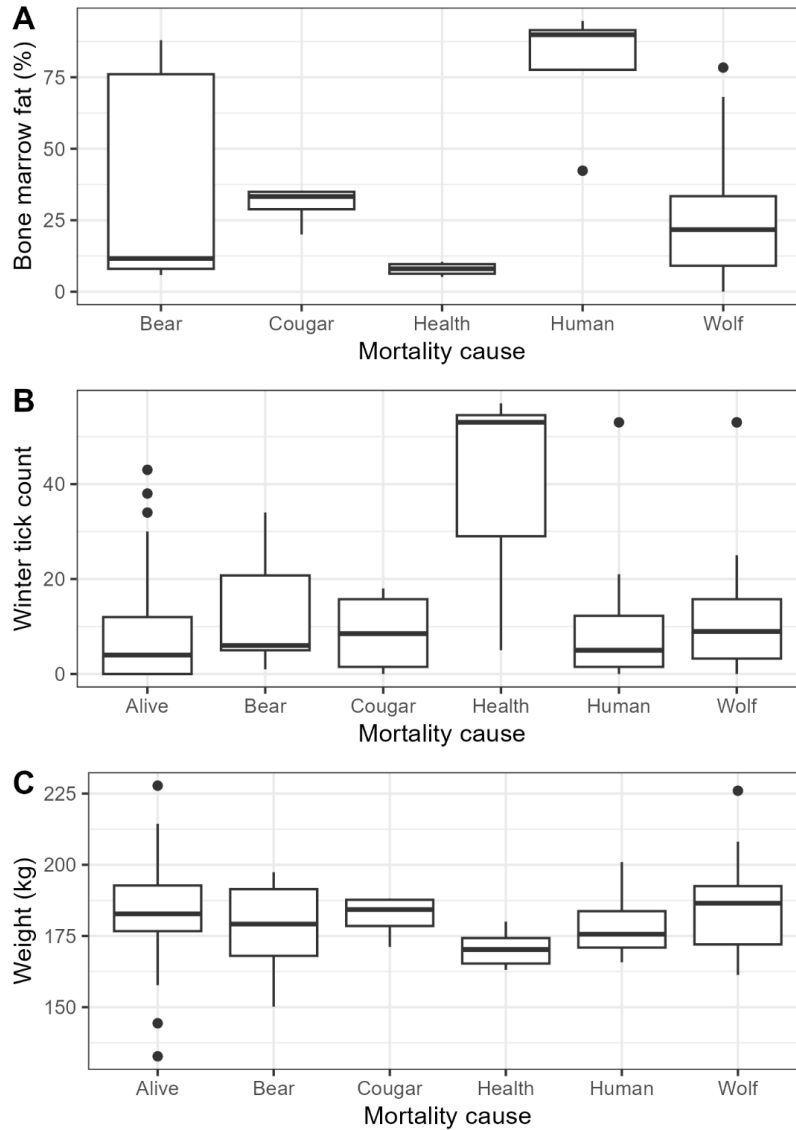


Figure 5.4 Body condition, including **A) bone marrow fat content, B) winter tick count at capture, and C) weight at capture, by mortality causes for juvenile moose captured at 7-8 months old and monitored for survival to November 1 of the year following birth in the Bonaparte Plateau and Prince George South, 2016-2021.**

Juvenile moose survival in relation to forest harvest and other risk factors

Due to limited mortality events, we pooled individuals across locations, years, and mortality causes. Sex ($\chi^2 = 8.52877$, $p = 0.0035$) and weight ($\chi^2 = 6.67154$, $p = 0.0098$) violated the proportional hazards assumption (Global $\chi^2 = 25.34315$, $p = 0.0133$) and to account for the time-dependent effects, we stratified these variables by age class (0 = calf, 1 = yearling). After stratification, all variables met the proportional hazards assumption (Global $\chi^2 = 20.2437$, $p =$

0.123). For most variables, the 1000-m buffer was most supported, except for long-term cutblock use (250-m), long-term road density use (250-m), and bear risk (500-m) (Table A5.3).

Use of forest harvest, combined with winter tick load or weight, most influenced juvenile moose survival (Table A5.4, Fig. 5.5). Use of higher road densities ($\beta \pm SE = 0.36 \pm 0.15$; HR = 1.44 (95% CI: 1.06-1.95)) and proportions of new cutblocks ($\beta \pm SE = 0.25 \pm 0.12$; HR = 1.29 (95% CI: 1.02-1.64)) increased juvenile risk (Fig. 5.5A-B), but older cutblocks did not ($\beta \pm SE = -0.22 \pm 0.14$; HR = 0.81 (95% CI: 0.61-1.07)). Juvenile mortality risk increased 43% for every additional 1-km of road per km². Higher tick infestations elevated mortality risk ($\beta \pm SE = 0.31 \pm 0.12$; HR = 1.37 (95% CI: 1.08-1.73); Fig. 5.5C). Each additional winter tick increased the hazard risk by 2%. Interactions between winter tick load and new cutblocks ($\beta \pm SE = 0.10 \pm 0.12$; HR = 1.37 (95% CI: 0.94-1.31)), older cutblocks ($\beta \pm SE = -0.22 \pm 0.81$; HR = 0.81 (95% CI: 0.92-1.41)), and road density ($\beta \pm SE = 0.10 \pm 0.12$; HR = 0.92 (95% CI: 0.72-1.18)) showed no trend. Age-adjusted weight showed no trend ($\beta \pm SE = 0.08 \pm 0.14$; HR = 1.08 (95% CI: 0.82-1.44)), except when stratified by age class ($\beta \pm SE = -1.11 \pm 0.32$; HR = 0.32 (95% CI: 0.18-0.61)). Lower capture weights elevated mortality risk of yearlings, whereas this effect was not pronounced for calves (Fig. 5.6A).

While the 'Forest harvest X Weight' model was supported (Table A5.4), interactions between age-adjusted weight and new cutblocks ($\beta \pm SE = -0.14 \pm 0.08$; HR = 0.87 (95% CI: 0.74-1.03)), older cutblocks ($\beta \pm SE = -0.14 \pm 0.12$; HR = 0.87 (95% CI: 0.69-1.09)), and road density ($\beta \pm SE = 0.04 \pm 0.15$; HR = 1.04 (95% CI: 0.78-1.40)) showed little trend. Sex ($\beta \pm SE = 0.39 \pm 0.29$; HR = 1.47 (95% CI: 0.84-2.59)) had little effect on risk, except when considering age ($\beta \pm SE = -1.92 \pm 0.74$; HR = 0.15 (95% CI: 0.03-0.62)). Female yearlings had 85% lower risk than yearling males, whereas hazards for male and female calves were more similar (Fig. 5.6B).

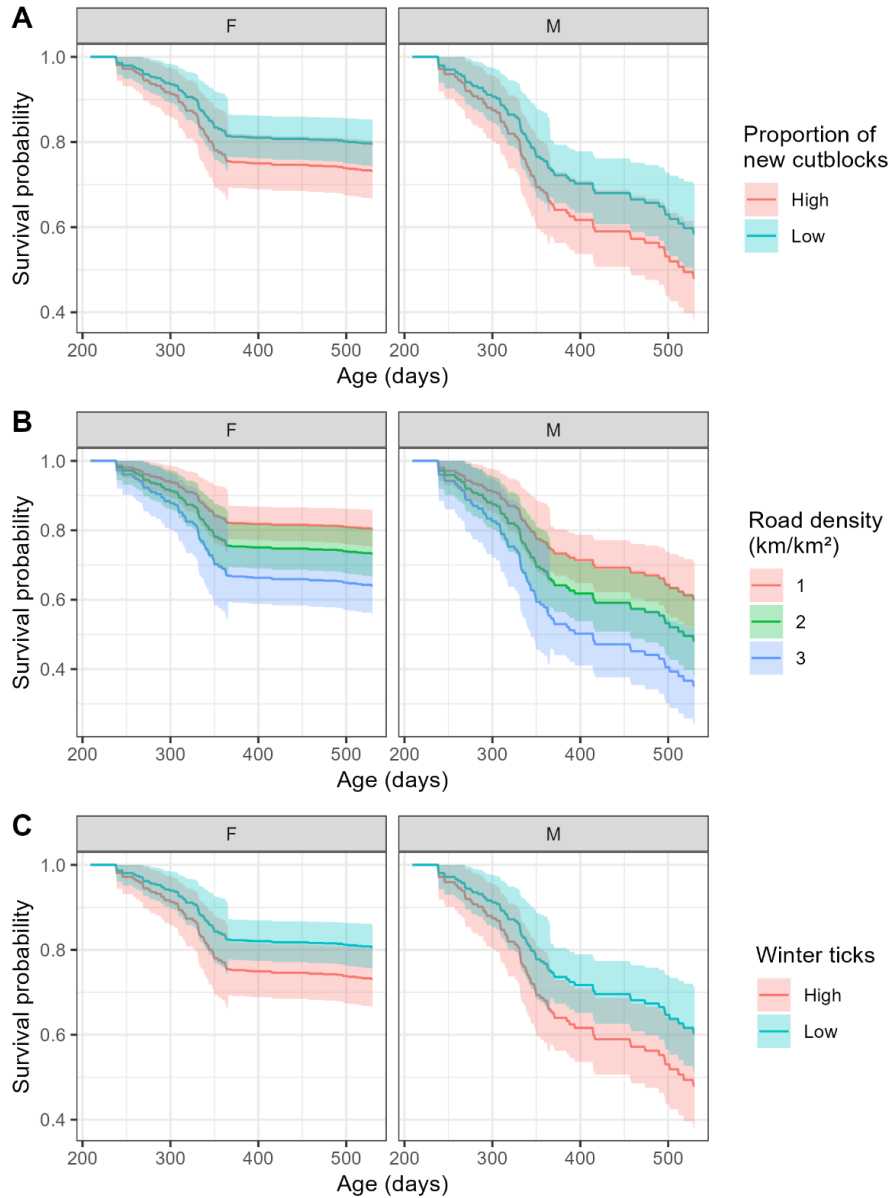


Figure 5.5 *Survivorship of juvenile moose in relation to forest harvest features and parasitism.* Predicted survivorship (95% confidence intervals) of juvenile moose as a function of sex and A) new cutblocks (low = 0, high = 0.23), B) road density, or C) winter tick load (low = 0, high = 13), in the Bonaparte Plateau and Prince George South, 2016-2021. For A and C, low and high values are 25% and 75% quantiles, respectively.

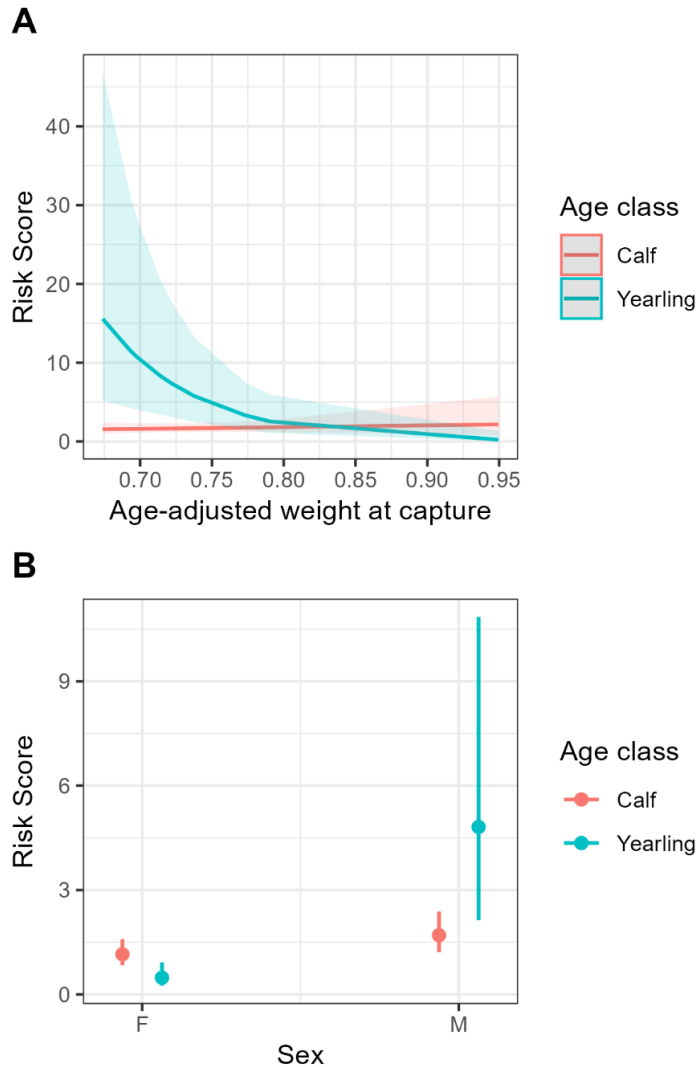


Figure 5.6 Mortality risk for juvenile moose in relation to weight, age, and sex. Risk scores (95% confidence intervals) of juvenile moose by age class (calf = <1 year old, yearling = >1 year) and A) age-adjusted weight (i.e., weight in kg/capture age) or B) sex, in Bonaparte Plateau and Prince George South study areas, 2016-2021.

5.4 Discussion

Globally, wildlife populations are declining and outside of wholesale habitat loss (257), mechanisms are difficult to discern. This is especially true when natural processes combine with, or are mediated by, anthropogenic stressors in latent processes manifesting as a single observable pattern (273). Using an extensive ecological analysis across 180 animals and two landscapes with significant resource extraction, we parsed apart natural and anthropogenic risks to declining moose. Forest harvest – new cutblocks and road densities – and heavier winter tick infestations

increased juvenile moose mortality risk. Yearling males, or those with low weights, had reduced survival. Health, long-term use, weather, forage, and predator occurrence did not modify the riskiness of forest harvest. Elevated juvenile vulnerability from recent logging, road networks, and winter tick infestations offer a potential explanation for population declines observed after widespread salvage logging and emphasize the need for species-centric approaches to landscape management.

Factors influencing juvenile moose survival

Anthropogenic disturbance – new cutblocks and roads – creates risky habitat for juvenile moose, and we largely attribute this elevated risk to amplification of predation and human-caused mortality events. Most juvenile mortalities were due to predation, primarily wolf, consistent with previous literature (46, 274, 275). Bear predation and humans were the next leading causes, although wolf predation alone exceeded these causes, and hazard from humans increased primarily for yearling bulls due to hunting (276). Thus, we attribute the riskiness of new cutblocks and roads to both sexes from predation, and to a lesser degree, yearling males from hunting, although we could not fully explore cause-specific risks. Likely, predation plays a more significant role in explaining moose population dynamics, as most mortalities were from predation, and hunters would need to harvest many juvenile females to effectively reduce populations.

Alternatively, risk posed to juveniles by forest harvest could be health-related, not just from predation and humans. With limited mortalities, we did not assess cause-specific risks but Mumma and Gillingham (39) linked adult female moose use of roads and new cutblocks to elevated apparent starvation risk (39). Younger cutblocks alter moose diets and may have lower-quality forage (214, 258). As most juvenile moose mortalities were predator- or human-caused, we primarily attribute the riskiness of forest harvest to these mechanisms. However, we focused on proximate causes, not ultimate, which likely deemphasizes the importance of health. Despite most mortalities occurring from predation, models including predation risk variables had limited support. This discrepancy highlights limitations in using predator occurrence layers to capture fine-scale predation dynamics. Our layers reflect predicted predator occurrence probabilities based on camera data modelled with habitat associations, which should reflect habitats where moose are more likely to encounter a predator but might not correspond to increased juvenile

vulnerability to predation (277). Additionally, cougars and grizzly bears preyed on juveniles, but were excluded from the predator layer due to data limitations. However, we expect this exclusion would have limited impacts on results, as most mortalities were attributed to wolves.

Nevertheless, roads and new cutblocks play an important role in shaping juvenile survival through the proximate mechanisms of predation and to a lesser degree, human-induced mortality.

Roads are used by both predators and humans for travel and hunting. Predators, in particular wolves, utilize linear features to move and hunt efficiently (53, 126). In PGS, wolves selected habitats near roads, which facilitated their movement, but moose kill-sites were not linked to roads (126). However, this result could be due to variable moose use of roads (40) or spatial separation of kills from roads if moose flee upon encountering wolves. Conversely, Kunkel and Pletscher (100) found moose kills by wolves were nearer roads than control sites, albeit at lower road densities. Evidently, roads facilitate predation events, whether through the search, encounter and/or kill phases (277), leading to increased juvenile risk. Additionally, higher road densities likely elevated juvenile hazard of being harvested by humans or struck by a vehicle. Road use increased adult female moose risk of being harvested by humans (39), and often hunter kills are nearby roads (259). While moose-vehicle collisions are less common on resource roads, they still occur (and did in this study), particularly when roads are nearby high-quality habitat (278, 279). While moose benefit from roads as movement corridors or forage subsidies, road accessible regions often have reduced moose densities, likely in part due to reduced juvenile survival from enhanced predation, human harvest, and/or moose-vehicle collisions (214).

While roads facilitate predator movement and human access, new cutblocks further expose moose to detection by predators and hunters. New cutblocks predominantly consist of large canopy openings with early seral vegetation, which attract moose for foraging, but have open sightlines and little hiding cover (40, 59). Older cutblocks may be less risky due to increased lateral cover from regenerating vegetation. Moose kill sites are more likely to occur in areas with reduced hiding cover from trees (100). In PGS, wolves select for new cutblocks, and moose kill-sites are more likely to occur in new and regenerating (9 – 24 years) cutblocks (126). Hunters also use new cutblocks to search for moose (163), and adult females have elevated risk of being harvested when using more new cutblocks over the previous week (39).

Forest harvest appears to be inherently risky for juvenile moose, regardless of modifying factors like weather, long-term use, forage, or health. While we expected weather to impact juvenile vulnerability (280), these metrics lacked supported. Possibly, unexplored variables (e.g., snow depth, crusting) are more important for survival, or microclimate (e.g. mature forest) use helped juveniles to buffer against weather effects. Long-term use also did not affect risk, indicating that encountering forest harvest features elevates juvenile hazard immediately, regardless of experience. Forage availability also had limited effects. We assessed use of forage availability daily, expecting trade-offs by moose between risk and forage, but possibly, longer-term scales might better explain survival due to cumulative effects on body condition. Lastly, interactions between health and forest harvest showed no trends, despite model support. Possibly, this was due to a mismatch of temporal scales, with body condition measured at capture but forest harvest use as a daily metric. Poor condition increases risky behaviors (124), which could increase mortality risk from forest harvest features, but this did not appear to be the case.

Even so, body condition did affect survival: both yearlings with lower age-adjusted weights and juveniles with higher winter tick loads had elevated mortality risk, regardless of habitat use. Low weights did not affect calf survival but contributed to increased hazard for yearlings. Possibly, body condition becomes more critical for yearling survival as they grow and are no longer buffered by maternal care. Low weights also result from winter ticks (208), as seen in our study, and accumulated adverse health effects from tick infestations could increase post-winter mortality risk.

High winter tick loads decreased the likelihood of juvenile recruitment. Winter ticks cause significant health effects on moose and elsewhere, are linked to population declines (24). With severe infestations, moose experience up to 8% daily loss of total blood volume, leading to anemia and intensified metabolic requirements to offset protein deficits (208). Excessive grooming from infestations causes hair loss and reduced foraging, further elevating energy demands (281). Juveniles have limited fat and high metabolisms, making them vulnerable to winter ticks (208). Infestations cause both direct juvenile mortality and indirect, by increasing juvenile vulnerability to predation (282, 283). Our focus on proximate mortality causes likely underestimated impacts of ticks on juveniles. However, we provide evidence that winter ticks play an important role in juvenile moose survival.

Conclusions

The combined mechanisms of predation in newly harvested areas with dense roads, combined with winter tick infestations, lead to suppressed juvenile moose survival. Our results have significant implications for managing moose populations in heavily harvested forested landscapes and could explain observed population declines in BC following significant salvage logging of beetle-killed forest. While regenerating cutblocks do benefit moose (214), numerous new cutblocks and roads likely compounded into significantly reduced recruitment in these moose populations by increasing the likelihood of juvenile mortality from predation. Forest harvest facilitates human-caused mortalities, but likely with a lessened impact on population dynamics than predation, as it primarily impacted yearling bulls. Elevated winter tick infestations, possibly amplified by forest harvest concentrating moose in fewer habitat patches (284), also elevated juvenile vulnerability.

