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Predator–prey co-occurrence in harvest blocks: Implications for caribou and forestry

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Abstract

Forest harvesting alters habitat, impacts wildlife, and disrupts ecosystem function. Across the boreal forest of Canada, forest harvesting affects ungulate prey species and their predators, with cascading impacts on other species, including threatened woodland caribou. We used camera and vegetation data and occupancy modeling to investigate what characteristics in and around forestry harvest blocks influenced the occupancy and co-occurrence of primary prey (elk, moose, mule deer, white-tailed deer) and predators (black bear, cougar, grizzly bear, wolf) in harvest blocks. Occupancy was linked to forage, the surrounding habitat and anthropogenic disturbance, and silviculture practices. Black and grizzly bear occupancy was influenced by the presence of deer, and bear–deer co-occurrence was influenced by site-specific silviculture practices and surrounding anthropogenic disturbance. In the context of caribou recovery, our results indicate that forestry within caribou ranges could consider site-specific silviculture practices and landscape-level planning to reduce use of harvest blocks by primary prey. Future caribou recovery efforts may also consider the roles of deer and bears in caribou predation risk. Our study provides the first insights into the impacts of forestry and silviculture on boreal forest predator–prey co-occurrence and provides practical management applications to mitigate the impacts of anthropogenic activities on the boreal forest ecosystem into the future.

KEYWORDS

caribou, co-occurrence, forestry, predator–prey

1 | INTRODUCTION

Large-scale landscape change is increasing across the globe, and habitat loss and alteration are among the largest threats to biodiversity (Maxwell et al., 2016; Theobald et al., 2020). Forest harvesting is a major contributor to landscape change worldwide, drastically altering habitat through the loss of forest cover and changes in forest species composition, with direct impacts on biodiversity (Curtis et al., 2018; Lindenmayer, 2009; Rocha-Santos et al., 2016). Within Canada, the boreal forest is changing rapidly, with approximately 650,000 hectares disturbed by forest harvesting each year, resulting in local biodiversity losses, changes in community composition, and population declines (Venier et al., 2014; White et al., 2017). While Canada currently contains the largest area of third-party-certified sustainable forests in the world (Mansuy et al., 2020), continued improvements in forest management present the opportunity to restore and maintain biodiversity within managed forests (Kremen & Merenlender, 2018; Spathelf et al., 2018).

In addition to the direct impacts of habitat loss, forest harvesting can have indirect impacts on wildlife, including changing forage availability and altering predator–prey dynamics (Finnegan et al., 2021; Fisher & Wilkinson, 2005; Serrouya et al., 2021). Removal of the forest canopy during harvesting increases light transmission to the forest floor, resulting in more abundant herbaceous vegetation and shrub species in the understory (Hart & Chen, 2006; Serrouya et al., 2021). This increase in forage availability can change the abundance and distribution of ungulates like deer (*Odocoileus virginianus* and *Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) (Laurent et al., 2021; Serrouya et al., 2021; Visscher & Merrill, 2009). In turn, changes in prey populations can lead to changes in the abundance and distribution of their predators like black bears (*Ursus americanus*), cougars (*Puma concolor*), grizzly bears (*Ursus arctos*), and wolves (*Canis lupus*) (Knopff et al., 2014; Latham et al., 2011; Nielsen et al., 2017). Across Canada, these altered predator–prey dynamics associated with anthropogenic disturbances like forest harvesting have resulted in widespread declines in caribou (*Rangifer tarandus*) populations due to apparent competition (DeCesare et al., 2010). Specifically, because of changes in populations of deer, elk, and moose, caribou are experiencing unsustainable mortality rates from the shared predators of primary prey and caribou (DeCesare et al., 2010; Hervieux et al., 2013; Latham et al., 2011). Boreal and central mountain caribou are currently designated as threatened under the Species at Risk Act in Canada (Environment Canada, 2012, 2014). Because apparent competition is recognized as the primary threat to caribou populations, federal recovery efforts in Canada are focused on habitat restoration and management of known caribou predators (bears, cougars, and wolves) and the main apparent competitors of caribou (deer, elk, and moose; hereafter primary prey) (Apps et al., 2013; Environment Canada, 2014; McKay et al., 2021). Where caribou ranges contain managed forests, identifying the attributes of forestry harvest blocks associated with the most overlap between predators and primary prey species could help to inform habitat restoration priorities and forest management practices to decrease the spatial overlap between caribou, primary prey, and their shared predators.

