Landsc Ecol (2025) 40:93
https://doi.org/10.1007/s10980-025-02095-z

RESEARCH ARTICLE

Silviculture shapes the spatial distribution of wildlife in managed landscapes

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Received: 27 December 2024 / Accepted: 4 April 2025

Abstract

Context Silviculture—managing tree establishment for landscape objectives—influences ecological outcomes of forests. While forest harvest impacts on wildlife are well-documented, silvicultural treatment effects remain unclear.

Objectives We investigated how forest harvest and silviculture shape predator and ungulate distributions and interactions, providing ecological insights for forest management.

Methods We deployed two camera arrays in extensively harvested North American landscapes to evaluate relationships between forest harvest, silviculture, and predator and ungulate occurrences.

Results Forest harvest, silviculture, and predator/prey activity shape wildlife occurrences. Wolf (*Canis lupus*), influenced by moose (*Alces alces*), decreased with regenerating (9–24 years) clearcuts, new (0–8 years) clearcuts with reserves, and fertilized cutblocks. Wolves increased with regenerating/older (25–40 years) clearcuts with reserves. Coyote (*C. latrans*) increased in manually or chemically brushed cutblocks at high or low deer occurrence, respectively. Black bear (*U. americanus*), influenced by prey, increased with regenerating prepared cutblocks and fewer new prepared cutblocks. Prey elevated lynx (*Lynx canadensis*) occurrence with regenerating prepared or older unprepared cutblocks. Depending on predators, mule deer (*Odocoileus hemionus*) decreased with regenerating and older prepared cutblocks; white-tailed deer (*O. virginianus*) decreased with selection- and new even-aged cutblocks. Harvest

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-025-02095-z.

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age and wolves best explained moose, although silviculture mattered seasonally.

Conclusions Silviculture shapes wildlife distributions and interactions. Integrating these effects into research and forest management is essential for meeting ecological objectives.

Keywords Forest harvest · Predators · Silviculture · Ungulates · Wildlife camera traps · Wildlife occurrence

Introduction

Forestry is a prominent driver of change across landscapes globally (Hansen et al. 2013). 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 (Fisher and Wilkinson 2005; Lindenmayer and Noss 2006). Any landscape disturbance could alter ecosystem dynamics, but the unprecedented scale of forest harvest poses a critical threat to biodiversity (Paillet et al. 2010; Chaudhary et al. 2016). Understanding how forest management practices impact wildlife habitat and species relationships is important for resource managers in 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 (Palik et al. 2020). 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 (Fisher and Wilkinson 2005), the impacts of silvicultural treatments are poorly understood (Johnson and Rea 2023).

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 (Berger 2007; Fisher and Burton 2018; Johnson-Bice et al. 2023). 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 (Mumma et al. 2021; Boucher et al. 2022; Johnson-Bice et al. 2023). However, silvicultural treatments affect vegetation regrowth and thus habitat conditions, potentially impacting use of forest harvest features by predators and ungulates (McKay and Finnegan 2022, 2023). 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 (Johnson and Rea 2023; McKay and Finnegan 2023). Other treatments, such as herbicide applications, may reduce forage quality (Ulappa et al. 2020; Werner et al. 2022). Decreased forage availability and/or quality could decrease ungulate occurrence which, in turn, reduces the attractiveness of these treated cutblocks to predators (McKay and Finnegan 2022, 2023). 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 (Taylor et al. 2006; Bogdanski et al. 2011). Salvage logging in this region removed both beetle-impacted and live trees primarily through clearcutting, converting the landscape into a patchwork of massive cutblocks that often exceeded standard size and adjacency/green-up constraints (where adjacent blocks can only be harvested once cutblocks have reached a specified threshold of tree growth), and did not mimic natural disturbance given their scale and limited retention (Lewis 2009). These drastic landscape changes coincided with ungulate population declines (Kuzyk 2016; Kuzyk et al.

2018). Landscape-mediated changes to predator–prey dynamics were identified as a potential contributing factor for declines (Kuzyk and Heard 2014). 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 (Francis et al. 2021; Mumma et al. 2021; Boucher et al. 2022). 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 (Boucher et al. 2022), and that prey presence would strengthen these associations.