To reduce the negative effects of forest harvest on juvenile moose, managers should reduce the hunting efficiency afforded to predators and hunters by roads and new cutblocks. The rapid, extensive development of the forest harvest footprint on the landscape – including both resource roads and cutblocks – should be minimized. Forest harvest often benefits moose populations (214), but rapid and large-scale forest harvest – as observed in BC – likely contributes to juvenile moose using these features, which comes at a great risk to their survival. We recommend reducing road densities (particularly in high-quality habitats that attract juveniles), minimizing road construction to the extent possible, and rehabilitating roads immediately post-harvest to reduce predator travel and human access (168, 209). As juveniles likely will continue using new cutblocks, habitat complexity should be maintained in these features to disrupt sightlines and minimize predation, which could be accomplished through cutblock configuration, variable retention, buffering important habitat, and/or silvicultural treatments (41, 217, 285). Alternative forage sources should be retained (e.g., unharvested burns) to reduce juvenile attraction to new cutblocks. Forest harvest should ensure that remaining high-quality moose habitat is not concentrated to reduce winter tick transmission (284). To benefit most of the population, managers must ensure these changes are spatially distributed across the landscape.

Mitigating the adverse impacts of forest harvest to survival of vulnerable life stages, like juveniles, is crucial to conserve wildlife populations. Currently, forestry-dominated landscapes are largely managed based on generic size, shape, and allowable-cut regulations. This species-agnostic approach is generalizable but misses the important cumulative ecological and biological processes linked to species declines across taxa. Considering the cumulative impacts of anthropogenic and natural stressors on populations is key when managing landscapes to ensure resilient ecosystems and sustainable resource extraction. As climate change will likely intensify landscape dynamics leading to salvage logging, like insect outbreaks and wildfires (36, 286), rethinking forest management to explicitly support wildlife population objectives is more urgent than ever.

General Conclusions

Persistence of wildlife populations depends in part on the balance of local reproductive success relative to mortality rates (in combination with dispersal), with these demographic rates shaped by ecological factors such as resource availability, and predation risk (42, 287). Yet anthropogenic disturbances disrupt these processes: fragmenting landscapes, altering habitat quality and availability, and causing cascading effects on community dynamics (5-7). Through this dissertation, I explored how widespread salvage logging impacts older calf moose, their maternal females, and their predators in two declining moose populations in interior British Columbia, leveraging data from extensive animal collaring efforts and two wildlife camera trap arrays. Salvage logging of bark beetle-impacted forests in BC exemplifies how anthropogenic landscape change intensifies selective pressures for moose. By altering predator-prey dynamics and habitat selection patterns for both calf and maternal female moose, the rapid overharvesting of forests via salvage logging creates hazardous landscapes that exacerbate predation risks and jeopardize juvenile survival, contributing to population declines.

In this system, wolves take advantage of new and regenerating cutblocks, as well as associated linear features, to move and hunt efficiently (Chapter 1). Forestry roads facilitate wolf movement between habitat patches, potentially increasing prey encounter rates. Younger cutblocks improve detectability of prey through clear sightlines and create predictable early seral habitats for wolves to search. Kill sites of moose were disproportionately linked to new and regenerating cutblocks, indicating that salvage logging facilitates encounter, attack, and/or capture stages of predation in these habitats.

Inexperienced juvenile moose select for these risky, early seral cutblocks, which exposes them to a greater risk of perishing, primarily from wolf predation (Chapters 2). Recruited calves avoided cutblocks, or only selected those with additional cover, whereas non-recruited calves did not. All calves avoided forestry roads, likely due to predator and human use. When spatially separated from their mothers, selection of these risky features by semi-independent calves increases. Likely, calves are unable to ideally weigh the costs and benefits of using certain forest harvest features, leading to some being predated. Potentially, forest harvest creates an ecological trap, wherein the selection of younger cutblocks by juvenile moose due to available forage

(Chapter 1) combines with the use of these habitats by wolves for facilitated hunting (Chapter 2) to ultimately reduce juvenile moose fitness due to elevated predation.

Conversely, risky behaviors in maternal females – selection of early seral forage in both cutblocks and wildfire burns – may benefit their reproductive success by offsetting nutritional deficiencies, likely arising from winter tick infestations and/or reproductive investments in previous calves (Chapter 3). Adult females are experienced and less vulnerable to predation than calves (43), allowing them to more successfully exploit these risky but resource-rich habitats. However, mirroring the same habitat selection strategies appears to not have the same beneficial outcomes on survival for calves, likely due to their heightened vulnerability to predation. As calves closely follow their maternal female, this highlights the importance of retaining shelter habitats adjacent to forage to benefit both juvenile and adult moose.

Forest harvest not only influences moose space-use patterns but also reshapes predator and ungulate distributions and interactions (Chapter 4). Only moose were best explained by forest harvest successional patterns, with reduced occurrence in most cutblock age classes, as a function of wolf activity. Otherwise, the occurrences of all other ungulate and predator species examined were driven by a combination of forest harvest patterns, silvicultural treatments (primarily site preparation and stand tending), and predator/prey occurrence frequency. However, silvicultural treatments did impact moose occurrence seasonally. Possibly, differing silvicultural treatments explain variation in moose and wolf responses to forest harvest between study areas and seasons. Forest harvest has broad implications for moose populations through shifts in predation risk, predator-prey dynamics, and interspecific competition across these disturbed landscapes, depending on silvicultural treatments and forest successional stages.

Together, compounded by natural stressors such as parasitism, these dynamics coalesce into a heightened risk of mortality for juvenile moose when navigating heavily logged landscapes (Chapter 5). Use of forest harvest features – new cutblocks and higher road densities – increases juvenile mortality risk, presumably from increased predator and hunter efficiency in these habitats. Juveniles with higher winter tick infestations, and lower weights, also had a higher mortality risk, likely due to elevated vulnerability to predation. However, forest harvest appears inherently risky, regardless of modifying factors such as juvenile condition. Thus, transforming much of the landscape to an early successional stage creates a system that challenges juvenile survival through intensified predation, contributing to population declines.

Not all forest harvest may be inherently bad for moose; in fact, it is often the opposite (214). Moose are disturbance-associated species, benefiting from peaks in plant productivity following forest clearing events such as wildfires or forest harvest, with their populations also often peaking in the years following these disturbances (59, 97, 288). However, rapid and large-scale forest harvest, combined with natural stressors like predation and parasitism, is not conducive to the survival of inexperienced and vulnerable juvenile moose, as evidenced in this dissertation. These drastic habitat alterations intensified selective pressures for juveniles, outweighing the benefits of abundant (but possibly lower quality) early seral forage from cutblocks (97, 158, 289), and leading to population declines – as observed in our study areas and across interior British Columbia (20, 31).

While potentially lucrative over the short-term (37, 290), the implementation of salvage logging should be re-thought, particularly as land use and climate change intensifies the ecological processes leading to salvage logging, such as insect outbreaks and wildfires (36, 291, 292). Insect outbreaks are expected to shift northward and/or intensify as the climate warms, as observed with mountain pine beetle in *Pinus* species (36). Other pest species may also reach outbreak levels, such as spruce beetle (*Dendroctonus rufipennis*) in Engelmann spruce (*Picea engelmannii*) or western balsam bark beetle (*Dryocoetes confuses*) in subalpine fir (*Abies lasiocarpa*) (293). Wildfire regimes are intensifying across North America, with the drastic impacts already seen across western Canada (291). Almost 5 million hectares burned in the province of BC between the start and end of this dissertation, greatly exceeding previous records (233). In many regions, these wildfires have been the next target for salvage logging. Further, while salvage logging is thought to mitigate future disturbances, a growing body of evidence indicates that salvage logging removes disturbance legacies (i.e., the features that persist through disturbances) that contribute to landscape resilience and contributes to, or potentially triggers, further disturbances (67, 294). For example, salvage logging creates abundant, dry shrubs and ground fuel that intensifies wildfires, or weakens trees along cutblock edges and alters their attractiveness to bark beetles, leading to infestations (294). Given the uncertainty about the frequency and severity of these future stochastic disturbances, the potential for the compounding impacts of salvage logging with natural disturbances, and the impacts upon wildlife and their habitats, the long-term ecological consequences of salvage logging should be further considered, and policies surrounding this practice should be re-evaluated to improve sustainability.

With the possible large scale of natural disturbances, an argument could be made that economic value must be recovered – to some degree – from burnt, insect-killed, or otherwise disturbed forests. However, if not carefully managed, salvage logging (and forest harvest itself) will cause biodiversity declines (37), as observed with moose. Policies must be implemented that limit the adverse ecological impacts of salvage logging on forested ecosystems, balancing economic gains with ecological costs. Natural disturbances, such as wildfires and insect outbreaks, are often an essential component of functioning ecosystems, with their legacies impacting recovery trajectories and rates, determining succession, and thus, supporting ecosystem resilience (295). Resource managers should prioritize preserving these disturbance legacies to maintain ecosystem structure and processes that enable recovery post-disturbance (295). In the case of moose, preserving some of these disturbance legacies (e.g., beetle-killed trees) and promoting natural regeneration in disturbed forests would maintain habitat complexity, reducing predator hunting efficiency, in addition to minimizing moose attraction to higher-risk forage habitats, such as new cutblocks. Forest harvest, including salvage logging, should also aim to emulate natural disturbances by retaining a mix of live trees, standing damaged/dead trees, decaying wood, and understorey vegetation, to maintain habitat complexity through structural legacies (296).

Habitat complexity is important for many species, including moose, and should be maintained in salvage-logged landscapes. Policies should ensure maximum cutblock size thresholds are maintained for salvage logging, in combination with adjacency constraints wherein a mix of live and damaged trees are retained adjacent to cutblocks. This would ensure that landscapes are not drastically cutover, retaining habitat heterogeneity with a mix of hiding cover and forage availability that would support wildlife populations. Implementing more selection logging, rather than clearcutting, to only remove a portion of the damaged timber while retaining a mix of live and disturbance-damaged trees would also support ungulates through maintained habitat complexity and cover. If salvage logging continues with clearcuts, there should be additional retention of disturbed forest, particularly within cutblocks (as currently most tree reserves are small and not internal for clearcuts in BC) (38, 297). Further, areas of high value to ungulates, such as calf rearing habitats, should be retained even if disturbed, and buffered from logging. Following salvage logging, managers should ensure forage species for ungulates are interspersed with replanted trees to ensure adequate forage availability. Further,

silvicultural treatments that adversely impact ungulate forage, such as herbicide applications, or attract predators, should be avoided (158, 216, 217, 258). Road construction should be as limited as possible during forest harvest, and deactivation and rehabilitation of these forestry roads should occur immediately following completion of harvest to reduce predator hunting efficiency across the landscape (209, 285).

Encouragingly, aerial surveys across interior BC are indicating signs of moose populations stabilizing and possibly even increasing, roughly two decades after the bark beetle outbreaks, widespread forest harvest, and identification of moose population declines (26). Likely, these promising population changes result from vegetation regeneration post-harvest, which provides both adequate forage and increased lateral cover within cutblocks to limit visibility of moose from predators and hunters (97). Together with the decommissioning and rehabilitation of some forestry roads, predator and hunter search efficiency has likely reduced, supporting moose survival and reproductive success. However, it remains unclear whether the landscape's carrying capacity will remain depressed, such that moose populations stabilize at a lower level. This is a possible outcome given intensified disturbance regimes combined with government-incentivized salvage logging and reducing productivity of planted pine monocultures in aging, previously salvage-logged cutblocks. Alternatively, moose populations could rebound to previous levels as vegetation regenerates and habitat heterogeneity increases, particularly if salvage logging and forest harvest policies are altered to increase sustainability while still providing early seral forage. To better understand these population dynamics and declines, age-structured matrix models should be employed, incorporating the impacts of forest harvest on juvenile survival rates and maternal reproductive success identified in this study. Additionally, long-term monitoring should continue for moose populations and their predators, as declines and their mechanisms may have been identified earlier, and the longer-term impacts of salvage logging remain poorly explored. By integrating these management considerations into practice and maintaining long-term population monitoring, managers can adapt to abrupt population changes, promote sustainable forest harvest (including salvage logging) and support wildlife populations, particularly their vulnerable juveniles.

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Appendix 1: Supplementary Information from Chapter 1

A1.1 Study area

The area is composed primarily of lodgepole pine (*Pinus contorta latifolia*) and hybrid spruce (*Picea glauca x engelmanni*) in the Sub-Boreal Spruce biogeoclimatic (BEC) zone, with highest elevations characterized by the Engelmann Spruce Subalpine Fir BEC zone (68). Winter moose density declined in PGS from $630 \pm 102/1000 \text{ km}^2$ in 2011/2012 to $400 \pm 78/100 \text{ km}^2$ in 2016/2017 (68). Other ungulate species in the study area are mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), and domestic cattle (*Bos taurus*).

A1.2 Wolf capture

All wolf captures were completed following Canadian Council on Animal Care guidelines and the British Columbia Wildlife Act (permit: PG17-272811). Immobilizations were completed using tiletamine-zolazepam (Telazol/Zoletil) at a 225 mg/mL concentration, with a volume of 1.5-1.8 mL administered at a 6 mg/kg dosage. For aerial darting, we used Pseudart 2-cc aerial darts with a 0.5" barb, injected into the wolf's hindquarters. For net-gunning, wolves were captured using a net deployed from a hand-held net gun, then darted at a low power setting once the net restricted movement. Aerial darting and net-gunning were completed from Bell 206 helicopters. Trapping was completed on nights with temperatures $>-8^{\circ}\text{C}$ using steel foot-hold traps with rubberized offset jaws (Livestock Protection EZ Grip #7), with a drag hook on 8' chain. Traps were placed on trails in areas with low risk to humans and domestic animals, with warning signs posted for the public. Attractants were used at the traps (gland lure, beaver castor, wolf urine and fresh wolf scats). Traps were checked in the morning or every 4-5 hours if ambient temperatures exceed 25°C (or traps were closed/removed). When trapped, wolves were restrained using a 4-6' noose pole and chemically immobilized via hand-injection. All captured wolves were examined for previous or capture-related injury, blindfolded, and monitored for vital signs throughout handling.

A1.3 Integrated step selection analysis

Step lengths were drawn from a gamma distribution parameterised using the step length data at the population level for each season, described by the tentative shape (influences the form/shape of the distribution; b_1) and scale (influences amount of stretch or compression of gamma distribution; b_2) parameters. Turn angles were sampled from a von Mises distribution (equal probability of left and right turns, with mean around zero). Integrated step selection analysis (iSSA) expands beyond previous step selection approaches by incorporating the log of the step length, $\ln(\text{Step length})$, as a term within the model alongside habitat covariates, augmenting the tentative movement kernel which is no longer confounded by the process of habitat selection (84). Additionally, $\ln(\text{Step Length})$ can be included as an interaction term to quantify the relationship between movement and habitat features.

Cutblock sizes and ages were determined using Reporting Silviculture Updates and Land Status Tracking System (RESULTS), obtained from DataBC (<https://data.gov.bc.ca/>). Cutblock ages were classified as new (0-8 years since harvest) and regenerating (9-24 years since harvest), based on average cutblock age thresholds identified by Mumma and Gillingham (39). In addition, we included the variables ‘edge in’ (distance to edge of forest when inside the forest) and ‘edge out’ (distance to edge of forest when outside of the forest) to describe use of edge habitat (89, 298). We log-transformed both edge habitat variables. Forestry increases the amount of edge habitat within a landscape, and edge habitats may attract ungulates – and thus, wolves – due to their juxtaposition of hiding cover and foraging areas (299, 300). One caveat is that these edge habitat variables contain limited information on how edge use varies based on edge boundary size. It is possible that wide edge boundaries would provide ecologically different features for wolves and their prey, as compared to narrow boundaries.

We used the Digital Road Atlas (DRA), obtained from DataBC (<https://data.gov.bc.ca/>), to calculate Euclidean distance (m) to the nearest linear feature from the start and end of the step. We log-transformed distance to the nearest linear feature. In addition, we created a raster of linear feature densities (km/km^2) across the landscape and used this layer to extract linear feature density at the start and end of the step. Linear features attract wolves, particularly in the summer, due to facilitation of travel (49, 53). Areas with high linear feature densities may be avoided by

wolves due to increased human use (74). A caveat of this dataset is that it does not differentiate between the conditions of linear features (e.g. degree of vegetation growth).

Land cover was determined from the Vegetation Resources Inventory (VRI), obtained from the Ministry of Forests, Lands, Natural Resource Operations & Rural Development (FLNRORD) (141). Land cover was reclassified into categories of deciduous-leading stands, coniferous-leading stands, mixed forest stands, pine-leading stands (i.e., predominantly *Pinus* sp.), and non-forest (reference category). Deciduous-leading stands may be selected by wolves for hunting, as these stands provide forage for prey species, including moose in all seasons (74). Coniferous-leading stands provide shelter and snow interception for both wolves and their prey, as well as moose forage in the winter (301, 302). Pine-leading stands were considered separate from other coniferous stands (spruce, fir), as we expected most pine to be impacted by MPB within this region. MPB-killed pine stands provide reduced shelter and snow interception, as compared to other coniferous-leading stands. We used the Water and Wetland GeoBase Land Cover dataset, obtained from DataBC (<https://data.gov.bc.ca/>), to determine the log-transformed distance to the nearest waterbody. Waterbodies can act as a travel corridor for wolves and riparian areas can provide hunting opportunities for beaver (*Castor canadensis*) and moose (303). Lastly, we used the R package ‘MODISsp’ (304) to obtain MODIS (moderate resolution imaging spectroradiometer) 16-day interval normalized difference vegetation index (NDVI) data to represent plant productivity. NDVI values range between -1 to 1, with -1 representing water, 0 representing barren ground or rock, and values nearing 1 representing high plant productivity (305). In the summer, areas with high NDVI values may attract ungulates for foraging (306) and therefore, may be selected by wolves due to increased hunting opportunities. In winter, higher NDVI values represent vegetation with reduced snow cover (e.g. conifers) which could be selected by wolves for ease of travel, shelter, and hunting opportunities, while lower NDVI values represent areas with little vegetation or bare soil (305). We resampled all land cover layers to the coarsest resolution (250 m).

A1.4 Resource selection strength

We calculated resource selection strength using equations provided by Avgar, Lele (93). We calculated selection-free movement rates (km/hr) using the following formula:

$$\frac{1}{b_2} \times (b_1 + \beta_{\ln(\text{Step length})} + (\beta_{1\dots n} \times x_{1\dots n}))$$

Where b_1 is the gamma shape parameter, b_2 is the gamma scale parameter, $\beta_{\ln(\text{Step length})}$ is the beta coefficient estimate for $\ln(\text{Step length})$ and $x_{(1\dots n)}$ is the beta coefficient estimates for interactions of $\ln(\text{Step length})$ and covariates within the model.

A1.5 Moose mortality sites

We used the Find Points Cluster Identification Program (Version 2) (83) to identify potential kill sites for each wolf. Location clusters were determined using a 100 m search radius over 2 weeks (336 hours). The cluster algorithm was run monthly to identify possible kill sites.

Cluster sites with 15 wolf GPS locations or more were checked for signs of a kill site. Sites with smaller clusters were visited randomly. Moose killed between November and March were often buried by snow by the time the cluster algorithm was run so were typically visited following snow melt. Cluster sites were accessed using a truck or helicopter, but accessibility limited some site visits. As well, the COVID-19 pandemic limited or delayed field visits, particularly during 2020. Therefore, field visits to potential kill sites occurred days to months following clustering occurrence or were not always possible.

At each potential kill site, the area was searched for evidence of prey species (bones, hair), sex (antlers or pedicels, pelvis) and age (size, tooth eruption and wear, incisor for cementum annuli aging). Searches started at the cluster centroid and occurred within a 100-m radius, with a focus on landscape features (e.g., game trails, wolf bed sites) where evidence of a kill may be left.

The identification of carnivore kill sites of large-bodied prey species like moose using GPS cluster analysis is a common and reliable method; however, several assumptions exist in identifying kill sites using this method (307-310). We assumed that if a wolf killed a moose, handling time of the carcass would be enough for the kill site to be detected as a cluster. However, GPS cluster analysis may not identify sites with quickly consumed kills or where wolves are displaced from a kill. We assumed that evidence of a kill would be present at each kill site; however, it is possible that false negatives occurred due to carcasses being fully consumed, minimal remains being undetected under cover or carcasses having been moved by scavengers. These challenges are magnified for small-bodied prey like moose neonates, and a 1-hour fix

schedule is unlikely to detect these kill sites (308, 310-312). As such, we are not able to assess the landscape characteristics that are more likely to lead to wolf predation on neonates. Lastly, while we identified and removed scavenged bear kills and hunter kills from the data set, we assumed that all remaining kill sites were wolf kills. However, it is possible that some of these moose were scavenged.