In the province of Alberta in western Canada, clearcutting is the most common method of forest harvesting, and the complete removal of the forest canopy has immediate and long-term impacts on understory forage and wildlife use of harvest blocks (Hart & Chen, 2006; Laurent et al., 2021; Serrouya et al., 2021). In addition, to facilitate the re-establishment of commercial tree species in regenerating harvest blocks, a range of silviculture practices are applied after forest harvesting, including site preparation, tree planting, and stand tending (Lieffers et al., 2003; Wagner et al., 2006). Various silviculture practices result in different amounts of site disturbance and removal of understory vegetation, and by modifying the amount of forage available, silviculture practices can influence the use of harvest blocks by wildlife (Cardoso et al., 2020; Stelfox et al., 1976; Tomm et al., 1981). Wildlife use of harvest blocks may also be influenced by landscape-level characteristics including the surrounding habitat and density of anthropogenic disturbance (Kearney et al., 2019; Muhly et al., 2019) and the presence or absence of other wildlife species (Fisher & Ladle, 2022; Ladle et al., 2018; Rota et al., 2016). In the context of the natural and anthropogenic processes occurring within and around harvested areas, wildlife response to harvest blocks is likely influenced by both natural and anthropogenic factors at the site- and landscape scales (Kearney et al., 2019; Tomm et al., 1981), which may also influence the co-occurrence of predator and prey species (Fisher & Ladle, 2022; Muhly et al., 2011; Murphy et al., 2021).

Despite the recognized links between forestry, primary prey, predators, and caribou declines (Hervieux et al., 2013; Serrouya et al., 2021), current research directly investigating co-occurrence of predators and primary prey is limited, with most research in North America focused on co-occurrence of predators (Ladle et al., 2018; Lombardi et al., 2020). In addition, there is a lack of published information on how forest harvesting influences the occupancy and co-occurrence of primary prey and predators within caribou ranges (but see Fisher & Ladle, 2022). Focused on providing information that could be used for landscape management for caribou conservation, we used camera trap data from four caribou population ranges in west-central Alberta and single-species and multi-species occupancy modeling (Fiske & Chandler, 2011; Mackenzie et al., 2006; Rota et al., 2016) to (i) assess occupancy of primary prey (elk, moose, mule deer, and white-tailed deer) and shared predators of caribou and primary prey (black bear, cougar, grizzly bear, and wolf) in clearcut harvest blocks (hereafter “harvest blocks”), and (ii) to understand what site-specific and landscape-scale characteristics in and around harvest blocks influence the occupancy and co-occurrence of primary prey and predators. Camera traps are increasingly applied in wildlife research as a relatively inexpensive and noninvasive approach to monitor species occurrence and habitat use, with the advantage of detecting multiple species (Burton et al., 2015; Caravaggi et al., 2017). Occupancy models are well suited to camera data, as they account for imperfect detection of species by estimating detection probabilities based on repeat sampling, and when geographic closure assumptions are not met (e.g., highly mobile species), occupancy models can estimate the probability that a species uses a site in relation to explanatory variables (Mackenzie, 2006, Gould et al., 2019). Multispecies occupancy models provide further information about underlying predator–prey dynamics by estimating species co-occurrence, testing for dependence between two or more species, and investigating the influence of explanatory variables on the probability of co-occurrence of prey and predators (Murphy et al., 2021; Rota et al., 2016).