Methods

Study area description

Our camera arrays were set up across two study areas with high levels of forest harvest in interior BC: Prince George South (PGS; 11,052 km^2) and the Bonaparte Plateau (6776 km^2) (Fig. 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 (Fig. S1). The mountain pine beetle outbreak began in the late 1990s following favourable weather and decreased wildfire activity, and significantly impacted much of the mature lodgepole pine (*P. contorta*) forest in this region (Taylor et al. 2006). In response, the annual allowable cut was raised to salvage beetle-impacted trees. Salvage logging in the study areas was primarily completed through clearcutting with little retention, often bypassing forest management plans set to maintain sustainability (e.g., cutblock size limitations, adjacency/green-up constraints) and thus, removing much of the mature forest across both study areas (Fig. 1). Widespread forest harvest across both landscapes led to an increase in new cutblocks and associated forestry roads (Mumma et al. 2021), which, in addition to wildfire (which significantly impacted Bonaparte in recent years, Fig. S1), and has lead to further salvage logging), has created increasingly connected, early successional landscapes.

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. 1; Section S1). Fifty camera sites per array were selected using stratified random sampling, with each landscape divided into 1 × 1-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 m 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,

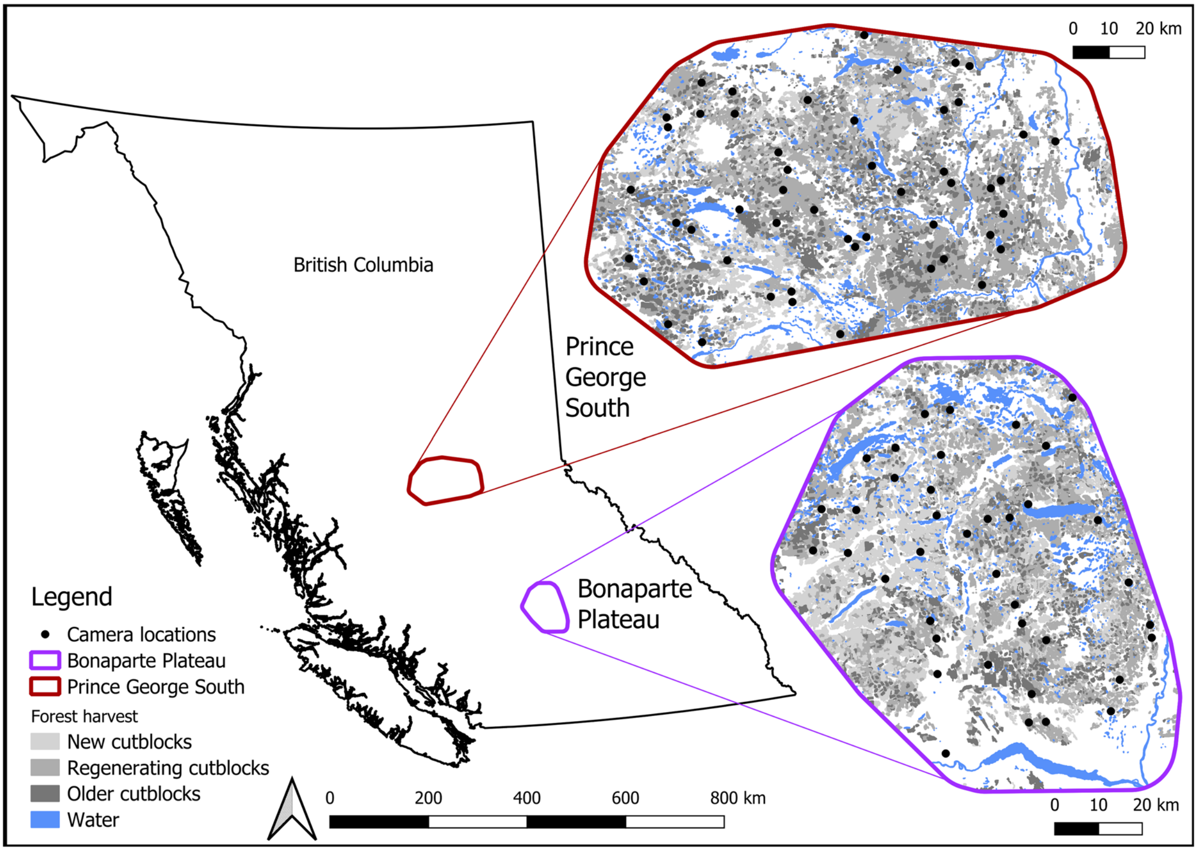

Fig. 1 Wildlife camera arrays, Prince George South (PGS; red) and Bonaparte Plateau (purple), in British Columbia, Canada. Camera sites (black points) were deployed in PGS in May 2021–2022 and the Bonaparte Plateau in May 2022–2023. New (0–8 years), regenerating (9–24 years), and older cutblocks (25–40 years) are in grey, and water in blue. Areas outside of cutblocks generally represent unharvested forests, cutblocks > 40 years, agriculture, and private land

in front of the camera as a long-lasting attractant (Franklin et al. 2019; Stewart et al. 2019; Holinda et al. 2020). Predators are elusive and lure ensures adequate detections for modelling, with limited effect on ungulates (Stewart et al. 2019; Holinda et al. 2020). Lure moves animals in front of the camera over short distances, but landscape features explain most variation in animal movement (Stewart et al. 2019). 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 (Greenberg et al. 2019). We treated any detections exceeding a 30-min threshold as independent events (Burton et al. 2015).

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 (Holland et al. 2004). Around each camera site, we created circular buffers every 500 m (radii: 500 to 2500 m) 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 (Government of BC 2024b). Wildlife occurrence often depends on cutblock age class due successional vegetation regeneration (Fisher and Wilkinson 2005) 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 et al. (2021), which correspond with delineations in Fisher and Wilkinson (2005). 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 (Bergman et al. 2006; Boucher et al. 2022). 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 heterogenous 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 (Werner et al. 2022). Prepared sites have lower tree seedling mortality and faster growth, but potentially less ungulate forage (Hawkins et al. 2006). 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 (Boan et al. 2011; McKay and Finnegan 2023).