A total of 4330 potential kill sites were identified using GPS cluster analysis. Of these, we were able to search 292 of 497 sites of clusters with ≥ 15 wolf locations and 305 of 3833 sites with < 15 wolf GPS points. In total, 597 cluster locations were searched. Clusters were investigated on average 99.3 ± 2.9 days (mean \pm SE) following the latest date the kill could have occurred. From the ground-truthed clusters, we identified 158 kill sites of moose. Of these, 145 kill sites of moose were identified from clusters with ≥ 15 wolf GPS locations. As well, we identified kill sites of other species (black bear = 2, cattle = 3, deer = 4, elk = 1), 18 rendezvous sites, 8 den sites, 39 active beaver areas, 3 bait sites, and 1 moose-wolf stand-off site. On average, kill sites of moose were 4.16 ± 0.37 m (mean \pm SE) from the centroid of the wolf GPS location cluster. Kill sites were primarily of adult moose ($n = 112$), followed by calves > 3 months old ($n = 38$), and 8 moose of an unknown age class. The sex of most carcasses was unknown ($n = 80$), but 61 were identified as female.

We generated fifty random locations (137) for each mortality site within the PGS study area boundary, and buffered each location by 883 m – the average successful pursuit distance of a moose by a wolf (313). Within each buffer, we determined the proportion of deciduous-leading stands, coniferous-leading stands, mixed forest stands, pine-leading stands, new cutblocks, and regenerating cutblocks. We determined mean values for distance to linear feature, linear feature density, distance to edge (both inside and outside of the forest), NDVI and distance to water. We log-transformed all distance variables. Due to the limited sample size, we pooled kill sites from all wolf individuals for analysis.

A1.6 Tables

Table A1.1 Summary of radio-collared wolves with movement data for summer (April 1 – September 30) and winter (October 1 – March 31), 2018-2020.

Wolves were only included within the analysis if sufficient data (>7 collared days) was available.

ID	Pack	Sex	Winter 2018	Summer 2018	Winter 2019	Summer 2019	Winter 2020	Summer 2020	Fate
1	A	M	x						Dispersed
2	B	M		x	x				Dispersed/shot
3	C	M	x	x	x				Offline
4	D	M	x	x	x				Dispersed
5	E	M			x	x	x		Offline
6	D	M			x	x			Dispersed
7	E	M				x	x	x	Active
8	D	F							Shot; insufficient data
9	F	M					x	x	Offline
10	G	M					x	x	Active
11	F	F						x	Offline

Table A1.2 Candidate models examining the relationship between salvage logging features and successful wolf kills of moose in the Prince George South study area, 2018-2020.

Model name	Covariates
Prey	Pine + Deciduous + Mixed Forest + Coniferous + ln(Distance to water) + NDVI + ln(Edge in) + ln(Edge out)
Linear feature network	Linear feature density + ln(Distance to linear feature)
Cutblock	New cut + Regenerating cut + New cut:Cut size + Regenerating cut:Cut size
Prey + Linear feature network	Pine + Deciduous + Mixed Forest + Coniferous + ln(Distance to water) + NDVI + ln(Edge in) + ln(Edge out) + Linear feature density + ln(Distance to linear feature)
Prey + Cutblock	Pine + Deciduous + Mixed Forest + Coniferous + ln(Distance to water) + NDVI + ln(Edge in) + ln(Edge out) + New cut + Regenerating cut + New cut:Cut size + Regenerating cut:Cut size + ln(Step length):New cut
LFN + Cutblock	Linear feature density + ln(Distance to linear feature) + New cut + Regenerating cut + New cut:Cut size + Regenerating cut:Cut size

Global	Pine + Deciduous + Mixed Forest + Coniferous + ln(Distance to water) + NDVI + ln(Edge in) + ln(Edge out) + Linear feature density + ln(Distance to linear feature) + New cut + Regenerating cut + New cut:Cut size + Regenerating cut:Cut size
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Table A1.3 Spearman’s rank correlation coefficient (r_s) medians from cross validations assessing fits of integrated step selection analysis models for each wolf individual in summer (April 1 – September 30) and winter (October 1 – March 31) in Prince George, 2018-2020.

Season	Model	r_s
Summer	Prey	0.74
	Linear feature network	0.72
	Cutblock	0.61
	Prey + Linear feature network	0.77
	Prey + Cutblock	0.76
	LFN + Cutblock	0.76
	Global	0.81
Winter	Prey	0.57
	Linear feature network	0.48
	Cutblock	0.35
	Prey + Linear feature network	0.57
	Prey + Cutblock	0.58
	LFN + Cutblock	0.56
	Global	0.66

Table A1.4 Model selection using Akaike’s information criterion (AIC) and for logistic regressions relating habitat features to wolf kill-sites of moose in Prince George South, 2018-2020. LFN = linear feature network.

Model	K	AIC	Δ AIC	AIC Weight	Log likelihood
Prey + Cutblock	11	1318.21	0	0.87	-648.09
Global	13	1322.03	3.82	0.13	-647.99
Prey	9	1336.12	17.91	0	-659.05
Prey + LFN	11	1338.85	20.64	0	-658.41
LFN + Cutblock	5	1362.51	44.31	0	-676.25
Cutblock	3	1364.29	46.08	0	-679.14

A1.7 Figures

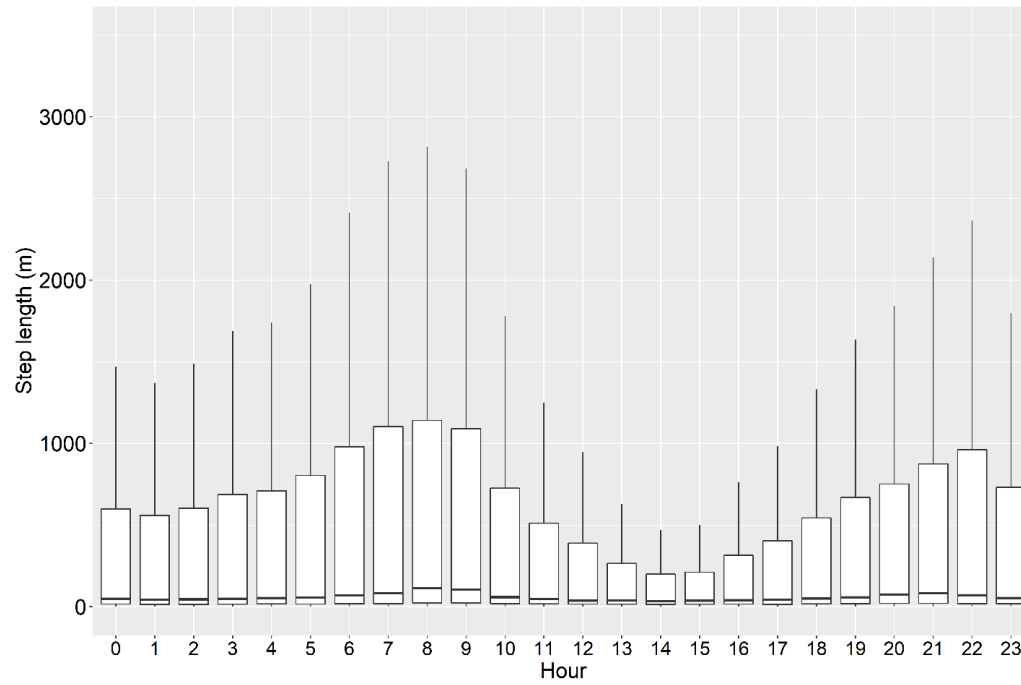


Figure A1.1 Variation in step length (m) by hour for wolves in Prince George South, 2018-2020.

Appendix 2: Supplementary Information from Chapter 2

A2.1 Figures

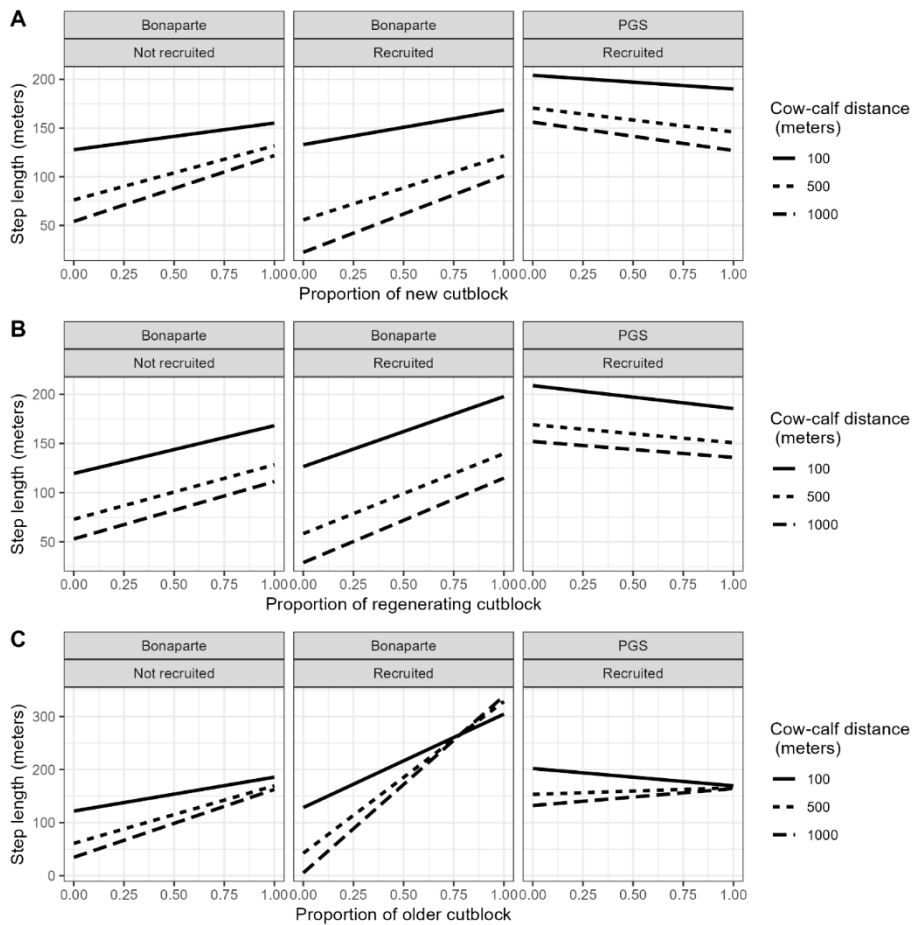


Figure A2.1 Movement rate of moose calves in relation to forest harvest features, cow-calf distances, study area, and calf fate. Step length (meters) of moose (*Alces alces*) calves in relation to cow-calf distance (meters) and A) new (0-8 years since harvest), B) regenerating (9-24 years), and C) older (25-40 years) cutblocks, based on the most supported integrated step selection analysis models for recruited (survived from 7-8 months to 1 year old) and not recruited (did not survive) calves with Bonaparte and Prince George South (PGS) study areas, British Columbia, Canada, 2016/2017 (Bonaparte) and 2017/2018 (PGS) to 2020/2021. Non-recruited PGS calves were not included as their top model did not include the interaction between movement, cow-calf distance, and environmental variables.

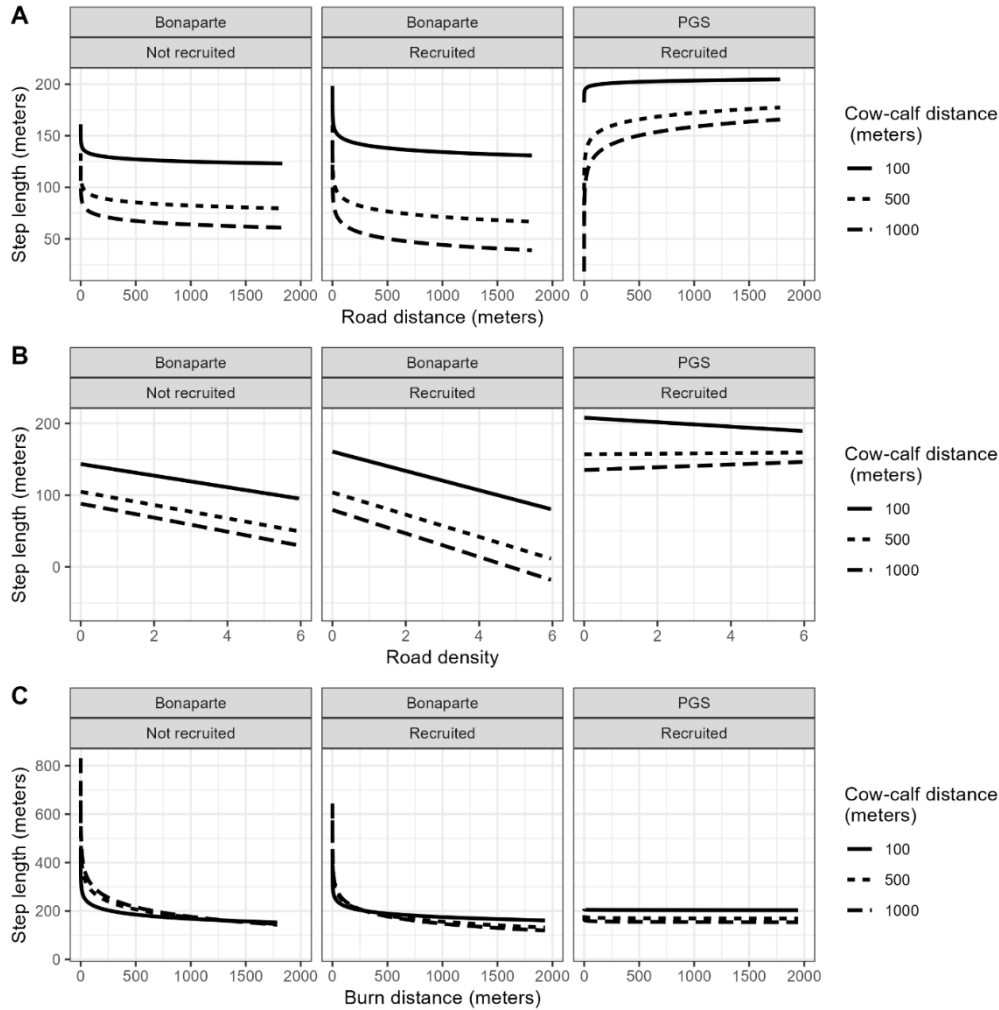


Figure A2.2 Movement rate of moose calves in relation to roads, burns, cow-calf distance, study area, and calf fate. Step length (meters) of moose (*Alces alces*) calves in relation to cow-calf distance (meters) and A) road distance (meters), B) road density (km/km^2), and C) burn distance (meters), based on the most supported integrated step selection analysis models for recruited (survived from 7-8 months to 1 year old) and not recruited (did not survive) calves with Bonaparte and Prince George South (PGS) study areas, British Columbia, Canada, 2016/2017 (Bonaparte) and 2017/2018 (PGS) to 2020/2021. Non-recruited PGS calves were not included as their top model did not include the interaction between movement, cow-calf distance, and environmental variables.

A2.2 Tables

Table A2.1 Model selection results using Akaike’s Information Criterion (AIC) for candidate models explaining log-transformed distances between moose calves (*Alces alces*) and their maternal female, based on whether the calf was recruited (i.e., survived from 7-8 months old to 1 year) or not (i.e., Recruited variable), age (approximate calf age in days, based on the mean calf birth date of May 21), sex (male or female), and location (Prince George South or Bonaparte study areas). Bias adjusted cross-validation (CV) scores (with standard error) based on 10-fold cross validation with 5 repeats are reported for each model. ‘*’ denotes an interaction with lower-order terms included.

Model structure	Parameters	AIC	Δ AIC	Weight	Log-likelihood	CV
Recruited*Age*Sex + Recruited*Age*Location	14	133857.1	0	0.58	-66914.6	1.122688 (0.00029)
Recruited*Age*Location + Age*(Sex + Location)	12	133857.7	0.62	0.42	-66916.9	1.122824 (0.00029)
Recruited*(Age + Sex + Location) + Age*(Sex + Location)	12	134086.6	229.47	0	-67031.3	1.128635 (0.00031)
Recruited*(Age + Sex) + Age*(Sex + Location)	11	134087	229.87	0	-67032.5	1.128635 (0.00031)
Recruited*(Age + Location) + Age*(Sex + Location)	11	134087.1	229.94	0	-67032.5	1.128635 (0.00031)
Age*(Recruited + Sex + Location)	10	134087.4	230.29	0	-67033.7	1.128635 (0.00031)
Recruited*Age*Sex + Age*(Sex + Location)	12	134090.4	233.28	0	-67033.2	1.128586 (0.00030)
Recruited*Sex*Location + Age*(Sex + Location)	13	134172	314.85	0	-67073	1.13105 (0.00031)
(Recruited + Age)*(Sex + Location)	11	134176.1	318.95	0	-67077	1.13105 (0.00031)
Recruited*Sex + Age*(Sex + Location)	10	134176.4	319.32	0	-67078.2	1.13105 (0.00031)
Recruited*Location + Age*(Sex + Location)	10	134176.6	319.49	0	-67078.3	1.13105 (0.00031)
Recruited + Age*(Sex + Location)	9	134176.9	319.82	0	-67079.5	1.13105 (0.00031)
Age*(Sex + Location)	8	134177.2	320.09	0	-67080.6	1.13128 (0.00031)

Table A2.2 Beta coefficient estimates with confidence intervals from the most supported model explaining log-transformed distances between moose calves (*Alces alces*; 7-8 months old to 1 year) and their maternal female from Bonaparte and Prince George South study areas. Covariates describe whether the calf was recruited (i.e., survived from 7-8 months old to 1 year; reference category) or not (i.e., Recruited variable), age (approximate calf age in days, based on the mean calf birth date of May 21), sex (male [reference category] or female), and location (Prince George South [reference category] or Bonaparte study areas). ‘:’ denotes an interaction.

Predictors	Estimates	Confidence Intervals
Intercept	4.64	2.90 – 6.37

Age	0.37	0.30 – 0.43
Sex [Male]	0.29	-1.60 – 2.17
Location [PGS]	0.49	-1.25 – 2.22
Recruited [Recruited]	-0.99	-2.92 – 0.95
Age:Sex [Male]	-0.02	-0.08 – 0.04
Age:Location [PGS]	-0.36	-0.42 – -0.30
Age:Recruited [Recruited]	-0.23	-0.30 – -0.17
Sex [Male]:Recruited [Recruited]	0.80	-1.42 – 3.03
Location [PGS]:Recruited [Recruited]	-0.49	-2.58 – 1.61
Age:Sex [Male]:Recruited [Recruited]	0.09	0.02 – 0.15
Age:Location [PGS]:Recruited [Recruited]	0.51	0.44 – 0.57

Table A2.3 Model selection results for integrated step selection analyses assessing the impact of maternal proximity on moose calf movement and habitat selection. Model selection results using Akaike's Information Criterion (AIC) for integrated step selection analysis candidate models examining the habitat selection and movement of the subset of recruited (survived from 7-8 months to 1 year old) and not recruited (did not survive) moose (*Alces alces*) calves with collared maternal females in Bonaparte and Prince George South (PGS) study areas, British Columbia, Canada, 2016/2017 (Bonaparte) and 2017/2018 (PGS) to 2020/2021.