Although immediate recovery efforts for caribou in Alberta are focused on reducing wolf predation (Hervieux et al., 2014), long-term solutions will require habitat restoration and adaptive management to reduce the abundance and distribution of primary prey species within caribou ranges (Environment Canada, 2012, 2014). Identifying the attributes of harvest blocks associated with the highest occupancy and/or co-occurrence of primary prey and predators will provide practical information for best forest management practices to limit the distribution and overlap of primary prey and shared predators in managed forests within caribou ranges. This information may also be used to mitigate the impacts of forestry on predator–prey dynamics across the boreal forest of Canada.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was in west-central Alberta in Treaty 8 territory, traditional and current lands of the Aseniwuche Winewak, Dene-zaa, Métis, Nêhiyawak, Simpcw, Stoney, and Tsuut'ina Peoples, and incorporated the occupied ranges of three central mountain caribou populations (A La Pêche, Narraway, Redrock Prairie Creek), and one boreal caribou population (Little Smoky), along with a 25 km buffer surrounding the annual ranges (Figure 1). Alberta caribou population estimates and 95% confidence intervals (CIs) based on the most recently available information include: A La Peche: 152 caribou (142–162), Narraway: 94 (38–75), Redrock Prairie Creek: 153 (CIs unavailable), and Little Smoky: 94 (69–129) (pers. comm. Barry Nobert, Government of Alberta). The region includes areas of intact caribou habitat interspersed with anthropogenic disturbances (harvest blocks, belowground pipelines, roads, seismic lines, and wellsites) and large-scale natural disturbances (wildfires). Forest management agreements are allocated to a number of companies in the area, including ANC Timber Ltd., Canfor Corporation, Dunkley Lumber Ltd., Millar Western Forest Products Ltd., Norbord Inc., West Fraser Timber Co. Ltd., and Weyerhaeuser Company, and harvest blocks within the study area are in the subalpine, upper foothills, lower foothills, and central mixedwood natural subregions (Natural Regions Committee, 2006). The subalpine is dominated by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), white spruce (*Picea glauca*), and subalpine fir (*Abies lasiocarpa*), the upper foothills are dominated by lodgepole pine and white spruce, the lower foothills are dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*), and the central mixedwood is dominated by aspen (*Populus tremuloides*) and white spruce (Natural Regions Committee, 2006). Primary prey within the study area include elk, moose, mule deer, and white-tailed deer, and caribou predators include black bears, cougars, grizzly bears, and wolves (Apps et al., 2013; Environment Canada, 2014; McKay et al., 2021).

2.2 | Study design

As our main goal was to inform forestry management practices, our research objective was to investigate characteristics that predicted predator and prey use of harvest blocks by directly comparing occupancy between blocks, rather than to investigate landscape features and vegetation characteristics driving regional occupancy and habitat use in our study area. As a result, we did not employ a grid cell design across the study area, and all camera sites were within harvest blocks. We used a stratified random design with strata based on harvest block age, ecosite type (natural subregion, soil type, and moisture regime), and the density of anthropogenic features (harvest blocks, pipelines, roads, seismic lines, and wellsites) surrounding each harvest block, defining three categories of disturbance density (low, medium, high) using natural breaks. To improve independence between camera sites, we limited sites to include only those harvest blocks ≥3 km apart, based on published mean daily movement rates and home ranges for deer and elk (D'Eon & Serrouya, 2005; Fryxell et al., 2008; Webb et al., 2010). However, we recognize that geographic closure assumptions were unlikely to be met for more highly mobile species (i.e., predators), and we interpret occupancy as the probability that each species used the harvest block rather than the probability that the species occupied the harvest block, in which case detecting the same individuals at multiple locations is unlikely to bias results (Gould et al., 2019; Mackenzie, 2006; Murphy et al., 2021).