Fertilization, brushing, and spacing impact vegetation present in a cutblock. Fertilizers are typically slow-release inorganic fertilizers that improve stand growth and development (Reid et al. 2017), but also enhance shrub and herb abundance (Lindgren and Sullivan 2013). 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 (Lindgren et al. 2006), 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 (Boucher et al. 2022). We quantified road density (km/km^2) using Digital Road Atlas data (GeoBC 2024). 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) (Government of BC 2024c), unharvested burn (proportion of burns < 40 years) (Guindon et al. 2020; BC Wildfire Service 2024; Government of BC 2024a), distance to water (GeoBC 2021) and mean elevation (Government of Canada 2024). We defined unharvested conifer as forest stands dominated by ≥ 65% coniferous species, and deciduous forest as a combination of deciduous-leading forests (≥ 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, and coyote; deer terms for lynx; 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 (Zager and Beecham 2006). Lynx prey upon small mammals and birds but will eat deer (Fuller 2004; Poszig et al. 2004). Coyotes select small prey but will hunt deer and moose, primarily juveniles but also adults (Benson and Patterson 2013; Shi et al. 2021; Jensen et al. 2022; Hayward et al. 2023). 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 (Burnham and Anderson 2002), we constructed candidate models describing our hypotheses on how forest harvest, silviculture, roads, predator/prey occurrence, and their combinations, influence species occurrence (Table S1). 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 or if detected in one array only, a random effect for site. We only assessed species exceeding 30 weekly detections, as below this threshold, estimates may become unstable (Wisz et al. 2008).

We fit binomial generalized linear mixed-effects models for each species using *glmmTMB* (Brooks et al. 2017). Our response variable was weekly species occurrence at each site (0 = absence, 1 = presence). Given the high mobility of our focal species and our goal to measure this habitat use through the occurrence metric, we treated zeros (non-detections) as ecological signals (i.e., true zeroes) rather than errors (Fisher and Burton 2018). We chose not to use occupancy models, which estimate the contribution of imperfect detection to non-detections and thus can misinterpret these non-detections from temporary emigration instead as detection error (MacKenzie et al. 2003; Fisher and Burton 2018). 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 (McGarigal et al. 2016), 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 assessed model residuals and checked for zero-inflation using the R package DHARMa (Martin et al. 2005; Hartig and Hartig 2017) no zero-inflation was detected for all species of interest. We used AICc to assess model support, with $\Delta\text{AICc}<2$ indicating substantial support (Burnham and Anderson 2002). Using the most supported model(s) for each species, we completed model validation using tenfold cross validation, repeated 5 times (Roberts et al. 2017), and used the R package *ggeffects* (Lüdecke 2018) to produce model predictions. All statistical analyses were completed using R version 4.3.3. (R Core Team 2024).