Location	Status	Model	Parameters	AIC	ΔAIC	AIC Weight	Log-likelihood
Bonaparte	Recruited	Global	92	387538.8	0	0.85	-193677
		Multiplicative - Movement	72	387542.3	3.46	0.15	-193699
		Additive	50	387625.7	86.86	0	-193763
		Multiplicative - Habitat selection	72	387629.7	90.89	0	-193743
		Base	46	437579.9	50041.06	0	-218744
	Not recruited	Multiplicative - Movement	74	76706.51	0	0.98	-38279.1
		Global	96	76714.43	7.92	0.02	-38261
		Additive	50	76728.87	22.36	0	-38314.4
		Multiplicative - Habitat selection	74	76740.14	33.62	0	-38296
		Base	46	84627.5	7920.98	0	-42267.7
PGS	Recruited	Multiplicative - Movement	73	256634.9	0	0.99	-128244
		Global	96	256645.3	10.4	0.01	-128227

	Additive	50	256682.4	47.42	0	-128291
	Multiplicative - Habitat selection	74	256697.5	62.57	0	-128275
	Base	46	288163.7	31528.79	0	-144036
Not recruited	Additive	50	102034.3	0	1	-50967.1
	Multiplicative - Movement	74	102051.8	17.52	0	-50951.8
	Multiplicative - Habitat selection	74	102059.4	25.19	0	-50955.6
	Global	94	102068.8	34.52	0	-50940.2
	Base	46	108062.3	6028.05	0	-53985.1

Table A2.4 Beta coefficient estimates \pm standard error for standardized covariates from the most supported integrated step selection analysis models examining the subset of recruited (survived from 7-8 months to 1 year old) and not recruited (did not survive) moose (*Alces alces*) calves with collared maternal females in Bonaparte and Prince George South (PGS) study areas, British Columbia, Canada, 2016/2017 (Bonaparte) and 2017/2018 (PGS) to 2020/2021. Terms are grouped based on whether they examine habitat selection (environmental covariates extracted from the end of the step) or movement (environmental covariates extracted from the start of the step and interacted with step length, SL, and log-transformed step length, Log(SL)). Bolded terms indicate significance (beta estimates do not overlap 0). All distance metrics were log-transformed. ‘:’ denotes an interaction between covariates. Note, for recruited Bonaparte calves, we could not include the terms ‘SL:Cow-Calf distance:Conifer’ and ‘Log(SL):Cow-Calf distance:Conifer’ due to model convergence errors.

Type	Term	Bonaparte		PGS	
		Recruited	Not recruited	Recruited	Not recruited
Habitat Selection	Cow-Calf distance	-3.587 \pm 0.191	-3.232 \pm 0.503	-4.307 \pm 0.073	-3.269 \pm 0.468
	New Cut	-0.094 \pm 0.06	0.029 \pm 0.056	-0.058 \pm 0.069	-0.014 \pm 0.115
	Regenerating Cut	-0.077 \pm 0.053	-0.083 \pm 0.138	-0.181 \pm 0.075	0.001 \pm 0.051
	Older Cut	-0.149 \pm 0.045	-0.154 \pm 0.117	-0.077 \pm 0.056	-0.217 \pm 0.187
	Road Distance	0.084 \pm 0.031	-0.017 \pm 0.034	0.096 \pm 0.03	0.012 \pm 0.029
	Road Density	0.058 \pm 0.045	-0.012 \pm 0.098	-0.087 \pm 0.052	0.069 \pm 0.098
	Burn Distance	-0.093 \pm 0.073	0.116 \pm 0.216	0.023 \pm 0.051	0.041 \pm 0.06
	Water Distance	0.019 \pm 0.045	0.041 \pm 0.063	-0.029 \pm 0.035	-0.031 \pm 0.061
	Elevation	0.239 \pm 0.337	-0.548 \pm 0.483	0.435 \pm 0.526	0.315 \pm 0.286

	Slope	-0.013 ± 0.029	0.041 ± 0.062	0.01 ± 0.057	0.112 ± 0.102
	Conifer	0.198 ± 0.068	-0.118 ± 0.142	0.26 ± 0.08	0.285 ± 0.136
	MixedDeciduous	0.203 ± 0.074	-0.159 ± 0.157	0.184 ± 0.093	0.294 ± 0.157
	Cow-Calf distance:New Cut	0.053 ± 0.033	-	-	-
	Cow-Calf distance:Regenerating Cut	0.034 ± 0.033	-	-	-
	Cow-Calf distance:Older Cut	-0.044 ± 0.027	-	-	-
	Cow-Calf distance:Road Distance	0.031 ± 0.021	-	-	-
	Cow-Calf distance:Road Density	0.07 ± 0.03	-	-	-
	Cow-Calf distance:Burn Distance	-0.059 ± 0.064	-	-	-
	Cow-Calf distance:Water Distance	0.006 ± 0.031	-	-	-
	Cow-Calf distance:Elevation	0.051 ± 0.058	-	-	-
	Cow-Calf distance:Slope	0.004 ± 0.022	-	-	-
	Cow-Calf distance:Conifer	0.05 ± 0.055	-	-	-
	Cow-Calf distance:MixedDeciduous	0.056 ± 0.051	-	-	-
Movement	SL	-0.164 ± 0.027	-0.353 ± 0.081	-0.18 ± 0.03	-0.146 ± 0.04
	Log(SL)	0.599 ± 0.02	0.504 ± 0.056	0.788 ± 0.029	0.361 ± 0.033
	SL:Cow-Calf distance	0.094 ± 0.019	-0.206 ± 0.078	0.088 ± 0.03	0.044 ± 0.044
	Log(SL):Cow-Calf distance	-0.262 ± 0.015	-0.168 ± 0.053	-0.364 ± 0.026	-0.281 ± 0.038
	SL:New Cut	-0.05 ± 0.029	0.084 ± 0.062	-0.003 ± 0.029	-0.049 ± 0.043
	Log(SL):New Cut	0.009 ± 0.024	-0.033 ± 0.048	-0.012 ± 0.028	0.029 ± 0.038
	SL:Regenerating Cut	-0.055 ± 0.027	0.152 ± 0.094	-0.063 ± 0.027	0.103 ± 0.049
	Log(SL):Regenerating Cut	-0.001 ± 0.021	-0.002 ± 0.06	-0.003 ± 0.027	-0.052 ± 0.042
	SL:Older Cut	-0.033 ± 0.031	0.204 ± 0.084	0.106 ± 0.05	-0.16 ± 0.058
	Log(SL):Older Cut	-0.044 ± 0.025	-0.094 ± 0.055	-0.025 ± 0.034	0.121 ± 0.046
	SL:Road Distance	-0.013 ± 0.025	0.023 ± 0.089	0.052 ± 0.022	0.137 ± 0.053
	Log(SL):Road Distance	-0.018 ± 0.028	-0.067 ± 0.061	-0.055 ± 0.028	-0.058 ± 0.046
	SL:Road Density	-0.03 ± 0.034	0.007 ± 0.109	-0.009 ± 0.031	0.075 ± 0.051
	Log(SL):Road Density	0.012 ± 0.029	-0.124 ± 0.071	-0.043 ± 0.029	0.043 ± 0.048
	SL:Burn Distance	0.101 ± 0.03	-0.081 ± 0.092	0.002 ± 0.039	-0.002 ± 0.034
	Log(SL):Burn Distance	-0.035 ± 0.02	-0.078 ± 0.066	-0.007 ± 0.034	0.031 ± 0.033
	SL:Water Distance	0.005 ± 0.028	0.153 ± 0.085	-0.007 ± 0.021	0.023 ± 0.042

Log(SL):Water Distance	0.067 ± 0.021	0.025 ± 0.064	-0.016 ± 0.025	-0.029 ± 0.035
SL:Elevation	0.054 ± 0.034	-0.079 ± 0.093	0.047 ± 0.032	-0.11 ± 0.047
Log(SL):Elevation	-0.048 ± 0.024	-0.143 ± 0.062	0.03 ± 0.037	0.08 ± 0.043
SL:Slope	-0.121 ± 0.031	-0.058 ± 0.074	0.034 ± 0.035	0.011 ± 0.051
Log(SL):Slope	0.028 ± 0.023	-0.009 ± 0.047	-0.034 ± 0.027	-0.055 ± 0.036
SL:Conifer	-0.011 ± 0.013	-0.21 ± 0.136	-0.040 ± 0.021	-0.061 ± 0.084
Log(SL):Conifer	-0.014 ± 0.016	0.198 ± 0.11	0.03 ± 0.051	0.013 ± 0.085
SL:MixedDeciduous	-0.052 ± 0.029	-0.167 ± 0.153	-0.06 ± 0.038	-0.169 ± 0.091
Log(SL):MixedDeciduous	0.023 ± 0.024	0.217 ± 0.12	0.077 ± 0.054	0.098 ± 0.09
SL:Cow-Calf distance:New Cut	0.128 ± 0.02	0.157 ± 0.058	-0.083 ± 0.033	-
Log(SL):Cow-Calf distance:New Cut	-0.057 ± 0.016	-0.074 ± 0.047	0.062 ± 0.026	-
SL:Cow-Calf distance:Regenerating Cut	0.178 ± 0.021	0.169 ± 0.085	-0.039 ± 0.03	-
Log(SL):Cow-Calf distance:Regenerating Cut	-0.071 ± 0.017	-0.137 ± 0.055	0.059 ± 0.022	-
SL:Cow-Calf distance:Older Cut	-0.01 ± 0.023	0.124 ± 0.09	0.094 ± 0.035	-
Log(SL):Cow-Calf distance:Older Cut	-0.024 ± 0.017	0.039 ± 0.058	0.004 ± 0.029	-
SL:Cow-Calf distance:Road Distance	-0.013 ± 0.018	-0.031 ± 0.079	0.108 ± 0.029	-
Log(SL):Cow-Calf distance:Road Distance	0.039 ± 0.021	0.004 ± 0.053	0.01 ± 0.02	-
SL:Cow-Calf distance:Road Density	0.074 ± 0.028	0.027 ± 0.106	0.123 ± 0.032	-
Log(SL):Cow-Calf distance:Road Density	0.034 ± 0.022	-0.052 ± 0.067	-0.057 ± 0.025	-
SL:Cow-Calf distance:Burn Distance	-0.031 ± 0.024	-0.336 ± 0.099	-0.144 ± 0.041	-
Log(SL):Cow-Calf distance:Burn Distance	0.011 ± 0.017	0.116 ± 0.062	0.127 ± 0.039	-
SL:Cow-Calf distance:Water Distance	-0.036 ± 0.02	0.036 ± 0.082	-0.028 ± 0.019	-
Log(SL):Cow-Calf distance:Water Distance	-0.024 ± 0.016	0.11 ± 0.07	0.01 ± 0.018	-
SL:Cow-Calf distance:Elevation	0.054 ± 0.026	-0.15 ± 0.108	-0.057 ± 0.022	-
Log(SL):Cow-Calf distance:Elevation	-0.027 ± 0.018	0.079 ± 0.072	-0.031 ± 0.025	-
SL:Cow-Calf distance:Slope	0.018 ± 0.023	0.029 ± 0.071	-0.039 ± 0.023	-
Log(SL):Cow-Calf distance:Slope	-0.021 ± 0.016	0.048 ± 0.043	0.021 ± 0.018	-
SL:Cow-Calf distance:Conifer	-	-0.227 ± 0.127	0.013 ± 0.055	-
Log(SL):Cow-Calf distance:Conifer	-	0.057 ± 0.124	-0.117 ± 0.058	-
SL:Cow-Calf distance:MixedDeciduous	-0.022 ± 0.023	-0.236 ± 0.146	-0.053 ± 0.057	-
Log(SL):Cow-Calf distance:MixedDeciduous	0.011 ± 0.018	0.085 ± 0.129	-0.072 ± 0.055	-

Appendix 3: Supplementary Information from Chapter 3

A3.1 Study area description

Prince George South (PGS) is southwest of the city of Prince George, spans approximately 11,000 km², and is largely composed of the biogeoclimatic zones Sub-Boreal Spruce with some Engelmann Spruce Sub-Alpine Fir (68). Bonaparte is northwest of Kamloops, with an area of about 6,800 km². Bonaparte is characterized by a mix of Interior Douglas Fir, Sub-Boreal Pine and Spruce, Montane Spruce, Sub-Boreal Spruce, Engelmann Spruce Sub-Alpine Fir, Bunchgrass, and Ponderosa Pine biogeoclimatic zones (68, 314). Both study areas are part of a long-term moose (*Alces alces*) monitoring research project through the BC Ministry of Forests, which addresses concerns of moose population declines across BC (20, 68).

The study areas are multi-predator, multi-prey systems. Predators include grey wolves (*Canis lupus*), cougars (*Puma concolor*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*). Other wild ungulates include mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (*Cervus canadensis*). Domestic or feral ungulates include cattle (*Bos taurus*), sheep (*Ovis aries*) and horses (*Equus caballus*). Humans access both study areas for rural property use and recreational activities, including hunting and off-road vehicle recreation.

A3.2 Moose sampling

We focused on capturing adult female/calf pairs and calves of existing collared females. Moose were captured by chemical immobilization administered via Pseudart™ (Williamsport, PA, USA) or Dan-Inject™ (Kolding, Denmark) aerial darting systems from a helicopter. Aerial net-gunning was also used to capture moose (primarily calves), in combination with aerial darting. From 2012 to 2015/2016, adult female moose were chemically immobilized using carfentanil citrate (1.4 ml at 3 mg/mL; Chiron Compounding Pharmacy Inc, Guelph, ON) and xylazine hydrochloride (0.5 ml at 100 mg/mL; Chiron Compounding Pharmacy Inc, Guelph, ON), followed by reversal of naltrexone hydrochloride (9 ml at 50 mg/ml). In winter 2016/2017 onward, adults and calves were immobilized using 3.5 ml (adult females) and 2.0 ml (calves) of BAM II (a combination of 27.3 mg/mL butorphanol, 9.1 mg/mL azaperone and 10.9 mg/mL

medetomidine; Chiron Compounding Pharmacy Inc, Guelph, ON), which was reversed using naltrexone hydrochloride (1 ml at 50 mg/mL; Chiron Compounding Pharmacy Inc, Guelph, ON) and atipamezole hydrochloride (adult females: 7 ml, calves: 4ml; 25 mg/ml; Chiron Compounding Pharmacy Inc, Guelph, ON).

We fitted adults with either Vectronic Aerospace VERTEX Survey Globalstar (2 fixes/day) or Survey Iridium (>2 fixes/day) radio collars (Berlin, Germany). Because fix rates varied between collars, we resampled all GPS data to two fixes per day. Locations within the first five days after capture were removed to account for altered behavior following collaring (140).

During capture of adult females, we measured maximum rump fat using portable ultrasounds (FUJIFILM Sonosite M-Turbo[®], Ontario, Canada, and Ibex[®] Pro, Colorado, USA). Body fat (%) was calculated following Stephenson, Hundertmark (161), using the formula:
[2] $\text{Body fat} = 5.61 + 2.05 * \text{MAXFAT}$

Where MAXFAT is the mother's maximum rump fat.

We also measured winter tick load on adult females by counting ticks along four 10-cm transects within 10 cm x 10 cm rump and shoulder plots (68). A single value for winter tick load was calculated by totalling counts from both sampling plots.

Calves were equipped with expandable Vectronic Aerospace VERTEX Survey Iridium collars (Berlin, Germany; 6 fixes/day). Male calf collars had cotton spacers designed to rot-off after one year, as adult male neck circumference exceeded the maximum expandable calf collar size. Female calf collars used either two cotton layers or none, because the expanded collars fit an average adult female's neck size. Collars sent mortality alerts following 8 hours without movement. Mortality site investigations occurred within about 24-48 hours of receiving an alert to verify mortality, following a standardized protocol described in Procter, Anderson (68). Any calf mortalities within five days of capture were censored due to possible capture effects (140).

A3.3 Rationale for seasons

Summer forage impacts the body reserves of ungulates going into winter, affecting energy allocated for gestation (165, 315). Female moose alter habitat selection and movement patterns during rut, which peaks in the first two weeks of October (192). Most pregnancies occur in the first 10 days of rut, and gestation lasts on average 231 days (range: 216 to 240 days) (316). During early gestation, moose experience heavier snowfall, limited food availability, and winter

tick pressures (*Dermacentor albipictus*) (191, 283). Energy expenditure for gestation increases significantly during late gestation, corresponding to spring green-up (206). May 21 is the average calving date within the study areas, based on adult female movement patterns indicating parturition (68, 188, 274, 317). However, we defined the neonatal period starting from May 1 to capture all potential calving dates. During this period, neonates are most vulnerable to limiting factors such as predation (43, 318). Lactation peaks during the neonatal period and calves are weaned by the following rut (within about four months old) (176). Energy requirements for mothers are highest during lactation in the neonatal period, and after which, both the mother and juvenile must build up sufficient body fat to survive the winter (165, 191, 192, 319).

The seasons of weaning, autumn and early winter correspond to summer, rut, and early gestation, respectively. The different terms are used to differentiate lagged seasons from those when the radio-collared calf accompanied its mother.

Typically, female moose reproduce every year, although recruitment success varies (42, 192). The previous reproductive status of female moose was unknown within this study. It is possible that females were accompanied by a previous calf prior in summer, rut, and gestation, which would impact maternal habitat use and nutritional status of the female (320). However, we were unable to account for these unmonitored calves, as well as any twinning, in our analyses. Additionally, we had a low sample size of females in some seasons (particularly in unsuccessful females in Bonaparte) which may impact conclusions.

A3.4 Covariates

At each adult female moose location, we extracted environmental data from sources accessed through DataBC (catalogue.data.gov.bc.ca), unless otherwise specified. We resampled spatial layers to the coarsest resolution (30-m) and temporally matched spatial layers with dates of moose locations. All distance covariates were log-transformed.

We determined the proportion of new (0 to 8 years since logging) and regenerating (9 to 24 years) cutblocks within a 250-m buffer of locations, with cutblock age thresholds based on previously identified patterns of moose selection in interior BC (41, 144). We also assessed road density (km/km^2) with a 250-m buffer and the distance to the nearest road (meters) (145).

We reclassified forest landcover (141) into categories based on the leading tree species (deciduous, coniferous, pine, and mixed forest) and calculated the proportion of each forest type

within a 250-m buffer. In PGS, we identified collinearity between proportions of coniferous and mixed forest in all seasons and ran separate Cover, Risk-Avoidant Foraging, and Global models for each collinear variable.

We also determined the Euclidean distance (meters) to the nearest waterbody (i.e., wetlands, lakes, streams, and rivers) (142). For each season, we calculated maximum normalized difference vegetation index (NDVI) from Landsat satellite imagery using Google Earth Engine, as a measure of plant productivity in summer and vegetative cover in winter (148, 306). We extracted the maximum NDVI at each moose location. Additionally, we calculated the distance of each moose location to the nearest edge of the closest forest of any size (141, 144) when moose were outside of the forest (meters).

We used a Digital Elevation Model (143) to determine elevation (meters), slope (degrees: 0-90°) and aspect (radians) at each location. Aspect was transformed to measures of E-W (+1 = East, -1 = West) and N-S (+1 = North, -1 = South) using cosine and sine functions, respectively.

We identified burned areas using a combination of Historical Fire Perimeters (146) and delta Normalized Burn Ratio (dNBR) (147) calculated from pre-fire (previous year) and post-fire cloud-free Landsat satellite imagery using Google Earth Engine (148). Post-fire images were obtained from the fire year, between June 1 to September 30 after the fire was extinguished. We used the Historical Fire Perimeters to determine the potential extent of fires and then delineated burned areas in these perimeters based on dNBR > 0.1 (149). From this burn layer, we determined the distance of each location to the nearest new (0-8 years since fire) and regenerating (9-24 years since fire) burn (meters).

A3.5 Tables

Table A3.1 Sample size (n) of successful (calf survival from 8 months to 1 year old) and unsuccessful (calf mortality between 8 months and 1 year of age) radio-collared adult female moose (Alces alces) included in seasonal resource selection functions for summer (July 1 – September 14 prior to parturition), rut (September 15 – October 15 prior to parturition), early gestation (October 16 – January 31), late gestation (February 1 – April 30), neonatal period (May 1 – June 30), weaning (July 1 – September 14), autumn (September 15 – October 15), early winter (October 16 – January 31), and late winter (February 1 – May 21 or date of calf mortality) in Prince George South (2015-2020) and Bonaparte (2016-2020), British Columbia, Canada.

Season	Prince George South		Bonaparte Plateau	
	Successful n	Unsuccessful n	Successful n	Unsuccessful n
Summer	6	6	23	4

Rut	6	6	23	4
Early Gestation	8	8	29	7
Late Gestation	9	8	30	7
Neonatal	9	8	28	7
Weaning	9	7	27	7
First Rut	9	7	27	7
Early Winter	9	7	27	7
Late Winter	21	7	36	19

Table A3.2 Model selection results for seasonal habitat selection analyses for moose mothers based on recruitment success in Prince George South. Akaike's Information Criterion corrected for small sample sizes (AIC_c) for candidate models examining seasonal habitat selection of successful (calf survival from capture at 8 months of age to 1 year old) and unsuccessful (calf mortality between capture and 1 year old) moose (*Alces alces*) mothers for summer (July 1 – September 14 prior to parturition), rut (September 15 – October 15 prior to parturition), early gestation (October 16 – January 31), late gestation (February 1 – April 30), neonatal (May 1 – June 30), weaning (July 1 – September 14), autumn (September 15 – October 15), early winter (October 16 – January 31), and late winter (February 1 – May 21 or date of calf mortality) in Prince George, 2016-2020. Bold numbers represent the most supported candidate model for each season. Brackets refer to collinear variables included within each model (either proportion of mixed forest- or coniferous-leading stands).