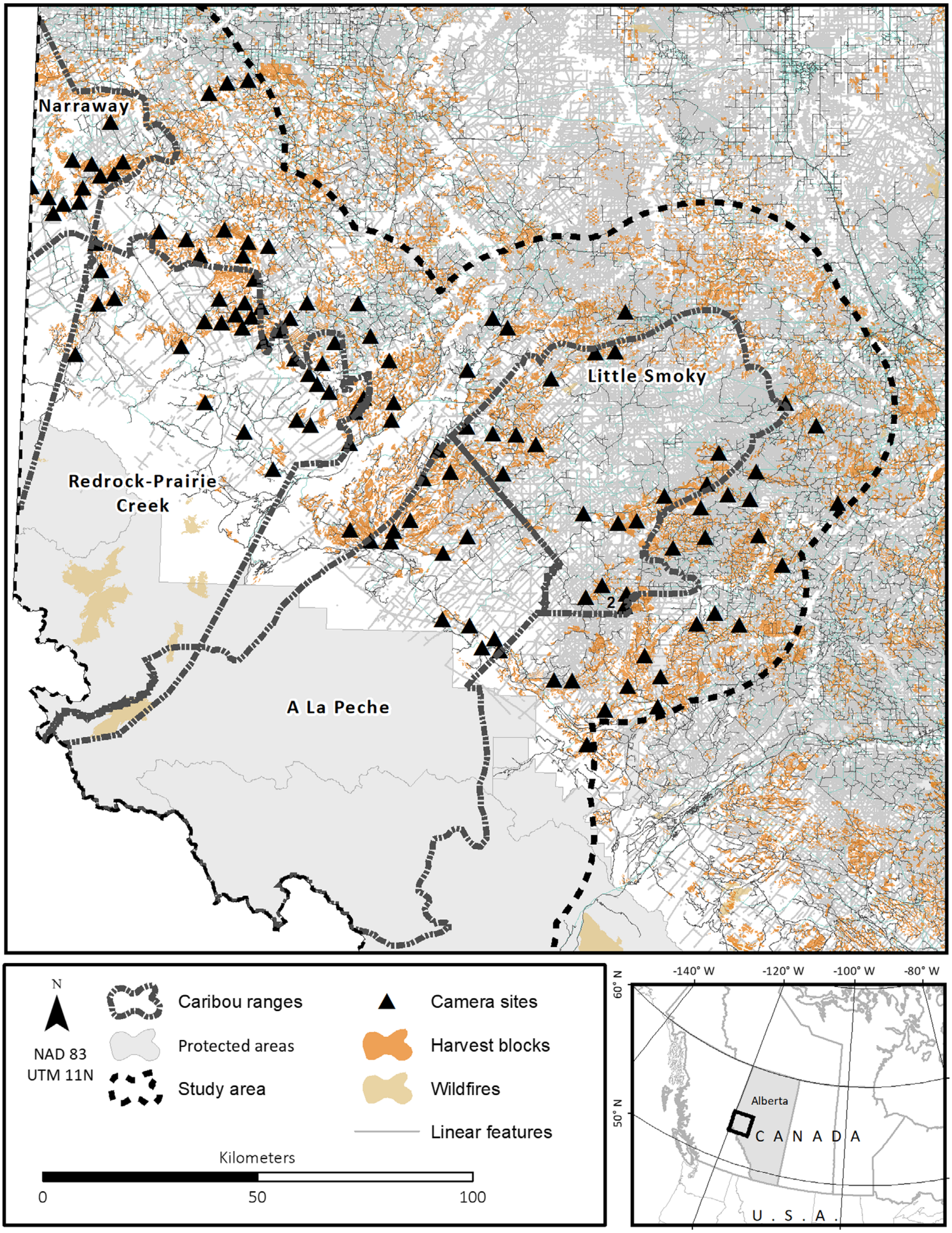

FIGURE 1 Map of study area in west-Central Alberta, Canada, including study area boundary, caribou ranges, protected areas, harvest blocks, wildfires, linear features, and locations of cameras deployed during 2018–2020. Inset indicates study area boundary within Alberta.

Low detection rates affect the accuracy of occupancy estimates, and many camera trap studies increase detection probabilities using nonrandom placement of cameras on active wildlife trails (Fisher & Burton, 2018; Shannon et al., 2014). However, the presence and quality of wildlife trails was inconsistent in our study area, and nonrandom camera placement can bias results (Kolowski & Forrester, 2017). As our goal was to directly compare occupancy between harvest blocks, we generated study sites at block centroids, setting up cameras (Browning Dark Ops HD Pro or Bushnell Trophy Cam) in clearings within 50 m of the centroid. To mitigate potentially low detection rates, we applied 28 g of O'Gorman's Long Distance Call scent lure in a tube secured into the ground 5 m in front of each camera (Burton et al., 2015; Murphy et al., 2021; Stewart et al., 2018). We revisited each site within 2–3 months, at which time we reapplied 28 g of scent lure. The timing of scent lure application was consistent across sites, and although the effect of the lure likely deteriorated over time, we consider the influence of lure on detection rates to be approximately equal across sites. We secured cameras onto trees or posts at a height of 1 m and programmed cameras to take three rapid-fire photos in succession when motion or heat triggered, as well as two automatic photos per day (2 h after sunrise and 2 h before sunset). Cameras generally collected data at each site for 1 year, but in cases where camera malfunctions resulted in large periods of missing data, we redeployed cameras at the same site for an additional year. All photos were reviewed and classified by trained personnel using TimeLapse2 Image Analyzer software (Greenberg & Godin, 2013) following established guidelines to determine wildlife species. We treated wildlife detection events as independent when they occurred at least 30 min apart (Murphy et al., 2021).