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 (sample size of weekly detections PGS = 250, Bonaparte = 96), mule deer (PGS = 177, Bonaparte = 428), white-tailed deer (PGS = 30, Bonaparte = 40), coyote (PGS = 220, Bonaparte = 241), grey wolf (PGS = 37, Bonaparte = 60), lynx (PGS = 21, Bonaparte = 107), and black bear (PGS = 196, Bonaparte = 433) in both arrays (Fig. S2). While we detected elk, wolverine, grizzly bear, bobcat, and cougar, we considered the detections insufficient for modeling (Fig. S2).

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 1; Fig. S3). Wolf occurrence increased with denser roads (Fig. S3), more regenerating/older clearcuts with reserves, and less regenerating clearcuts, new clearcuts with reserves, and/or fertilized cutblocks (Table 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. 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. 2B) but exhibiting gradual increases with unfertilized cutblocks (Fig. 2C). Higher elevations and deciduous forest were positively associated with wolf occurrence (Table 2), but no pattern was observed for new clearcuts, older clearcuts, and selection cuts.

Coyote occurrence was linked to cutblock brushing and deer (Table 1; Fig. S4). Coyote occurrence decreased with more unbrushed cutblocks, and less manually brushed cutblocks (Table 2). As deer occurrence frequency increased, coyote occurrence decreased with higher proportions of chemically brushed cutblocks (Fig. 2D) but increased more rapidly with higher proportions of manually brushed cutblocks (Fig. 2E) or lower proportions of unbrushed cutblocks (Fig. 2D). Additionally, coyotes were associated with younger trees and less conifer forest (Table 2; Fig. S4).

Ursids

Black bear occurrence was linked to site preparation based on harvest age, road density, and prey (including cattle) (Table 1; Fig. S5). Black bear occurrence was linked to more frequent prey occurrence, less new prepared cutblocks, lower road densities (Fig. S5), and more regenerating prepared cutblocks (Table 2). Black bear occurrence increased with more new prepared cutblocks when prey occurred infrequently but decreased when prey occurrence frequency increased (Fig. 3A). Black bears decreased more rapidly in areas with more new unprepared cuts when prey occurred frequently (Fig. 3B). Additionally, black bear occurrence increased with older forests, deciduous forest, burnt habitat, and distance to water (Table 2; Fig. S5).

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 1 and 2; Fig. S6). Lynx occurrence was highest with frequent mule deer or deer occurrences (Fig. S6). Frequent prey occurrences were linked to rapid increases in lynx occurrence in areas with more regenerating prepared (Fig. 4A) or older unprepared cutblocks (Fig. 4B). No pattern was evident for prey modifying the relationship between lynx occurrence and other cutblock age classes, with or without site preparation (Table 2). However, lynx occurrence increased with higher proportions of older prepared and regenerating unprepared cutblocks (Table 2). Lynx occurrence decreased with lower road densities (Fig. S6). While a model including the interaction between road density and mule deer was supported, there was no trend in covariate (Table 1; Fig. S6). Additionally, lynx occurrence was positively associated higher elevations and conifer forest.

Ungulate occurrence in response to silviculture and predator occurrence

Moose occurrence was best explained by cutblock age class interacting with wolf occurrence frequency (Table 1). Moose decreased with more new and older cutblocks, and less regenerating cutblocks (Table 2). When wolves occurred frequently, moose occurrence

Table 1 Akaike's Information Criterion corrected for small sample sizes (AICc) results for the top five models (ranked by ΔAICc) explaining wolf (*Canis lupus*), black bear (*Ursus americanus*), coyote (*C. latrans*), lynx (*Lynx canadensis*), 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
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
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 2 Odds ratios (with lower and upper confidence levels) for all coefficients explaining wolf (*Canis lupus*), black bear (*Ursus americanus*), coyote (*C. latrans*), lynx (*Lynx canadensis*), 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	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
Intercept	0.258 (0.143, 0.465)	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	1.238 (1.043, 1.470)	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		0.949 (0.643, 1.401)					0.205 (0.094, 0.447)
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		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)	
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)	