Success	Candidate Model	Summer	Rut	Early Gestation	Late Gestation	Neonatal	Lactation	Autumn	Early Winter	Late Winter
Successful	Cover (Coniferous)	5676.36	2262.81	9161.8	11910.69	8643.36	10363.81	4300.17	18681.83	34322.31
	Cover (Mixed Forest)	5677.38	2278.19	9147.18	11993.96	8646.96	10391.76	4295.47	18710.18	34297.72
	Disturbance Avoidance	5436.84	2018.65	9025.02	11603.85	8438.42	10232.83	4082.35	18358.06	34170.10
	Topography	5635.78	2295.83	9236.52	11710.85	8657.35	10412.42	4326.62	18967.85	34148.91
	Risk Avoidant Foraging (Coniferous)	5586.57	2142.34	9124.13	11524.31	8555.54	10234.49	4199.29	18415.66	33847.01
	Risk Avoidant Foraging (Mixed Forest)	5599.46	2150.35	9109	11559.71	8543.72	10218.38	4193.6	18457.11	33872.78
	Resources	5622.72	2241.84	9178.45	11823.9	8357.41	10202.96	4295.7	19018.7	34128.49
	Disturbance Resources	5469.52	2099.52	9063.09	11813.34	8511.99	10319.17	4156.41	18480.65	34254.31
	Cutblock Resources	5666.21	2163.81	9063.21	12036.05	8597.14	10340.89	4176.74	18488.89	34348.55
	Risk-Prone Foraging	5357.78	2008.32	8982.63	11501.21	8113.29	9945.46	4057.98	18297.09	34015.84
	Global (Coniferous)	5298.33	1940.21	8959.08	11194.73	8084.09	9898.25	4055.35	18194.16	33690.00
	Global (Mixed Forest)	5322.71	1951.42	8925.22	11199.7	8062	9891.96	4045.65	18210.81	33693.78
Unsuccessful	Cover (Coniferous)	5972.01	2387.18	8638.02	9055.48	5644.56	6932.21	2798.92	9823.43	7930.49
	Cover (Mixed Forest)	5976.01	2402.15	8684.42	8989.48	5645.97	6955.13	2815.49	9773.17	7648.89
	Disturbance Avoidance	5729.93	2340.64	8556.53	8738.2	5445.63	6734.93	2763.39	9787.69	7644.83
	Topography	5824.67	2443.54	8993.41	9162.64	5543.86	6730.62	2848.09	10122.56	7859.71
	Risk Avoidant Foraging (Coniferous)	5711.52	2279.68	8537.13	8814.31	5399.6	6649.7	2680.5	9767.29	7529.54
	Risk Avoidant Foraging (Mixed Forest)	5706.67	2286.9	8626.18	8762.07	5406.64	6646.99	2687.16	9691.72	7364.46

Resources	5925.77	2409.84	8901.56	8888.51	5625.52	6892.94	2770.55	9964.92	7972.04
Disturbance Resources	5749.52	2408.29	8559.65	8816.97	5529.09	6738.67	2790.35	9822.49	7810.42
Cutblock Resources	5986.59	2474.78	8618.92	8877.54	5566.39	6961.73	2877.8	9884.93	7898.33
Risk-Prone Foraging	5599.91	2328.92	8506.76	8587.73	5436.61	6634.24	2722.66	9703.91	7682.63
Global (Coniferous)	5511.87	2230.84	8317.44	8494.08	5205.3	6452.85	2585.18	9430.67	7459.35
Global (Mixed Forest)	5502.3	2232.33	8364.32	8454.45	5203.77	6441.19	2584.33	9364.48	7312.29

Table A3.3 Model selection results for seasonal habitat selection analyses for moose mothers based on recruitment success in the Bonaparte Plateau. Akaike's Information Criterion corrected for small sample sizes (AIC_c) for candidate models examining habitat selection of successful (calf survival from capture at 8 months of age to 1 year old) and unsuccessful (calf did not survive from capture to 1 year old) moose (*Alces alces*) mothers in summer (July 1 – September 14 prior to parturition), rut (September 15 – October 15 prior to parturition), early gestation (October 16 – January 31), late gestation (February 1 – April 30), neonatal (May 1 – June 30), weaning (July 1 – September 14), autumn (September 15 – October 15), early winter (October 16 – January 31), and late winter (February 1 – May 21 or date of calf mortality) in Bonaparte, 2015-2020. Bold numbers represent the most supported candidate model for each season.

Success	Candidate Model	Summer	Rut	Early Gestation	Late Gestation	Neonatal	Lactation	Autumn	Early Winter	Late Winter
Successful	Cover	22968.87	9531.85	36811.05	36786.72	23441.67	27786.23	11155.84	42301.02	68140.94
	Disturbance Avoidance	22917.9	9414.21	36671.17	36976.37	23145.81	27609.57	11010.25	41824.34	68338.95
	Topography	22575.77	9136.56	36475.26	36451.24	23039.61	27603.67	10972.2	42274.94	67902.17
	Risk Avoidant Foraging	21917.52	8934.02	35995.64	36147.44	22844.74	26887.33	10739.85	41676.31	67517.78
	Resources	22791.46	9597.58	36573.45	36839.4	22989.01	27380.78	11199.9	42322.69	68261.09
	Disturbance Resources	23210.13	9571.43	36725.16	36994.52	23383.79	27815.34	11120.14	42087.38	68436.31
	Cutblock Resources	23217.13	9581.61	36825.81	37012.35	23444.26	27838.75	11181.13	42194.64	68615.96
	Risk-Prone foraging	22611.58	9350.3	36404.37	36971.02	22712.31	27051.47	10976.29	41739.06	68111.58
	Global	21879.56	8915.93	35862.77	36002.53	22405.08	26727.55	10635.06	41348.15	67252.67
	Unsuccessful	Cover	3906.88	1616.43	7034.17	7778.88	5303.59	6244.85	6807.58	11362.1
Disturbance Avoidance		3704.5	1559.4	6929.98	7614.98	5199.2	6114.65	6721.47	11276.48	15171.18
Topography		3830.24	1634.7	6759.15	7947.44	5143.4	6357.3	6906.78	11457.37	15210.34

Risk Avoidant									
Foraging	3719.66	1604.12	6650.36	7726.45	5067.13	6090.42	6598.99	11116.68	14911.48
Resources	3894.92	1633.02	6970.62	7912.21	5211.19	6386.45	6855.17	11350.63	15487.35
Disturbance Resources	3783.84	1570.64	6934.04	7637.56	5246.2	6256.88	6865.06	11367.54	15231.36
Cutblock Resources	3928.04	1632.51	7037.13	7833.13	5332.03	6391.33	6878.6	11364.97	15378.98
Risk-Prone foraging	3650.59	1521.92	6859.36	7465.56	4962.86	6076.53	6599.64	11176.83	15046.95
Global	3521.91	1505.41	6553.31	7445.49	4788.83	5948.11	6452.19	11015.28	14625.04

Table A3.4 Cross validation scores for the top candidate resource selection functions for successful (calf survived from capture to 1 year) and unsuccessful (calf did not survive to 1 year) mother moose (Alces alces) in summer (July 1 – September 14 prior to parturition), rut (September 15 – October 15 prior to parturition), early gestation (October 16 – January 31), late gestation (February 1 – April 30), neonatal (May 1 – June 30), weaning (July 1 – September 14), autumn (September 15 – October 15), early winter (October 16 – January 31), and late winter (February 1 – May 21 or date of calf mortality) in Prince George South (PGS) and Bonaparte, British Columbia, Canada. Brackets represent the collinear variable included in the model: proportion of mixed forest (MF) or coniferous-leading stands (C).

Study Area	Season	Successful		Unsuccessful	
		Model	Accuracy	Model	Accuracy
PGS	Summer	Global (C)	0.90	Global (MF)	0.90
	Rut	Global (C)	0.91	Global (C)	0.87
	Early Gestation	Global (MF)	0.91	Global (C)	0.90
	Late Gestation	Global (C)	0.91	Global (MF)	0.91
	Neonatal	Global (MF)	0.91	Global (MF)	0.91
	Weaning	Global (MF)	0.91	Global (MF)	0.90
	Autumn	Global (MF)	0.90	Global (MF)	0.90
	Early Winter	Global (MF)	0.90	Global (MF)	0.90
	Late Winter	Global (C)	0.91	Global (MF)	0.91
Bonaparte	Summer	Global	0.90	Global	0.80
	Rut	Global	0.89	Global	0.77
	Early Gestation	Global	0.90	Global	0.88
	Late Gestation	Global	0.91	Global	0.90
	Neonatal	Global	0.91	Global	0.90
Weaning	Global	0.91	Global	0.90	

Autumn	Global	0.91	Global	0.87
Early Winter	Global	0.90	Global	0.88
Late Winter	Global	0.91	Global	0.91

Table A3.5 Body fat (current and lagged) for mother moose by calf recruitment success. Current (matching calf capture date) and lagged (1 year prior to calf capture) body fat (%) for successful (calf survived from capture at about 8 months to 1 year old) and unsuccessful (calf mortality between 8 months and 1 year) adult female moose (*Alces alces*) in Prince George South (PGS) and Bonaparte, British Columbia, Canada. Body fat was measured as ingesta-free body fat (I61), using ultrasound rump fat measurements taken between December – January.

Region	Calf Recruited	N	Mean body fat ± SE (%)	Min – Max body fat (%)	Lagged n	Lagged Mean body fat ± SE (%)	Lagged Min – Max body fat (%)
Bonaparte	Successful	19	7.9 ± 0.3	5.6 – 10.4	11	9.4 ± 0.6	7.6 – 13.8
	Unsuccessful	5	8.3 ± 0.9	6.1 – 10.7	4	10.1 ± 0.8	8.8 – 12.3
PGS	Successful	16	7.9 ± 0.4	6.4 – 11.8	3	6.8 ± 0.7	5.6 – 7.9
	Unsuccessful	8	8.4 ± 0.6	6.8 – 10.9	3	10.3 ± 2.5	7.7 – 15.2

Table A3.6 Winter tick load (current and lagged) for mother moose based on calf recruitment success. Current (matching calf capture date) and lagged (1 year prior to calf capture) winter tick (*Dermacentor albipictus*) loads for successful (calf survived from capture at about 8 months to 1 year old) and unsuccessful (calf mortality between 8 months and 1 year) adult female moose (*Alces alces*) in Prince George South (PGS) and Bonaparte, British Columbia, Canada.

Region	Calf Recruited	N	Mean Tick Load ± SE	Min – Max Tick Load	Lagged n	Lagged Tick Load ± SE	Lagged Min – Max Tick Load
Bonaparte	Successful	21	3.8 ± 1.6	0 – 28	9	9.4 ± 3.7	0 – 28
	Unsuccessful	7	10.3 ± 7.4	0 – 54	4	2.8 ± 1.8	0 – 8
PGS	Successful	19	2.7 ± 0.6	0 – 11	6	2.0 ± 0.5	0 – 3
	Unsuccessful	11	7.5 ± 1.5	1 – 15	3	9.7 ± 4.1	3 – 17

Table A3.7 Previous rearing success of mother moose based on current recruitment success. Previous calf presence (the year prior to calf capture) during mid-winter (January – February) surveys for successful (calf survived from capture at about 8 months to 1 year old) and unsuccessful (calf mortality between 8 months and 1 year) adult female moose (*Alces alces*) in Prince George South (PGS) and Bonaparte, British Columbia, Canada.

Previous Mid-Winter Calf Presence	Prince George South		Bonaparte	
	Successful	Unsuccessful	Successful	Unsuccessful
Yes	5	2	9	0
No	7	3	8	4

Table A3.8 Beta coefficients for models assessing the relationship of maternal health and previous rearing success with current recruitment success for mother moose. Beta coefficient estimates and cross-validation accuracy for binomial generalized linear models comparing current and lagged body fat (%), current and lagged winter tick (*Dermacentor albipictus*) load, and previous maternal success between successful (calf survived from

capture at about 8 months to 1 year old) and unsuccessful (calf mortality between 8 months and 1 year) mother moose (Alces alces) in Prince George South (PGS) and Bonaparte, British Columbia, Canada. Current measures temporally matched the year of calf capture, while lagged measurements were taken 1 year prior to calf capture. PGS was the reference category for the study area covariate.

Model	Accuracy	Covariate	Estimate
Current Body Condition	0.72	Current body fat (%)	-0.22 ± 0.23
		Study Area (PGS)	-0.63 ± 0.67
Lagged Body Condition	0.67	Lagged body fat (%)	-0.87 ± 0.65
		Study Area (PGS)	-1.67 ± 1.28
Current Winter Tick Load	0.72	Current Tick Count	-0.75 ± 0.40
		Study Area (PGS)	-0.67 ± 0.62
Lagged Winter Tick Load	0.64	Lagged Tick Count	0.09 ± 0.49
		Study Area (PGS)	-0.09 ± 0.94
Previous Maternal Success	0.77	Mid-Winter Calf Presence (Yes)	1.19 ± 0.89
		Study Area (PGS)	-0.58 ± 0.79

Appendix 4: Supplementary Information from Chapter 4

A4.1 Study area descriptions

Our camera arrays were set up across two study areas with high levels of forest harvest in interior BC: Prince George South (PGS; 11052 km²) and the Bonaparte Plateau (6776 km²) (Fig. 4.1). Over the past two decades, both regions have experienced drastic landscape change through a combination of forest harvest, road construction, mountain pine beetle outbreak, and wildfire. Widespread forest harvest across both landscapes led to an increase in new cutblocks and associated forestry roads (41), which, in addition to wildfire, has created increasingly connected, early successional landscapes.

Bonaparte and PGS are home to a variety of predator and ungulate species. Predators include grey wolves (*Canis lupus*), black bears (*Ursus americanus*), grizzly bears (*U. arctos*), cougar (*Puma concolor*), coyotes (*C. latrans*), lynx (*Lynx canadensis*), bobcat (*L. rufus*; Bonaparte only), and wolverine (*Gulo gulo*; PGS only). Ungulate species include moose (*Alces alces*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (*Cervus canadensis*). Free-ranging domestic cattle (*Bos taurus*) and both domestic and feral horses (*Equus caballus*) are also present.

Bonaparte is typified primarily by a combination of Interior Douglas Fir, Sub-Boreal Pine and Spruce, and Montane Spruce biogeoclimatic zones, whereas PGS is largely dominated by the Sub-boreal Spruce zone (314). Both study areas are characterized by a mix of coniferous and deciduous forest, primarily comprised of the following species: lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas fir (*Pseudotsuga menziesii* var. *glauca*), spruce (*Picea engelmannii* × *glauca*), subalpine fir (*Abies lasiocarpa*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and black cottonwood (*P. balsifera*).

A4.2 Tables

Table A4.1 Candidate models describing our hypotheses on the effects of natural and anthropogenic disturbances on predators and ungulates. The ‘Basic model structures’ (A) describe the candidate models, with the ‘Silviculture’ term as a placeholder that is replaced by each of the silviculture variable groupings (B) to form our final candidate model set.

Category	Name	Structure
A) Basic model structures	Base model	Landcover
	Predator-prey occurrence model	Base + Predator/prey occurrence
	Silviculture models	Base + Silviculture + Roads
	Additive models	Base + Silviculture + Roads + Predator/prey occurrence
	Interaction models	Base + Silviculture X Predator/prey occurrence + Roads
	Interaction models	Base + Silviculture + Roads X Predator/prey occurrence
	Global models	Base + Silviculture X Predator/prey occurrence + Roads X Predator/prey occurrence
B) Silviculture variable groupings	Cutblock presence	Cutblock
	Cutblock age	New cutblock + Regenerating cutblock + Older cutblock
	Edge density	New cutblock edge density + Regenerating cutblock edge density + Older cutblock edge density
	Age system	Even-aged system + Uneven-aged system
	Age system by cutblock age	New even-aged system + Regenerating even-aged system + Older even-aged system + Uneven-aged system
	Silviculture system	Clearcut + Clearcut with reserves + Selection system
	Silviculture system by cutblock age	New clearcut + Regenerating clearcut + Older clearcut + Selection system + New clearcut with reserves + Regenerating/older clearcut with reserves
	Site preparation	Cutblock with site preparation + Cutblock without site preparation
	Site preparation type	Cutblock with mechanical site preparation + Cutblock with other site preparation + Cutblock without site preparation
	Site preparation by cutblock age	New cutblock with site preparation + Regenerating cutblock with site preparation + Older cutblock with site preparation + New cutblock without site preparation + Regenerating cutblock without site preparation + Older cutblock without site preparation
	Planting	Planted cutblock + Not planted cutblock

Planting by cutblock age	Planted new cutblock + Planted regenerating cutblock + Planted older cutblock + Not planted new cutblock + Not planted regenerating cutblock + Not planted older cutblock
Brushing	Brushed cutblock + Cutblock without brushing
Brushing type	No brushing + Mechanically brushed cutblock + Chemically brushed cutblock + Manually brushed cutblock
Brushing by cutblock age	New cutblock with no brushing + Regenerating cutblock with no brushing + Older cutblock with no brushing + New cutblock with brushing + Regenerating cutblock with brushing + Older cutblock with brushing
Fertilization	Fertilized cutblock + Not fertilized cutblock
Spacing	Spaced cutblock + Not spaced cutblock

Table A4.2 Model selection results for species assessed for seasonal occurrence in relation to forest harvest features, silviculture, and predator/prey occurrence based on wildlife camera trap data. Akaike's Information Criterion corrected for small sample sizes (AIC_c) results for the top five models (ranked by delta AIC_c) explaining black bear (*Ursus americanus*), coyote (*Canis latrans*), moose (*Alces alces*), and mule deer (*Odocoileus hemionus*) occurrence in early summer (May to June), late summer (July to October), and winter (November to April; excluding black bears) in Prince George South and the Bonaparte Plateau, British Columbia, Canada, 2021 to 2023.