To measure forest stand characteristics, hiding cover, and available forage at each camera site, we established a 100 m^2 vegetation sampling plot outside of each camera clearing, 5 m due south of the camera location (Figure S1). Within 100 m^2 plots, we measured diameters at breast height (DBH) for all trees present (Table S1), and recorded tree species composition and tree densities (stems/100 m^2) for trees $\geq$5 cm DBH, and sapling species composition and sapling densities for trees <5 cm DBH. We measured canopy cover using a spherical crown densiometer, and lateral (hiding) cover using a cover board. We established three 8 m^2 subplots within each 100 m^2 plot, at which we recorded percent cover of shrub and berry species preferred by deer, elk, moose, and bears (Table S2) (Nielsen et al., 2004; Strong & Gates, 2006; Visscher et al., 2006) and completed stem counts and basal diameter measurements to estimate available shrub biomass using equations from Visscher et al. (2006). Within each 8 m^2 plot we established three 1 m^2 subplots, within which we recorded percent cover of target herbaceous species (Table S2) and collected herbaceous biomass samples; these samples were later dried at 60°C for 72 h and weighed to the nearest 0.01 g. We averaged shrub and herbaceous vegetation results across the three 8 and 1 m^2 subplots for each site.

2.3 | Covariates for modeling probability of detection and occupancy

Imperfect detection of wildlife can depend on habitat and survey-related factors, and we selected site-specific covariates for predicting detection probability for each species based on sampling effort (total number of active camera days), camera field of view (camera type and size of clearing), and factors affecting visibility of wildlife (canopy cover, lateral cover, tree, and sapling densities) (Table 1) (Burton et al., 2015; Devarajan et al., 2020; Hofmeester et al., 2019). For predicting the probability of occupancy of each species, we included site-specific covariates to investigate the influence of the characteristics of the harvest block itself (forage, forest stand characteristics, hiding cover, silviculture), as well as the characteristics of the surrounding area (anthropogenic disturbance, surrounding habitat) (Table 1). We obtained forage, forest stand, and hiding cover data from field data collection as described in Section 2.2. We obtained silviculture data from forestry partners (ANC Timber Ltd., Canfor Corporation, Dunkley Lumber Ltd. [Foothills Forest Products], Millar Western Forest Products Ltd., Norbord Inc. [West Fraser], West Fraser Timber Co. Ltd, and Weyerhaeuser Company), and we derived anthropogenic disturbance densities from human footprint data obtained from the Alberta Biodiversity Monitoring Institute (ABMI, 2018). For the surrounding habitat, we obtained data regarding derived ecosite phase, nutrient regime, percent conifer and deciduous trees, and forest stand age from Government of Alberta open source data (Government of Alberta, 2020), and we extracted elevation values from a 30 m × 30 m resolution digital elevation model. Both predator and prey responses to landscape characteristics are scale-dependent (Ciarniello et al., 2007; DeCesare et al., 2012), and we investigated the characteristics of the area surrounding each harvest block at two scales (1 and 5 km radii; Table 1) generated using a moving window analysis in ArcGIS.

2.4 | Analysis and model selection

To account for potential seasonal variation in occupancy resulting from changes in vegetation and snowpack, we defined two seasons (Summer: April 8–November 7, Winter: November 8–April 7), approximately equivalent to snow-free/snow periods in in our study area, and corresponding with start and end dates for Narraway and Redrock Prairie Creek caribou seasons (MacNearney et al., 2016). We used a 14-day survey occasion, generated detection histories for each species by season, and pooled seasonal data across years (2018–2020) using "detectionHistory" in camtrapR (Niedballa et al., 2020). We classified each species as detected (1) at a site during a survey occasion if $\geq$1 photograph of the species was recorded during the survey occasion, and undetected (0) if no photos of the species were recorded during the survey occasion.

TABLE 1 Covariate groups and individual covariates investigated in model selection to predict detection probability and single and multispecies occupancy in harvest blocks for elk, moose, mule deer, white-tailed deer, black bears, cougars, grizzly bears, and wolves in west-Central Alberta, Canada, during 2018–2020, including units and ranges.