Table 2 (continued)

	Black bear	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
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)	
Older prepared cutblock:Predator/Prey						1.205 (1.041, 1.395)	
Cutblock without brushing			0.657 (0.541, 0.798)				
Older cutblock with brushing							
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)				
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)				

Table 2 (continued)

	Black bear	Grey wolf	Coyote	Lynx	Moose	Mule deer	White-tailed deer
Cutblock with manual brushing:Predator/Prey			1.195 (1.074, 1.328)				
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)

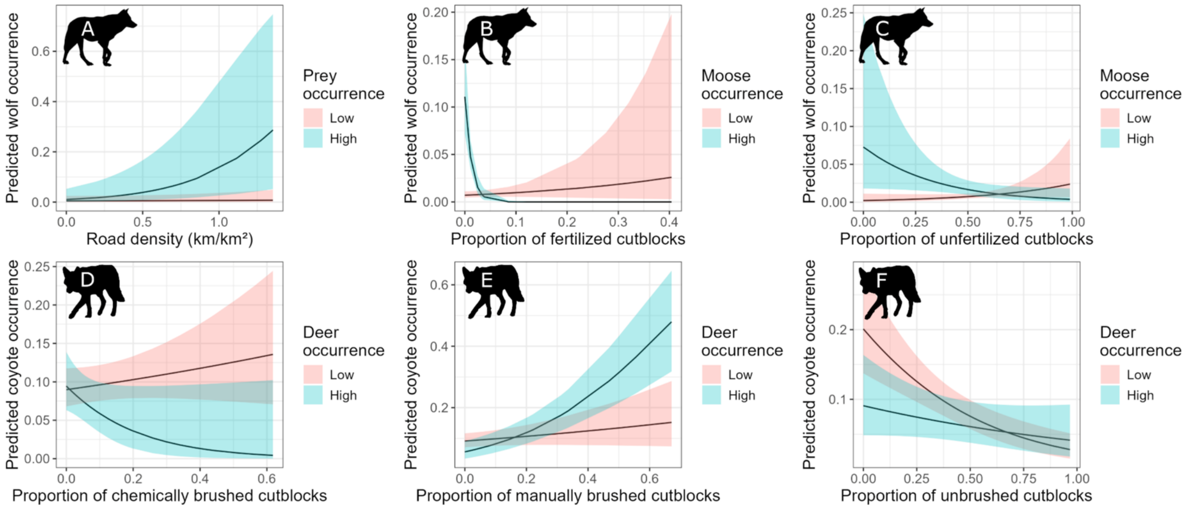

Fig. 2 Predicted occurrence of grey wolves (*Canis lupus*; **A**–**C**) and coyotes (*C. latrans*; **D**–**F**) in relation to road density (km/km^2; **A**) and silviculture metrics (**B**–**F**) as an interaction with prey (including cattle; **A**), moose (*Alces alces*; **B** and **C**), or deer (*Odocoileus 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)