Species	Season	Model	AIC_c	Delta AIC_c	AIC_c weight	Log-likelihood	Relative likelihood
Black bear	Early summer	Silviculture system by cutblock age + Roads + Prey (including cattle)	859.746	0	0.406	-413.873	1
	Early summer	Silviculture system by cutblock age + Roads X Cattle	860.088	0.343	0.342	-413.044	0.843
	Early summer	Silviculture system by cutblock age X Prey (including cattle) + Roads	863.485	3.739	0.063	-409.742	0.154
	Early summer	Silviculture system by cutblock age X Cattle + Roads X Cattle	864.946	5.201	0.03	-409.473	0.074
	Early summer	Site preparation by cutblock age X Prey (including cattle) + Roads	866.645	6.9	0.013	-411.323	0.032
	Late summer	Site preparation by cutblock age X Cattle + Roads	1570.78	0	0.346	-763.39	1
	Late summer	Site preparation by cutblock age X Cattle + Roads X Predation	1572.532	1.752	0.144	-763.266	0.417
	Late summer	Site preparation by cutblock age X Deer + Roads X Deer	1573.291	2.511	0.099	-763.646	0.285

Coyote	Late summer	Silviculture system by cutblock age X Prey (not including cattle) + Roads	1573.595	2.815	0.085	-764.797	0.245
	Late summer	Site preparation by cutblock age X Deer + Roads	1575.126	4.346	0.039	-765.563	0.114
	Early summer	Brushing type	523.972	0	0.118	-248.986	1
	Early summer	Site preparation type X Deer + Roads X Deer	524.344	0.372	0.098	-245.172	0.83
	Early summer	Brushing type + Roads + Mule deer	524.994	1.022	0.071	-248.497	0.6
	Early summer	Brushing type + Roads + Deer	525.078	1.106	0.068	-248.539	0.575
	Early summer	Site preparation X Deer + Roads X Deer	525.563	1.591	0.053	-247.781	0.451
	Late summer	Silviculture system by cutblock age X Mule deer + Roads	948.909	0	0.338	-452.455	1
	Late summer	Silviculture system by cutblock age X Deer + Roads	949.541	0.632	0.246	-452.771	0.729
	Late summer	Silviculture system by cutblock age X Mule deer + Roads X Mule deer	950.702	1.793	0.138	-452.351	0.408
Moose	Late summer	Silviculture system by cutblock age X Deer + Roads X Deer	951.031	2.122	0.117	-452.515	0.346
	Late summer	Silviculture system by cutblock age + Roads + Mule deer	952.272	3.363	0.063	-460.136	0.186
	Winter	Brushing type + Roads + Deer	1343.653	0	0.124	-657.827	1
	Winter	Brushing type + Roads + Mule deer	1343.899	0.246	0.11	-657.95	0.884
	Winter	Brushing X Deer + Roads	1344.102	0.449	0.099	-658.051	0.799
	Winter	Brushing type + Roads X Deer	1344.225	0.572	0.093	-657.113	0.751
	Winter	Brushing type + Roads X Mule deer	1344.273	0.619	0.091	-657.136	0.734
	Early summer	Age system by cutblock age + Roads X Predator	469.277	0	0.133	-219.638	1
	Early summer	Age system by cutblock age + Roads X Bear	469.576	0.299	0.115	-219.788	0.861
	Early summer	Age system by cutblock age + Roads X Coyote	469.935	0.658	0.096	-219.967	0.72
	Early summer	Age system by cutblock age X Wolf + Roads X Wolf	470.892	1.615	0.059	-216.446	0.446
	Early summer	Age system by cutblock age + Roads + Predator	471.187	1.91	0.051	-221.593	0.385
	Late summer	Site preparation type X Coyote + Roads	930.534	0	0.72	-449.267	1
	Late summer	Site preparation type X Coyote + Roads X Coyote	932.455	1.921	0.275	-449.227	0.383
	Late summer	Site preparation type X Wolf + Roads	941.187	10.653	0.003	-454.593	0.005
Late summer	Site preparation type X Wolf + Roads X Wolf	943.186	12.652	0.001	-454.593	0.002	
Late summer	Site preparation type + Wolf X Predation	949.013	18.479	0	-460.507	0	
Winter	Fertilization X Wolf + Roads	818.512	0	0.543	-395.256	1	

	Winter	Fertilization X Wolf + Roads X Wolf	820.307	1.795	0.221	-395.154	0.407
	Winter	Fertilization + Roads + Wolf	820.851	2.339	0.169	-398.425	0.311
	Winter	Fertilization + Roads X Wolf	822.829	4.317	0.063	-398.414	0.115
	Winter	Fertilization + Roads X Predator	830.91	12.398	0.001	-402.455	0.002
Mule deer	Early summer	Edge density X Canid + Roads	759.306	0	0.232	-363.653	1
	Early summer	Edge density X Canid + Roads X Canid	759.53	0.223	0.208	-362.765	0.894
	Early summer	Edge density X Predator + Roads X Predator	759.969	0.663	0.167	-362.985	0.718
	Early summer	Edge density X Predator + Roads	761.088	1.781	0.095	-364.544	0.41
	Early summer	Planting X Canid + Roads	762.803	3.497	0.04	-367.402	0.174
	Late summer	Site preparation by cutblock age X Predator + Roads	1390.024	0	0.72	-673.012	1
	Late summer	Site preparation by cutblock age X Predator + Roads X Predator	1391.924	1.9	0.278	-672.962	0.387
	Late summer	Planting by cutblock age X Wolf + Roads X Wolf	1402.486	12.462	0.001	-678.243	0.002
	Late summer	Planting by cutblock age X Wolf + Roads	1406.42	16.396	0	-681.21	0
	Late summer	Site preparation by cutblock age X Wolf + Roads	1410.676	20.652	0	-683.338	0
	Winter	Silviculture system X Predator + Roads	527.716	0	0.467	-247.858	1
	Winter	Silviculture system X Predator + Roads X Predator	529.714	1.999	0.172	-247.857	0.368
	Winter	Age system by cutblock age X Canid + Roads X Canid	531.475	3.76	0.071	-246.738	0.153
	Winter	Age system by cutblock age X Predator + Roads	532.84	5.125	0.036	-248.42	0.077
	Winter	Age system X Predator + Roads X Predator	533.296	5.58	0.029	-251.648	0.061

Table A4.3 Odds ratios (with lower and upper confidence levels) for all coefficients explaining black bear (*Ursus americanus*), coyote (*Canis latrans*), moose (*Alces alces*), and mule deer (*Odocoileus hemionus*) occurrence in early summer (May to June), late summer (July to October), and winter (November to April; excluding black bears) in Prince George South and the Bonaparte Plateau, British Columbia, Canada, 2021 to 2023.

	Black bear		Coyote			Moose			Mule deer		
	Early summer	Late summer	Early summer	Late summer	Winter	Early summer	Late summer	Winter	Early summer	Late summer	Winter
Intercept	0.441 (0.205, 0.950)	0.290 (0.168, 0.501)	0.107 (0.038, 0.303)	0.092 (0.075, 0.114)	0.088 (0.075, 0.104)	0.094 (0.069, 0.127)	0.067 (0.034, 0.131)	0.039 (0.031, 0.050)	0.277 (0.156, 0.490)	0.223 (0.056, 0.882)	0.009 (0.000, 0.319)

	Black bear		Coyote			Moose			Mule deer		
	Early summer	Late summer	Early summer	Late summer	Winter	Early summer	Late summer	Winter	Early summer	Late summer	Winter
Predator/Prey occurrence	1.799 (1.404, 2.305)	1.027 (0.747, 1.410)		1.304 (1.096, 1.552)	0.849 (0.702, 1.027)			1.856 (1.534, 2.247)		1.134 (0.939, 1.369)	0.737 (0.313, 1.733)
Uneven-aged (Selection) system	1.266 (1.034, 1.551)			1.249 (1.029, 1.516)		0.548 (0.310, 0.966)					1.346 (0.870, 2.083)
Clearcut											1.554 (1.000, 2.414)
Clearcut with reserves											0.789 (0.492, 1.267)
New clearcut	0.635 (0.470, 0.858)			1.095 (0.926, 1.295)							
Regenerating clearcut	1.228 (0.961, 1.570)			0.748 (0.548, 1.021)							
Older clearcut	0.914 (0.735, 1.136)			1.260 (1.011, 1.570)							
New clearcut with reserves	0.910 (0.728, 1.138)			0.885 (0.690, 1.136)							
Regenerating/older clearcut with reserves	1.191 (0.972, 1.461)			1.705 (1.381, 2.106)							
Clearcut:Predator/Prey occurrence											1.884 (0.854, 4.157)
Uneven-aged (Selection) system:Predator/Prey occurrence											2.969 (1.595, 5.524)
Clearcut with reserves:Predator/Prey occurrence											0.463 (0.283, 0.756)

	Black bear		Coyote			Moose			Mule deer		
	Early summer	Late summer	Early summer	Late summer	Winter	Early summer	Late summer	Winter	Early summer	Late summer	Winter
New cutblock with site preparation		1.142 (0.934, 1.396)								1.052 (0.875, 1.263)	
Regenerating cutblock with site preparation		1.029 (0.789, 1.344)								0.786 (0.627, 0.986)	
Older cutblock with site preparation		1.135 (0.891, 1.444)								0.694 (0.550, 0.876)	
New cutblock without site preparation		0.833 (0.659, 1.051)								1.191 (0.977, 1.451)	
Regenerating cutblock without site preparation		1.469 (1.088, 1.984)								1.306 (1.017, 1.679)	
Older cutblock without site preparation		0.950 (0.756, 1.192)								0.860 (0.719, 1.028)	
New cutblock with site preparation:Predator/Prey occurrence		0.706 (0.523, 0.952)								0.876 (0.678, 1.133)	
Regenerating cutblock with site preparation:Predator/Prey occurrence		0.967 (0.720, 1.299)								0.567 (0.428, 0.751)	
Older cutblock with site preparation:Predator/Prey occurrence		1.225 (0.928, 1.617)									
New cutblock without site preparation:Predator/Prey occurrence		1.032 (0.886, 1.203)								1.684 (1.401, 2.025)	
Regenerating cutblock without site preparation:Predator/Prey occurrence		0.952 (0.666, 1.360)								0.827 (0.670, 1.022)	

	Black bear		Coyote			Moose			Mule deer		
	Early summer	Late summer	Early summer	Late summer	Winter	Early summer	Late summer	Winter	Early summer	Late summer	Winter
preparation:Predator/Prey occurrence											
Older cutblock without site preparation:Predator/Prey occurrence		0.829 (0.583, 1.180)								0.453 (0.319, 0.644)	
Older cutblock with site preparation:Predator/Prey occurrence										1.103 (0.893, 1.363)	
Cutblock without brushing			0.982 (0.655, 1.472)		0.504 (0.382, 0.665)						
Cutblock with mechanical brushing			1.142 (0.971, 1.343)		1.054 (0.906, 1.225)						
Cutblock with chemical brushing			1.024 (0.687, 1.526)		1.003 (0.783, 1.285)						
Cutblock with manual brushing			1.474 (1.206, 1.800)		1.203 (1.065, 1.359)						
Cutblock with fertilization								1.787 (1.480, 2.157)			
Cutblock without fertilization								1.385 (0.957, 2.005)			
Road density	0.845 (0.687, 1.039)	0.832 (0.707, 0.978)	0.943 (0.688, 1.293)	1.235 (1.013, 1.506)	0.961 (0.806, 1.146)	1.032 (0.631, 1.689)	0.758 (0.399, 1.441)	0.917 (0.699, 1.203)	0.793 (0.632, 0.995)	0.989 (0.832, 1.177)	0.963 (0.601, 1.545)
Deciduous forest	1.137 (0.950, 1.361)	1.451 (1.180, 1.784)	0.869 (0.668, 1.131)	1.344 (1.149, 1.571)	0.922 (0.788, 1.079)	1.017 (0.734, 1.409)	1.177 (0.920, 1.506)	1.406 (1.087, 1.818)	0.916 (0.727, 1.152)	0.829 (0.691, 0.994)	1.161 (0.824, 1.636)

	Black bear		Coyote			Moose			Mule deer		
	Early summer	Late summer	Early summer	Late summer	Winter	Early summer	Late summer	Winter	Early summer	Late summer	Winter
Conifer forest	0.915 (0.707, 1.183)	1.326 (0.901, 1.952)	0.664 (0.442, 0.998)	1.025 (0.747, 1.407)	0.753 (0.573, 0.991)	0.656 (0.351, 1.225)	1.235 (0.761, 2.003)	0.883 (0.635, 1.227)	0.694 (0.517, 0.931)	0.821 (0.633, 1.064)	1.255 (0.739, 2.130)
Forest age	1.176 (0.959, 1.441)	1.145 (0.997, 1.315)	0.934 (0.711, 1.225)	0.746 (0.614, 0.907)	0.817 (0.694, 0.963)	1.101 (0.821, 1.478)	0.991 (0.790, 1.242)	1.211 (0.963, 1.524)	1.091 (0.898, 1.325)	0.837 (0.714, 0.982)	0.812 (0.571, 1.155)
Burn	1.028 (0.794, 1.331)	1.163 (0.909, 1.488)	0.964 (0.712, 1.306)	1.073 (0.841, 1.369)	1.039 (0.845, 1.277)	0.697 (0.486, 0.999)	0.976 (0.749, 1.272)	0.812 (0.622, 1.059)	1.077 (0.855, 1.355)	1.076 (0.881, 1.314)	1.162 (0.797, 1.693)
Elevation	0.943 (0.719, 1.237)	0.907 (0.718, 1.146)	0.843 (0.569, 1.248)	0.809 (0.649, 1.008)	1.032 (0.841, 1.266)	0.884 (0.680, 1.148)	1.291 (0.951, 1.752)	0.880 (0.700, 1.106)	1.434 (1.040, 1.977)	0.851 (0.663, 1.092)	0.091 (0.052, 0.161)
Distance to water	1.000 (0.822, 1.217)	1.149 (0.988, 1.336)	0.816 (0.613, 1.087)	1.093 (0.877, 1.363)	1.021 (0.855, 1.220)	1.152 (0.885, 1.500)	0.809 (0.650, 1.008)	0.878 (0.686, 1.124)	0.918 (0.752, 1.120)	0.843 (0.718, 0.990)	2.408 (1.774, 3.269)

A4.3 Figures

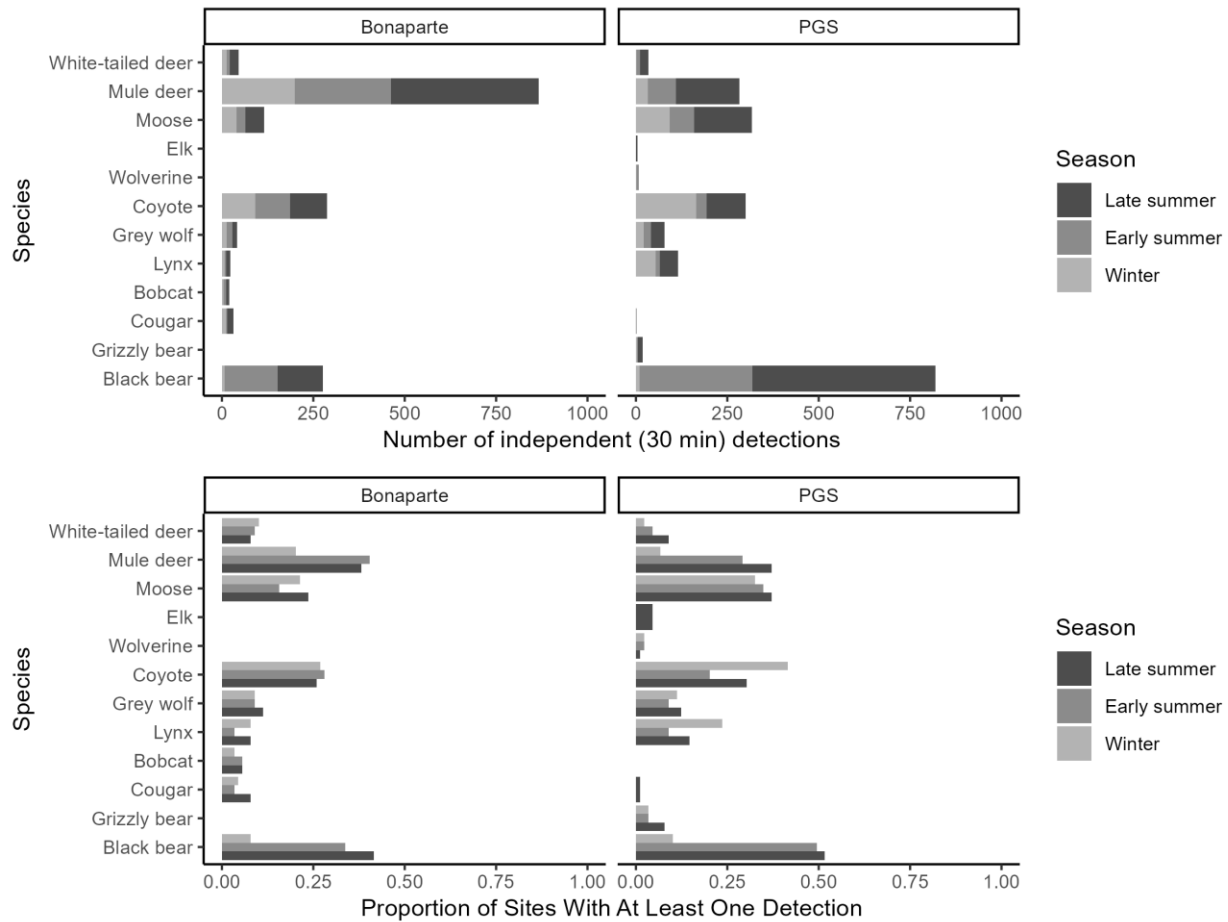


Figure A4.1 Summary of species detections from wildlife camera trap arrays across Bonaparte and PGS.

Ungulates, including white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), moose (*Alces alces*), and elk (*Cervus canadensis*), and predators, including coyote (*Canis latrans*), grey wolf (*C. lupus*), lynx (*Lynx canadensis*), bobcat (*L. rufus*), cougar (*Puma concolor*), grizzly bear (*Ursus arctos*), black bear (*U. americanus*), and wolverine (*Gulo gulo*), detected by remote wildlife camera traps in winter (November to April; light grey), early summer (May to June; medium grey) and late summer (July to October; dark grey) deployed in the Bonaparte (May 2022 – 2023) and Prince George South (PGS; May 2021 – 2022) study areas, summarized for each species as the A) number of independent detections (events separated by > 30 minutes) and B) proportion of sites with at least one detection

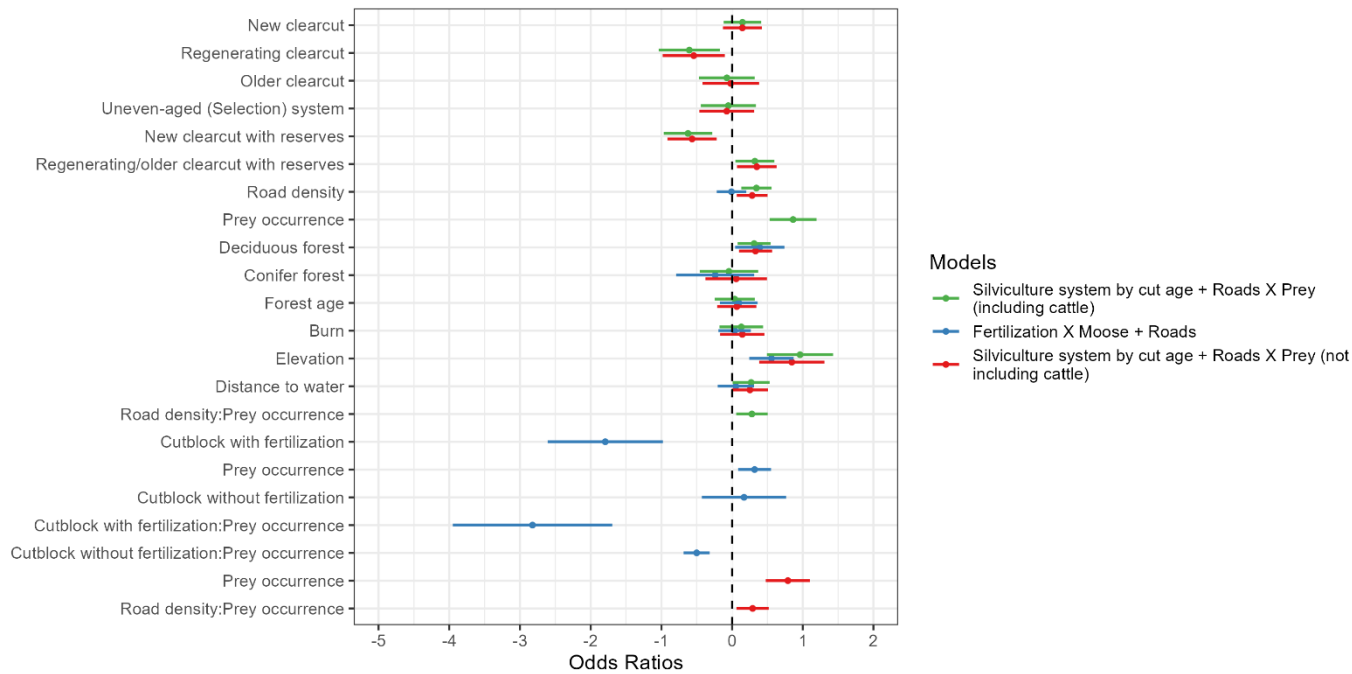


Figure A4.2 Beta coefficients for all supported models explaining grey wolf (*Canis lupus*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Prey occurrence is the relative abundance index for moose (*Alces alces*) or the summed relative abundance indices for all prey species, including moose, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), and when specified, domestic cattle (*Bos taurus*). Relative abundance indices are calculated as the total number of independent detections for each species at each site, divided by the total number of days the camera was functional