Model	Covariate group	Covariate	Range
Detection probability	Sampling effort	Total number of active camera trapping days at each site (by season)	11–329
	Field of view	Site width (m)	3.0–22.0
		Site length (m)	6.0–25.0
		Overall site area (m^2)	27–550
	Visibility	Canopy cover (%)	0–93
		Tree density (stems/100 m^2)	0–0.70
		Tree sapling density (stems/100 m^2)	0–7.99
		Lateral cover at 0–1 m height	0.33–100
		Lateral cover at 1–2 m height	0–100
	Scent lure	Number of times scent lure applied (by season)	1–2
Occupancy	Forage: tree saplings	Total sapling density (stems/100m^2)	0–7.99
		Total deciduous sapling density (stems/100m^2)	0–6.72
		Deciduous saplings (%)	0–100
		Coniferous saplings (%)	0–100
	Forage: shrubs	Target shrub species (% cover for each species), mean value across three subplots	0–80
		Other shrub species (% cover for all other species), mean value across three subplots	0–15
		Biomass of target shrub species (g/m^2), mean value across three subplots	0–304
	Forage: herbaceous	Target forb species (% cover for each species), mean value across three subplots	0–73
		Carex spp. (% cover), mean value across three subplots	0–7
		Target grass species (% cover), mean value across three subplots	0–73
		All forbs (% cover), mean value across three subplots	0–98
		All grasses (% cover), mean value across three subplots	0–45
		Biomass (g/m^2) of herbaceous species, mean value across three subplots	0.6–279.6
	Forest stand characteristics	Lodgepole pine (% of total)	0–100
		Spruce (black spruce + white spruce) (% of total)	0–100
		Coniferous (% cover) (see Table S1)	0–100
		Deciduous (% cover) (see Table S1)	0–100
		Tree density, trees >5 cm DBH (stems/100 m^2)	0–0.70
		Canopy cover (%)	0–93
		Harvest block age (years since harvested)	3–48
		Harvest block <25 years old (1) or >25 years (0)	0 or 1
	Hiding cover	Lateral cover at 0-1 m height (%)	0.33–100
		Lateral cover at 1-2 m height (%)	0–100
	Silviculture	Harvest block area (km^2)	0.024–2.604
		Harvest block perimeter (km)	0.085–18.899
		Perimeter to area ratio (km/km^2)	0.091–30.376
		Site preparation occurred (1), or did not occur (0)	0 or 1
		Planting occurred (1), or did not occur (0)	0 or 1
		Density of lodgepole pine planted (stems/hectare)	0–3205

TABLE 1 (Continued)

Model	Covariate group	Covariate	Range
		Density of white spruce planted (stems/hectare)	0–1962
		Density of black spruce planted (stems/hectare)	0–1747
		Total density of all trees planted (stems/hectare)	0–3456
		Stand tending occurred (1), or did not occur (0)	0 or 1
		Mechanical stand tending occurred (1), or did not occur (0)	0 or 1
		Chemical stand tending occurred (1), or did not occur (0)	0 or 1
		Herbicide application rate (L/ha)	0–6.02
	Anthropogenic disturbance	Proportional area of harvest blocks within a 1 km radius	0.114–0.959
		Proportional area of harvest blocks within a 5 km radius	0.028–0.776
		Density of pipelines within a 1 km radius (km/km^2)	0–3.34
		Density of pipelines within a 5 km radius (km/km^2)	0–1.755
		Density of roads within a 1 km radius (km/km^2)	0–2.98
		Density of roads within a 5 km radius (km/km^2)	0.207–1.220
		Density of seismic lines within a 1 km radius (km/km^2)	0–6.268
		Density of seismic lines within a 5 km radius (km/km^2)	0.241–5.362
		Density of all linear features combined within a 1 km radius (km/km^2)	0.243–8.437
		Density of all linear features combined within a 5 km radius (km/km^2)	0.870–6.952
		Density of active wellsites within a 1 km radius (wellsites/km^2)	0–0.757
		Density of active wellsites within a 5 km radius (wellsites/km^2)	0–0.031
	Surrounding habitat	Mean percent conifer within a 1 km radius	11.2–10.0
		Mean percent conifer within a 5 km radius	34.2–100
		Mean percent deciduous within a 1 km radius	0–79.3
		Mean percent deciduous within a 5 km radius	0–56.8
		Dominant derived ecosite phase within a 1 and 5 km radius	Various
		Dominant nutrient regime within a 1 and 5 km radius	Poor, medium, rich
		Mean forest stand age within a 1 km radius (years)	36–196
		Mean forest stand age within a 5 km radius (years)	58–179
	Terrain	Digital elevation model (m)	766–1590

Note: Only silviculture and anthropogenic disturbance covariates were investigated in multispecies models.