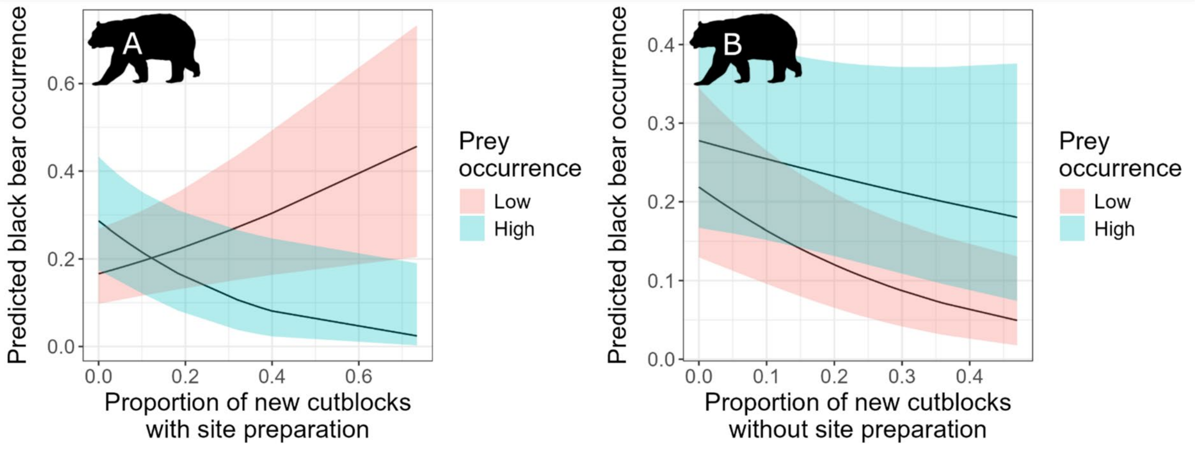

Fig. 3 Predicted occurrence of black bears (*Ursus americanus*) in relation to prey occurrence frequency (including cattle) and proportion of new cutblocks **A** with site preparation and **B** without site preparation, based on wildlife camera data from Prince George South (May 2021–2022) and the Bonaparte 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)

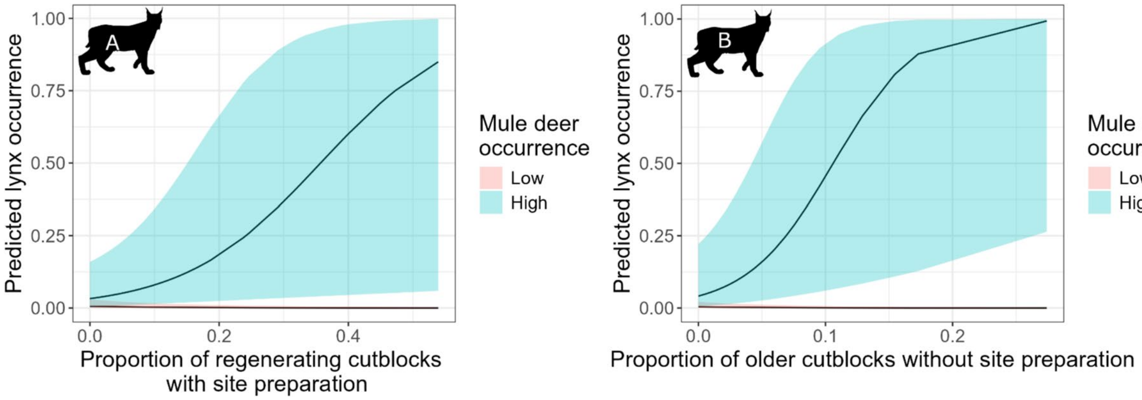

Fig. 4 Predicted occurrence of lynx (*Lynx canadensis*) in relation to mule deer (*Odocoileus hemionus*) occurrence and **A** proportion of regenerating cutblocks with site preparation or **B** proportion of older cutblocks without site preparation, based on wildlife camera data from Prince George South (May 2021–2022) and the Bonaparte Plateau (May 2022–2023). 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)

decreased (Table 2). Wolves modified moose relationships with cutblock age classes (Fig. 5A–C). Moose occurrence declined more rapidly in relation to higher proportions of new and older cutblocks when wolves frequently occurred (Fig. 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. 5B). Lower road density was linked to moose occurrence in one model, but not the other (Table 2). Although the interaction between road density and wolf occurrence frequency was included in one supported model, the coefficient showed no trend (Table 1; Fig. S7). Moose occurred at higher elevations, older forests, and deciduous forests (Table 2).

Mule deer occurrence was linked to site preparation based on cutblock age, roads, and their