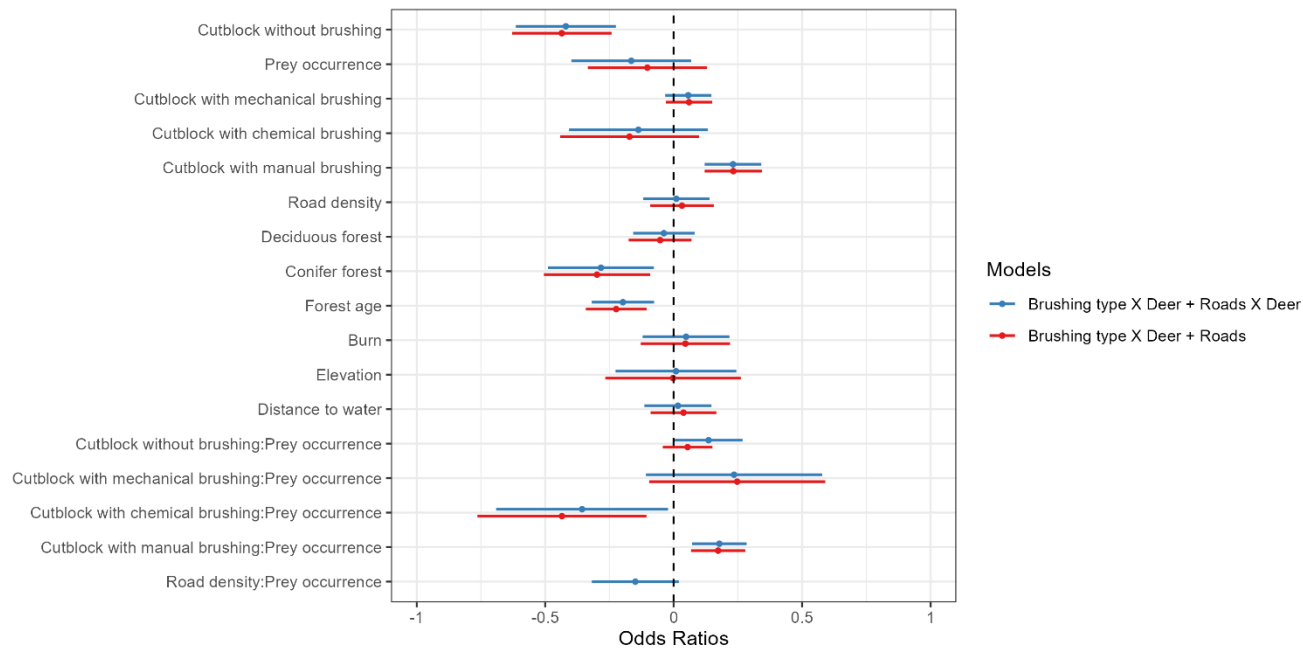


Figure A4.3 Beta coefficients for all supported models explaining coyote (*Canis latrans*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Prey occurrence (i.e., Deer) is the summed relative abundance indices for mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*), calculated as the total number of independent detections for each species at each site, divided by the total number of days the camera was functional

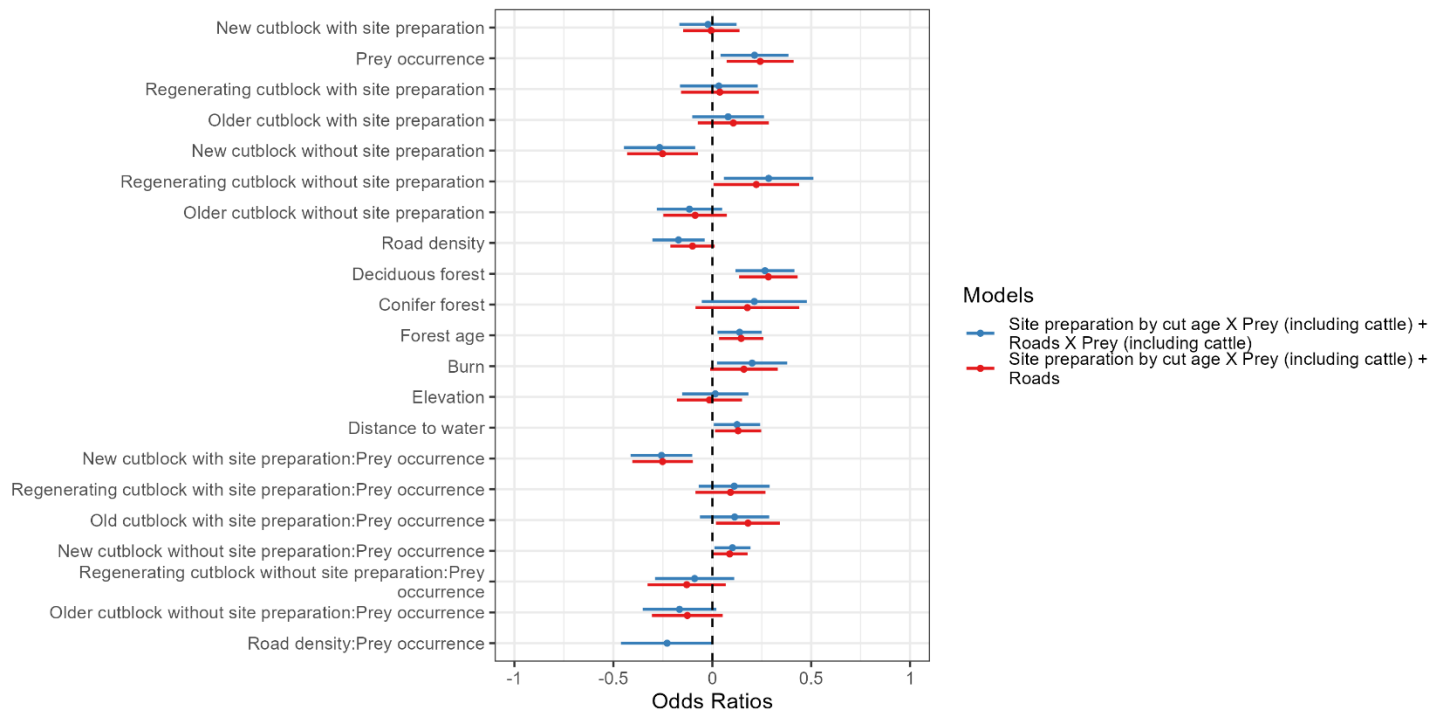
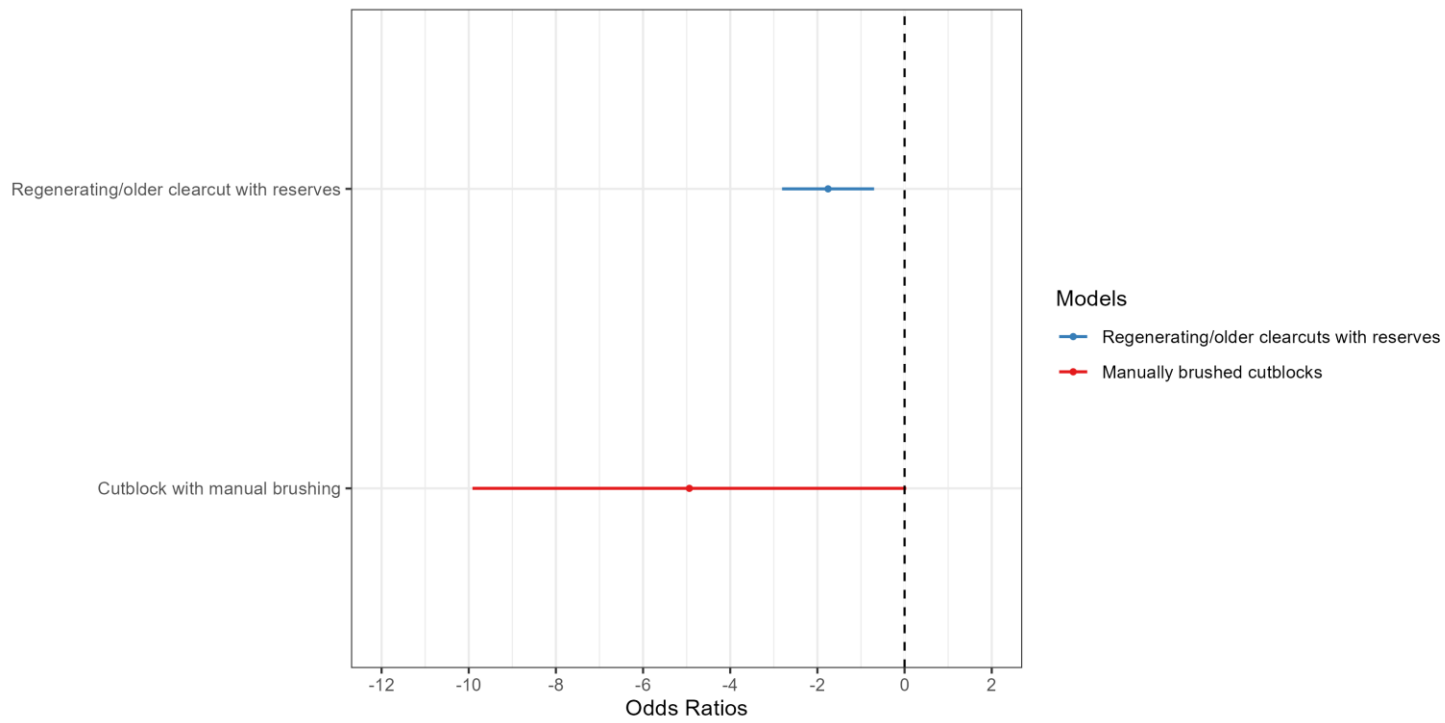


Figure A4.4 Beta coefficients for all supported models explaining black bear (*Ursus americanus*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Prey occurrence (i.e., Prey including cattle) is the summed relative abundance indices for all prey species, including moose (*Alces alces*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), and domestic cattle (*Bos taurus*). Relative abundance indices are calculated as the total number of independent detections for each species at each site, divided by the total number of days the camera was functional



*Figure A4.5 Beta coefficients for all supported models explaining grizzly bear (*Ursus arctos*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022), British Columbia, Canada. Data from the Bonaparte Plateau was not included in the grizzly bear analyses due to lack of detections*

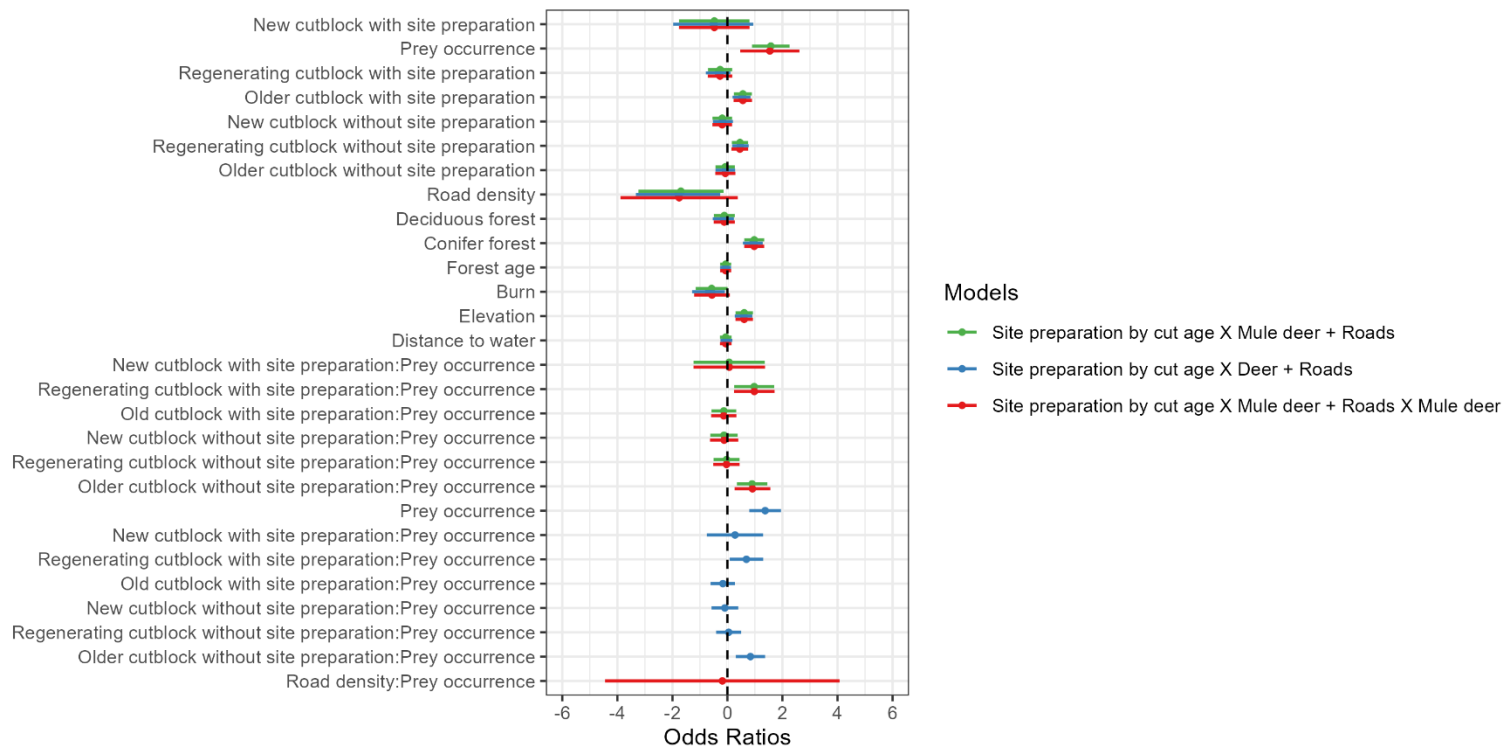
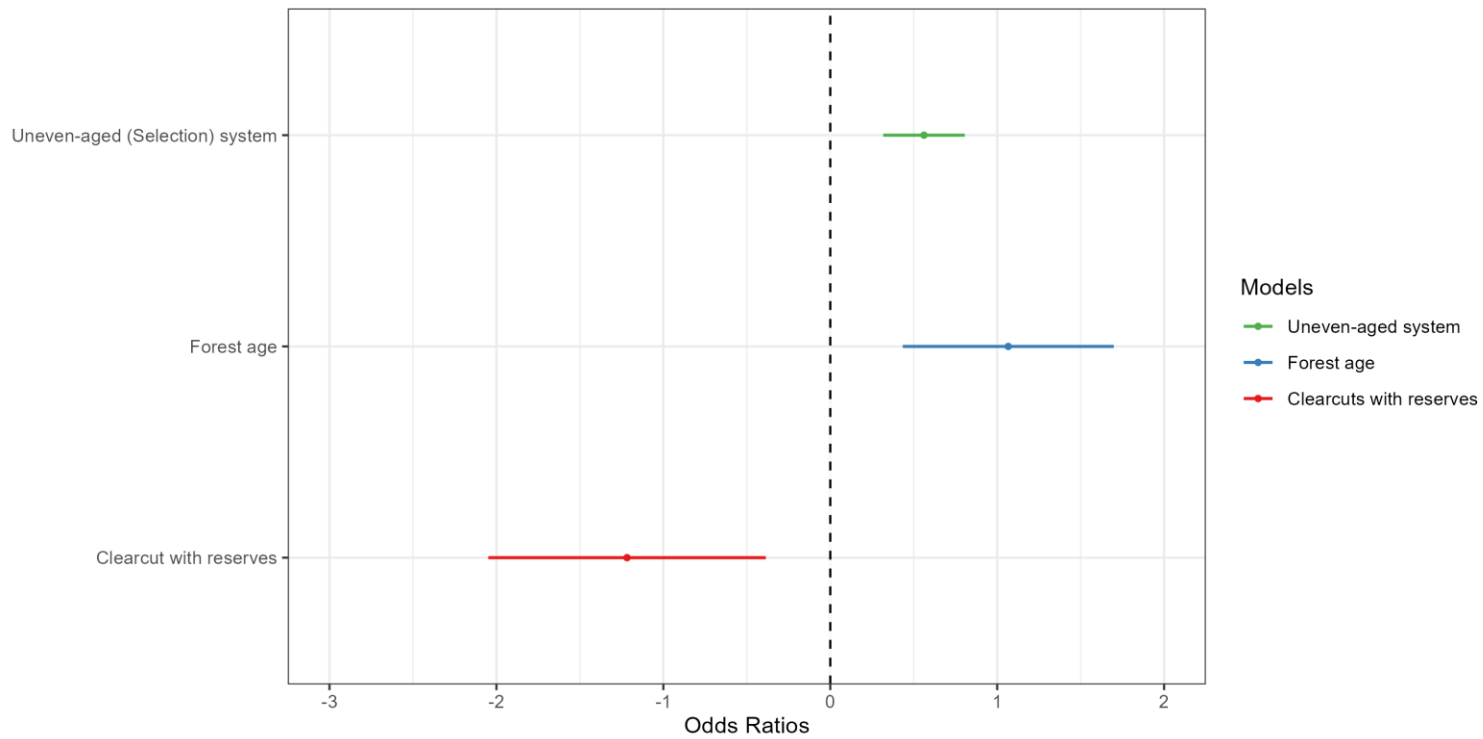


Figure A4.6 Beta coefficients for all supported models explaining lynx (*Lynx canadensis*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Prey occurrence is the relative abundance index for mule deer (*Odocoileus hemionus*) (i.e., Mule deer term), or the summed relative abundance indices for white-tailed deer (*O. virginianus*) and mule deer (i.e., Deer). Relative abundance indices are calculated as the total number of independent detections for each species at each site, divided by the total number of days the camera was functional



*Figure A4.7 Beta coefficients for all supported models explaining bobcat (*Lynx rufus*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Data from the Prince George South camera array was not included in the bobcat analyses due to lack of detections*

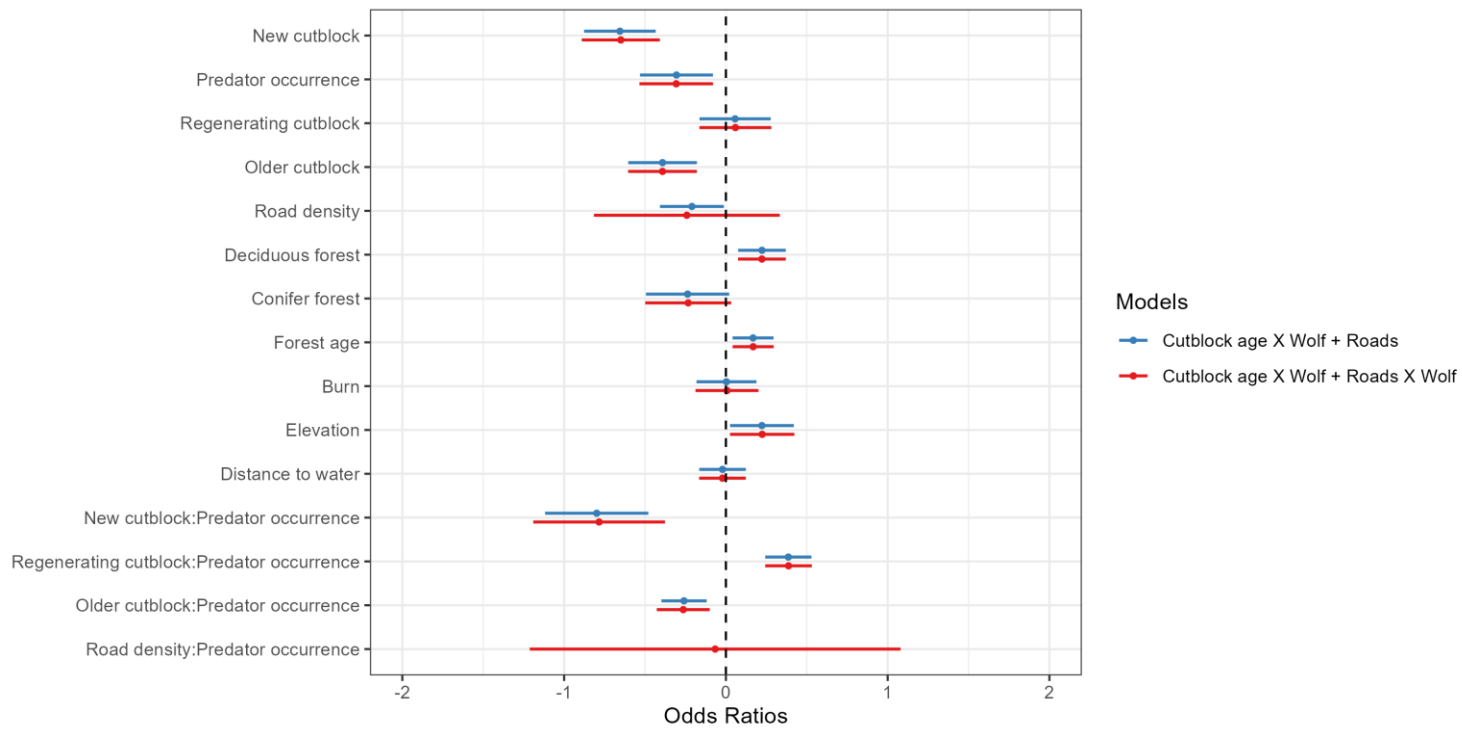


Figure A4.8 Beta coefficients for all supported models explaining moose (*Alces alces*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Predator occurrence is the relative abundance index for grey wolf (*Canis lupus*), calculated as the total number of independent wolf detections at each site, divided by the total number of days the camera was functional