We calculated naïve occupancy estimates based on the proportion of sites where each species was detected at least once, and we ran single-species occupancy models without covariates (i.e., assuming constant detection and occupancy) to estimate overall detection and marginal occupancy probabilities for each species and season at the scale of the study area (Cavada et al., 2019). Individual species vary in detection probability (Steenweg et al., 2019), and a low number of detections and low overall probability of detection can increase bias, decrease precision in occupancy estimates, and cause nonconvergence issues in the occupancy model selection process (Long et al., 2011; Mackenzie et al., 2002). This is particularly true when the total number of detection events for a species (d) and the number of sites where a species is detected (S_D) are nearly equal (Guillera-Arroita et al., 2010). We compared detection events and the number of sites with detections for each species and season (Table 2), and did not include species-seasons in our analysis if d was approximately equal to S_D.

Due to a lack of published information on how forest harvesting influences the occupancy and co-occurrence of primary prey and predators in our study area, we did not have justification to test a specific set of *a priori* models, and our initial analysis included many potential model covariates at multiple spatial scales (Table 1). To avoid over-parameterization and inclusion of uninformative parameters in final models, we grouped covariates into biologically relevant categories and used a multistep model selection process to identify covariates to include in the final detection probability and occupancy models for each species and season (Arnold, 2010; Estevo et al., 2017; Long et al., 2011). First, we ran univariate detection probability models for all detection covariates (Table 1) while holding occupancy constant, ranked these models using Akaike's information criterion (AIC; Akaike, 1983), and included all detection covariates with ΔAIC ≤ 4 in the global detection model. In the case of correlated covariates ($r \geq .6$), we retained the covariate with the better AIC ranking. Second, we tested the global model and all possible combinations of the detection probability covariates from Step 1 (to a maximum of five covariates), and selected the final detection probability model for each species and season based on the best AIC ranking (Gould et al., 2019; Majgaonkar et al., 2019). Third, we incorporated the final detection probability models for each species and season within univariate occupancy models to test occupancy covariates within each category (Table 1) and carried forward occupancy covariates if 90% CIs for coefficients did not include zero. Again, in the case of correlated covariates ($r \geq .6$), we retained the covariate with the better AIC ranking. Fourth, we compared univariate models for covariates carried forward from Step 3, ranked models using AIC, and identified covariates with ΔAIC ≤ 4 to include in the global model. Finally, we tested the global model and all possible combinations of occupancy covariates carried forward from Step 4 and ranked models using AIC to determine the final occupancy model for each species and season. We report coefficients from our final models if the 90% CI does not include zero, and we report results as mean beta coefficients (β) with 90% CIs.

We report observed co-occurrence for species pairs based on the proportion of sites where both species were detected, and we used multispecies occupancy models to estimate probability of species co-occurrence, test for dependence between species pairs, and determine whether anthropogenic disturbance and/or silviculture covariates influenced co-occurrence (Lahkar et al., 2021; Murphy et al., 2021; Rota et al., 2016). As the focus of our research was to examine how disturbance characteristics may affect predator–prey dynamics, we limited our multispecies analysis to predator–prey combinations, and we limited our investigation of covariates predicting co-occurrence to anthropogenic disturbance and silviculture covariates. To investigate how the occupancy of each species in a pair

TABLE 2 Number of 14-day survey occasions with detections (d), number of sites with at least one detection (S_D), naïve occupancy (ψ_n), and mean estimates of probability of detection (p) and probability of occupancy (ψ) with lower (LCL) and upper (UCL) 90% confidence intervals for each species by season at camera sites in harvest blocks in west-central Alberta, Canada during 2018–2020.