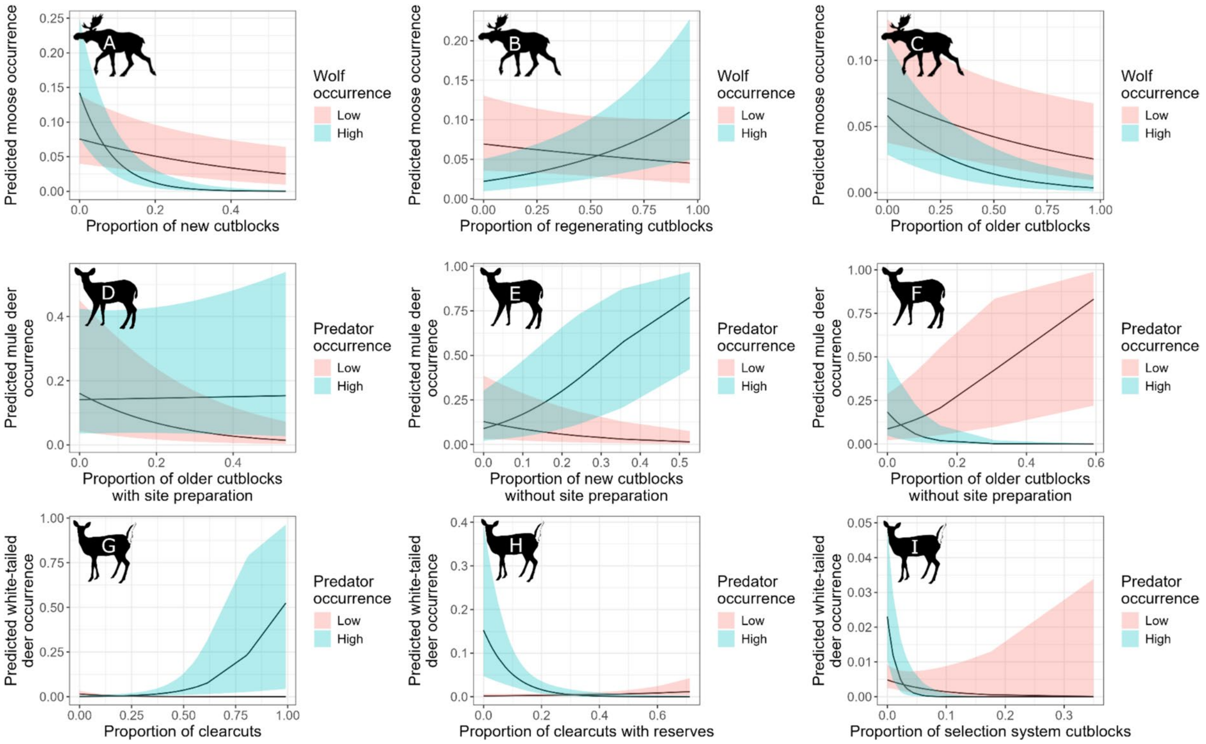

Fig. 5 Predicted occurrence of moose (*Alces alces*; **A**–**C**), mule deer (*Odocoileus hemionus*; **D**–**F**), and white-tailed deer (*O. virginianus*; **G**–**I**) in relation to silviculture, interacting with wolf (*Canis lupus*; **A**–**C**) or predator (**D**–**I**) occurrence frequency, based 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 95.th percentiles of relative abundance indices, respectively (wolf occurrence: low = 0, high = 0.013; predator occurrence: low = 0.011, high = 0.169)

interaction with predator occurrence (Table 1). Mule deer decreased with regenerating and older prepared cutblocks but showed no trend for other site preparation age classes (Table 2). A slight positive relationship between mule deer and predator occurrence existed in one supported model, but not the other (Fig. S8). Higher predator occurrence modified mule deer occurrence in relation to proportions of site preparation by cutblock age classes but not road densities (Table 2; Fig. 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. 5D and E). Conversely, mule deer occurrence was higher with more new unprepared cutblocks at higher predator occurrence levels (Fig. 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. 5F). Mule deer decreased with higher elevations, older forests, and conifer or deciduous forest (Table 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 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 2). Predator and bear occurrence frequency modified the relationship of white-tailed deer with silviculture systems and age systems, respectively (Table 1; Fig. S9). 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. 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. S9). White-tailed deer occurrence increased with more deciduous forest or burnt habitat, and in some cases, younger forests (Table 2).

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 species. 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). We only assessed species with sufficient detections for subsetting the data by season, including black bear (PGS: early summer = 146, late summer = 280; Bonaparte: early summer = 91, late summer = 99), coyote (PGS: winter = 137, early summer = 26, late summer = 78; Bonaparte: winter = 74, early summer = 65, late summer = 81), mule deer (PGS: winter = 21, early summer = 50, late summer = 106; Bonaparte: winter = 80, early summer = 136, late summer = 212), and moose (PGS: winter = 79, early summer = 54, late summer = 117; Bonaparte: winter = 31, early summer = 23, late summer = 42) (Fig. S2).