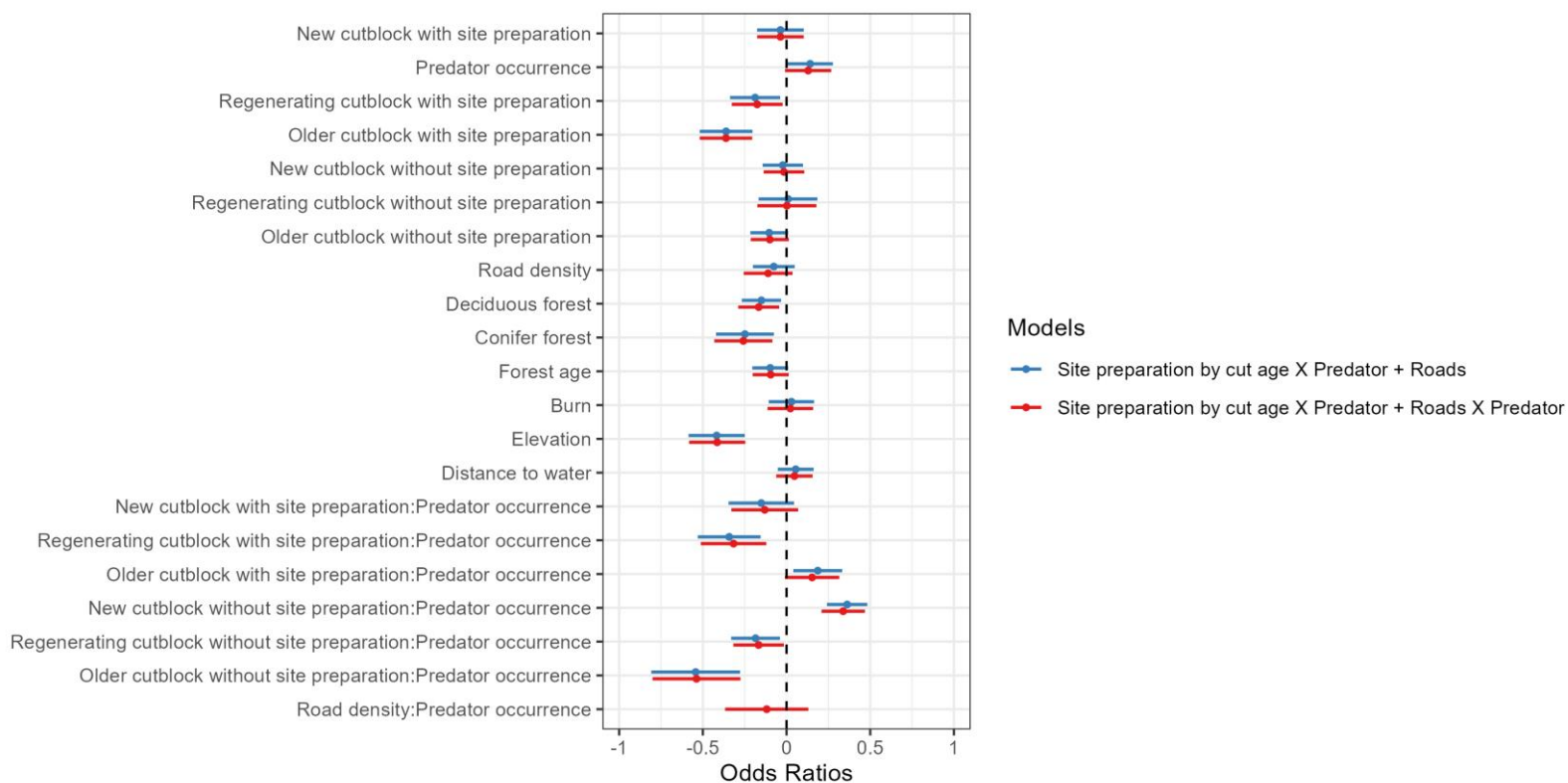


Figure A4.9 Beta coefficients for all supported models explaining mule deer (*Odocoileus hemionus*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Predator occurrence is the summed relative abundance indices for all predator species, including coyote (*Canis latrans*), grey wolf (*C. lupus*), lynx (*Lynx canadensis*), cougar (*Puma concolor*), grizzly bear (*U. arctos*), black bear (*Ursus americanus*), and wolverine (*Gulo gulo*). Relative abundance indices are calculated as the total number of independent detections for each species at each site, divided by the total number of days the camera was functional

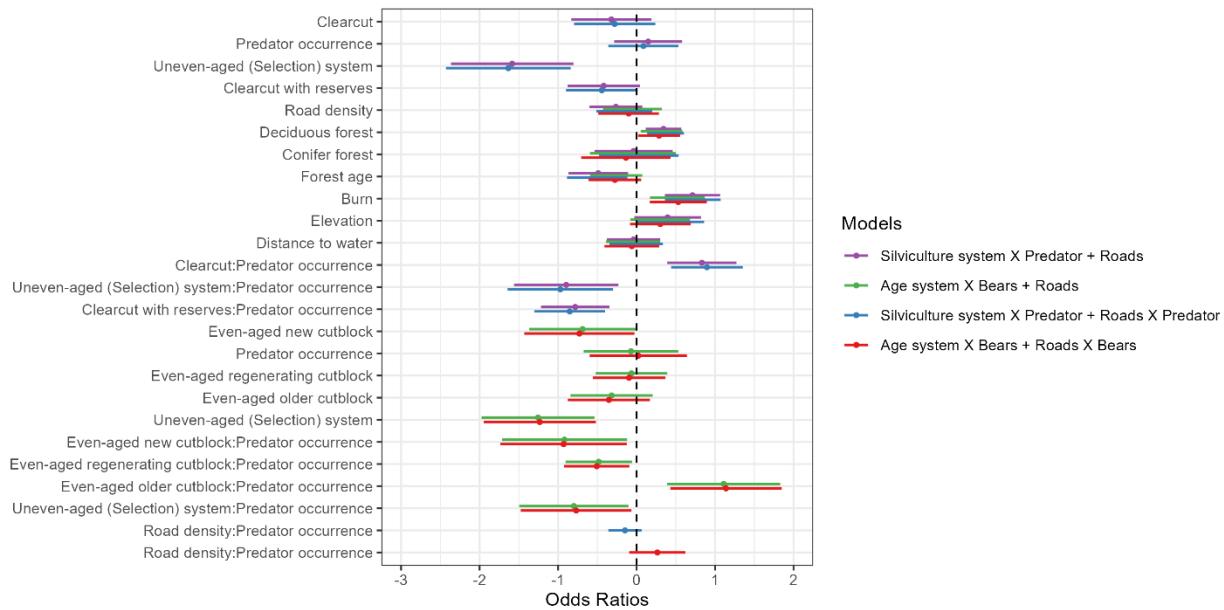


Figure A4.10 Beta coefficients for all supported models explaining white-tailed deer (*Odocoileus virginianus*) occurrence in relation to natural and anthropogenic features, based on wildlife camera trap data from Prince George South (May 2021 – 2022) and the Bonaparte Plateau (May 2022 – 2023), British Columbia, Canada. Predator occurrence is the summed relative abundance indices for all ursid species, including black bears (*Ursus americanus*) and grizzly bears (*U. arctos*) (i.e., Bears), or for all predator species, including coyote (*Canis latrans*), grey wolf (*C. lupus*), lynx (*Lynx canadensis*), cougar (*Puma concolor*), grizzly bear, black bear, and wolverine (*Gulo gulo*). Relative abundance indices are calculated as the total number of independent detections for each species at each site, divided by the total number of days the camera was functional

Appendix 5: Supplementary Information from Chapter 5

A5.1 Study area descriptions

Both Prince George South (PGS) and the Bonaparte Plateau are characterized by a mosaic of forested landscapes, including mature and regenerating stands of deciduous, conifer, or mixed species, fragmented by large cutblocks and extensive forestry roads. PGS is dominated by Sub-Boreal Spruce, with some Engelmann Spruce Sub-Alpine Fir. Bonaparte features a combination of Interior Douglas Fir, Sub-Boreal Pine and Spruce, Montane Spruce, Sub-Boreal Spruce, Engelmann Spruce Sub-Alpine Fir, Bunchgrass, and Ponderosa Pine biogeoclimatic zones. Wildfire is a common forest disturbance in both study areas. Both regions have resource extraction (primarily forest harvest), in addition to agriculture, recreational activities, and hunting. Primary predators of juvenile moose include wolves (*Canis lupis*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and cougars (*Puma concolor*). Other ungulate species in the study areas include mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), domestic cattle (*Bos taurus*), and domestic horses (*Equus caballus*).

A5.2 Juvenile moose capture

We randomly captured moose (*Alces alces*) calves of both sexes by net gunning and darting from a helicopter. We chose to capture older calves to avoid potential capture-induced abandonment and mortality of younger calves (43, 321). To capture calves from helicopter, we used aerial net gunning with a hand-held net gun. Calves were administered 2 mL BAM II (27.3 mg/mL butorphanol, 9.1 mg/mL azaperone and 10.9 mg/mL medetomidine; Chiron Compounding Pharmacy Inc, Guelph, ON). Throughout immobilization, we regularly monitored vital signs of calf moose. Following sampling and handling, calves were administered 1 mL of 25 mg/mL naltrexone hydrochloride and 4 mL of 25 mg/mL atipamezole hydrochloride for reversal. To account for calf growth, we used one or two cotton rot-off strips on male and female collars, respectively. Cotton strips allowed collars to drop off after approximately one to two years. Males only received one rot-off strip as adult males have a neck size that exceeds the expandable limit of the collar, and the thinner rot-off ensured an earlier drop date for the collar.

We measured calf weights (kg) and took morphological measurements of total length, chest girth, and shoulder height. When we could not weigh calves, we estimated weights using morphological measurements, which is commonly done for ungulates (322). To do so, we used linear regression to compare actual weights of weighed calves to their morphological measurements and used this model to provide estimates for calves that could not be weighed.

A5.3 Creation of predation risk layers

We deployed arrays of Reconyx™ HyperFire 2 Covert IR cameras (Reconyx, Holmen, WI) in Prince George South (n = 50) and Bonaparte (n = 39) during May 22, 2021 to May 14, 2022 and May 15, 2022 to May 19, 2023, respectively. Sites for camera deployment were selected using stratified random sampling based on quantiles of resource road density and cutblock age classes of new (0 to 8 years since harvest), regenerating (9 to 24 years), and older (25 – 40 years) age classes. Cameras were set-up on trees at a height of about 1.5 meters, typically facing north towards a game trail. We used commercial scent lure (O'Gorman's™ Long Distance Call) to improve detection probability (219, 221). Cameras captured daily timelapse photos at 12:00 pm every day to ensure camera functionality. Cameras were programmed to take 1 photo per trigger, using a high sensitivity and no delay for the quiet period. Images were classified using Timelapse Image Analyzer 2.0 software (222). We considered detections separated by at least 30 minutes to be independent (223). In PGS, we had the following daily occurrence sample sizes: 706 black bear, 17 grizzly bear, 71 grey wolf, and 1 cougar. In Bonaparte, we had the following daily occurrence sample sizes: 253 black bear, 0 grizzly bear, 40 grey wolf, and 29 cougar. Due to the limited occurrence of grizzly bear and cougar, we only modeled black bear and grey wolf occurrence.

At each camera site, we extracted environmental covariates from buffers of 500 to 2500-meters. We quantified variables describing: proportions of cutblock age classes (new, regenerating, and older), proportions of silvicultural treatments (site preparation, planting, brushing, spacing, fertilization, and silvicultural systems), proportion of unharvested conifer and deciduous forest, mean forest age (years), distance to the nearest water source (meters), proportion of unharvested <40 year old burns, and mean elevation (meters). We determined the most supported buffer size scale for each species based on Akaike's Information Criterion (AIC).

To create the predation risk layers, we related daily species occurrence (0 = absence, 1 = presence) to habitat features around each camera using binomial generalized linear mixed-effects models using *glmmTMB* (150). We checked for multicollinearity using Pearson's correlation coefficients and variance inflation factors. All covariates were scaled (mean = 0, standard deviation = 1) prior to modeling. We then used these results to create predicted predator occurrence rasters (30 meter resolution) for each species for both study areas.

A5.4 Quantifying forest harvest, predation risk, forage availability, and weather for juvenile moose

We created buffers around each juvenile moose location with radii of 250, 500, and 1000 meters, representing fine, medium, and broad scale habitat use, respectively. Within buffers, we extracted road density (km/km²) (145) and proportion of new (0 – 8 years since harvest) and older (9 – 40 years) cutblocks (144). We only used two cutblock age classes, unlike other moose studies (40, 41), due to the low mortality event sample size which limited model complexity. For each forest harvest metric, we calculated a daily average to represent short-term habitat use and averaged all days from capture to censoring/mortality to represent long-term use. Using predicted predator occurrence spatial layers created from wildlife camera trap data (Appendix 5), we extracted mean predation risk (i.e., predicted occurrence, 0 to 1) from wolves and bears in each buffer. Because bears hibernate from November–April (based on camera data), we set bear risk as 0 during these months. We also summed wolf and bear values together to create a single predation risk variable, because we were not differentiating mortality causes. We excluded grizzly bear and cougar from the analysis due to limited detections, which possibly affected the predictive accuracy of the spatial layers. We extracted a measure of forage availability based on mean delta-enhanced vegetation index (EVI), which represents plant productivity and is calculated by subtracting minimum EVI (leaf-off period) from maximum EVI (leaf-on period) (323). Using univariate analyses, we determined the most supported spatial scale for each variable for inclusion in models (243), based on Akaike's Information Criterion corrected for small sample sizes (AIC_c). For weather, we extracted mean winter (representing winter severity; October–March) and daily temperatures (Celsius) using Environment and Climate Change Canada weather records for Prince George (Longitude = -122.68, Latitude = 53.88) and Bonaparte Plateau (Longitude = -120.45, Latitude = 50.7). We scaled (mean = 0, standard

deviation = 1) all variables to facilitate coefficient comparisons. We checked for collinearity using Pearson's correlation coefficients ($|r| > 0.7$) and variance inflation factors ($VIF > 5$) following modeling, to ensure no problematic collinearity existed.

A5.5 Tables

Table A5.1 Sample size of 7- to 8-month-old moose captured from winter 2016/2017 to 2020/2021 in Bonaparte and Prince George South (PGS), British Columbia, Canada. Surviving juveniles remained alive from capture to approximately 18 months of age (November 1 in the year following their birth). Proximate mortality causes are listed for each study area and birth year.

Birth year	Study area	Females	Males	Alive	Wolf	Bear	Cougar	Human	Health
2016	PGS	0	0	-	-	-	-	-	-
	Bonaparte	12	8	7	4	1	0	3	5
2017	PGS	11	9	12	5	2	0	1	1
	Bonaparte	6	14	13	2	1	1	2	1
2018	PGS	7	12	11	4	4	0	1	0
	Bonaparte	9	11	13	4	1	1	1	0
2019	PGS	12	9	11	7	1	0	2	0
	Bonaparte	10	10	14	5	0	1	0	0
2020	PGS	14	6	15	5	0	0	0	0
	Bonaparte	11	7	15	2	0	1	0	0

Table A5.2 Annual survivorship (95% CI) of juvenile moose from capture at 7-8 months old to recruitment at approximately 18 months old (i.e., November 1 in the year following birth) for pooled data from the Bonaparte Plateau and Prince George South study areas in British Columbia, Canada.

Birth year	Survival (95% CI)
2016	0.35 (0.16, 0.55)
2017	0.60 (0.43, 0.73)
2018	0.58 (0.41, 0.72)
2019	0.58 (0.40, 0.72)
2020	0.79 (0.62, 0.89)

Table A5.3 Model selection results, based on Akaike's Information Criterion corrected for small sample sizes (AIC_c), to determine the best scale (buffers of 250, 500, and 1000 meters) for inclusion in survival analyses assessing juvenile moose mortality risks in the Bonaparte Plateau and Prince George South study areas, British Columbia, Canada, 2016-2021.

Variable	Buffer size (meters)		
	250	500	1000
Road density	671.349	670.7781	668.7649
New cutblocks	670.1043	669.8723	668.9643
Older cutblocks	669.7449	669.4416	669.4296
Wolf	671.3723	671.329	670.5644
Bear	671.3444	671.2257	671.4870
Predation risk	671.4807	671.484	670.9254

Long-term road density use	667.5588	668.9435	670.1193
Long-term cutblock use	667.5909	668.4317	669.7882

Table A5.4 Model selection using Akaike's Information Criterion corrected for small sample sizes (AICc) and concordance statistics (\pm standard error) for Andersen-Gill survival models assessing how forest harvest interacts with body condition, forage availability, long-term use, and weather to affect juvenile moose (*Alces alces*) survival from capture (7-8 months old) to recruitment (18 months old) in Bonaparte Plateau and Prince George South, British Columbia, Canada. All models include a factor for sex (male or female), stratified by age class (calf = prior to first birthday of May 21, or yearling = following first birthday to mortality or right censoring), and a cluster for individual ID. Models with "(RC)" have summed predation risk from wolves (*Canis lupus*) and bears (*Ursus americanus*), whereas models with "(RS)" have separate wolf and bear variables. 'LT' refers to long-term forest harvest use, whereas other variables were daily metrics. '*' denotes interactions, including all lower-order effects.

Model	Structure	Parameters	AICc	Δ AICc	AICc weight	Concordance
Forest harvest X Tick	(New cutblock + Older cutblock + Road density)*Tick + Weight + Weight:Age + Sex + Sex:Age	12	635.95	0	0.42	0.71 \pm 0.03
Forest harvest X Weight	(New cutblock + Older cutblock + Road density)*Weight + Weight:Age + Tick + Sex + Sex:Age	12	636.01	0.06	0.41	0.72 \pm 0.03
All additive (RC)	New cutblock + Older cutblock + Road density + Δ EVI + Temperature + Risk + Tick + Weight + Weight:Age + Sex + Sex:Age	13	639.9	3.63	0.07	0.72 \pm 0.03
Forest harvest X Condition	(New cutblock + Older cutblock + Road density)*(Tick + Weight) + Weight:Age Sex + Sex:Age	15	639.92	3.97	0.06	0.72 \pm 0.03
All additive (RS)	New cutblock + Older cutblock + Road density + Δ EVI + Temperature + Wolf + Bear + Tick + Weight + Weight:Age + Sex + Sex:Age	14	641.13	4.92	0.04	0.71 \pm 0.03
Forest harvest	New cutblock + Older cutblock + Sex + Sex:Age	6	652.86	16.91	0	0.64 \pm 0.03
Cutblocks X Roads	(New cutblock + Older cutblock)*Road density + Sex + Sex:Age	8	653.21	17.26	0	0.65 \pm 0.04
Forest harvest X Long-term use	(New cutblock + Older cutblock + Road density)*LT Road density + Sex + Sex:Age	11	654.58	18.63	0	0.65 \pm 0.04
Forest harvest X Forage	(New cutblock + Older cutblock + Road density)* Δ EVI + Sex + Sex:Age	10	654.87	18.92	0	0.66 \pm 0.03
Forest harvest X Temperature	(New cutblock + Older cutblock + Road density)*Temperature + Winter severity + Sex + Sex:Age	11	656.85	21.43	0	0.67 \pm 0.03

Forest harvest X Risk (RC)	(New cutblock + Older cutblock + Road density)*Risk + Sex + Sex:Age	10	657.38	21.48	0	0.66 ± 0.03
Null	Sex + Sex:Age	3	657.43	22.61	0	0.58 ± 0.03
Forest harvest X Bear	(New cutblock + Older cutblock + Road density)*Bear + Wolf + Sex + Sex:Age	11	659.16	23.21	0	0.65 ± 0.03
Forest harvest X Wolf	(New cutblock + Older cutblock + Road density)*Wolf + Bear + Sex + Sex:Age	11	659.86	23.91	0	0.65 ± 0.03
Forest harvest X Winter severity	(New cutblock + Older cutblock + Road density)*Winter severity + Temperature + Sex + Sex:Age	11	661.28	25.33	0	0.64 ± 0.03
Forest harvest X Risk (both)	(New cutblock + Older cutblock + Road density)*(Wolf + Bear) + Sex + Sex:Age	14	662.55	26.6	0	0.65 ± 0.03