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 S2). 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 S3). 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 S2). 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 S3). In late summer, coyote occurrence increased with older clearcuts, selection cutblocks, and regenerating/older clearcuts with reserves (Tables S2 and S3). 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 S3).

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 S2). In early summer, moose were linked to lower proportions of uneven-aged systems and burns, and increased predator occurrence frequencies (Table S3). 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 S3). 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 S2). In early summer, mule deer occurred more with higher edge densities of older cutblocks when canids occurred frequently (Table S3). 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.

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 (Fisher and Wilkinson 2005), 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 (Mumma et al. 2021), likely explaining the close relationship between moose occurrence and harvest age. Our results reflected those in Mumma et al. (2021), 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 (Francis et al. 2021; Mumma et al. 2021; Boucher et al. 2022). Wolves in PGS select new cutblocks and moose kill-sites were linked to both new and regenerating cutblocks (Mumma et al. 2021; Boucher et al. 2022). 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 (Fisher and Wilkinson 2005). 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 (Francis et al. 2021; Mumma et al. 2021), 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 grey wolf and white-tailed deer occurrences; site preparation impacted black bear, lynx, and mule deer; brushing impacted 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 (Haeussler et al. 2002; Boan et al. 2011). 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 (Reese and Robbins 1994; Latham et al. 2011; Francis et al. 2021). 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 (Beese et al. 2019), 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 (Beese et al. 2019), 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 (Lautenschlager and Sullivan 2002; Boan et al. 2011; Haeussler et al. 2017). 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 (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 (Haeussler et al. 2002, 2017). 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 (Haeussler et al. 2017). However, when prey occur infrequently, new prepared cutblocks may provide alternative foods, like graminoids, that are part of black bear diets (Mosnier et al. 2008; Haeussler et al. 2017). 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 predating on mule deer (Poszig et al. 2004), 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 (Ulappa et al. 2020), 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 (Lautenschlager and Sullivan 2002). Unexpectedly, coyotes were negatively associated with unbrushed cutblocks, indicating that vegetation disturbances are beneficial for this species (Kays et al. 2008). 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 (Beese et al. 2022).

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 (Dempster 2022). Spacing would influence habitat structure and tree growth, due to impacts on competition, canopy closure, light availability, and understory vegetation growth (Dempster 2022; Baah-Acheamfour et al. 2023). 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 (Berger 2007; Dickie et al. 2019; Boucher et al. 2022). 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 (Dickie et al. 2017; Boucher et al. 2022), 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 (Mosnier et al. 2008; Dickie et al. 2019), which may result in the unclear trend. Lynx occurrence decreased at higher road densities, supporting studies showing human avoidance by lynx (Squires et al. 2019).

Ungulates either were negatively associated with roads (moose) or exhibited no patterns (mule and white-tailed deer). Moose likely avoid roads due to wolves (Boucher et al. 2022). 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 (McKay and Finnegan 2022, 2023), 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 (Kuzyk et al. 2018), 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 forest management practices that support both timber production and biodiversity goals.

Acknowledgements We thank all staff from the Applied Conservation Macro Ecology lab at the University of Victoria for field work support, and the editor and anonymous reviewers who helped to improve the manuscript. We are grateful for funding support from the University of Victoria's Applied Conservation Macro Ecology lab, Government of BC, Habitat Conservation Trust Foundation, Ian McTaggart Cowan Professorship for author B.M.S., and a Natural Sciences and Engineering Research Council of Canada graduate scholarship for author N.B.

Author contributions All authors contributed to the study design, project administration, and funding acquisition. Nicole Boucher completed data collection, preparation, analysis, visualization, and wrote and edited the manuscript. All authors reviewed and provided meaningful contributions to the manuscript drafts. Dr. Jason Fisher and Dr. Brian Starzomski provided resources and supervision.

Funding Our research was supported with funding from the University of Victoria's Applied Conservation Macro Ecology lab, Government of BC, Habitat Conservation Trust Foundation, Ian McTaggart Cowan Professorship for author B.M.S., and a graduate scholarship from the Natural Sciences and Engineering Research Council of Canada for N.B.

Data availability Data and scripts are available on Borealis (https://doi.org/10.5683/SP3/068G7P).

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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