Species	d	S_D	ψ_n	p	LCL	UCL	ψ	LCL	UCL
Summer									
Caribou	0	0	0	0.000			0.000		
Elk	**92**	**46**	**0.393**	**0.115**	**0.092**	**0.138**	**0.493**	**0.394**	**0.592**
Moose	**398**	**98**	**0.837**	**0.266**	**0.246**	**0.286**	**0.879**	**0.822**	**0.936**
Mule deer	**127**	**57**	**0.487**	**0.128**	**0.107**	**0.149**	**0.593**	**0.496**	**0.690**
White-tailed deer	**530**	**107**	**0.915**	**0.335**	**0.315**	**0.355**	**0.933**	**0.891**	**0.975**
Black bear	**273**	**82**	**0.701**	**0.208**	**0.188**	**0.228**	**0.764**	**0.689**	**0.839**
Cougar	3	2	0.017	0.032	0.000	0.080	0.030	0.000	0.074
Grizzly bear	**69**	**36**	**0.308**	**0.095**	**0.072**	**0.119**	**0.424**	**0.317**	**0.531**
Wolf	**18**	**15**	**0.128**	**0.024**	**0.002**	**0.045**	**0.454**	**0.066**	**0.842**
Winter									
Caribou	0	0	0	0.000			0.000		
Elk	10	8	0.082	0.045	0.000	0.094	0.222	0.000	0.450
Moose	**100**	**53**	**0.541**	**0.146**	**0.117**	**0.175**	**0.693**	**0.574**	**0.812**
Mule deer	5	4	0.041	0.070	0.000	0.170	0.080	0.000	0.181
White-tailed deer	**39**	**28**	**0.286**	**0.075**	**0.042**	**0.109**	**0.525**	**0.317**	**0.733**
Cougar	1	1	0.010	0.001	0.000	0.003	n/a	n/a	n/a
Wolf	5	4	0.041	0.054	0.000	0.135	0.096	0.000	0.231

Note: Species with enough detections to build seasonal occupancy models are indicated in bold.

was dependent upon the occupancy of the other species, we predicted conditional occupancy probabilities as the probability of occurrence of species A conditional on the presence (i.e., detection) or absence (i.e., nondetection) of species B without covariates for each predator–prey species pair (Ladle et al., 2018; Mackenzie et al., 2004; Rota et al., 2016). As for single-species occupancy models, we determined which species pairs had enough detection events to predict seasonal co-occurrence by assessing the number of detection events and the number of sites where both species were detected (Table 3). Due to a low number of detections for some species, we examined co-occurrence of species during summer only, and focused on pairwise interactions (i.e., we did not estimate co-occurrence of three or more species). We incorporated the final single-species detection and occupancy models within the nested structure of all multispecies occupancy models, allowing us to account for habitat covariates predicting occupancy of each species unrelated to species dependence (i.e., marginal occupancy) while investigating the influence of anthropogenic disturbance and silviculture on species dependence (Estevo et al., 2017; Ladle et al., 2018). We used a multistep model selection process to identify covariates to include in final multispecies occupancy models for each species pair. First, we tested for species dependence by comparing models including only marginal detection and occupancy covariates against models with and without species dependence. Second, for species pairs where the model including species dependence was either the top-ranked model or with ΔAIC $\leq$2.0 in Step 1, we compared univariate models for anthropogenic and silviculture covariates, and carried covariates forward if 90% CIs for coefficients did not include zero. Third, we compared univariate models for covariates carried forward from Step 2, ranked models using AIC, and identified covariates with ΔAIC $\leq$4 to include in the global model. Finally, we tested the global model and all possible combinations of covariates carried forward from Step 3 and ranked models using AIC to determine the final multispecies occupancy model for each species pair (Lahkar et al., 2021; Rouse et al., 2021). We report coefficients from our final models if the 90% CI does not include zero, and we report results as mean beta coefficients (β) with 90% CIs.

We built occupancy models in R using "occu" and "occuMulti" from the unmarked package (Fiske & Chandler, 2011), we completed model selection using "dredge" and "modSel" from the MuMIn package (Bartón, 2015), and we standardized covariates in final models using "stdize" from the MuMIn package. We tested continuous covariates for correlation using Pearson's r, defining covariate pairs with r >.6 as correlated, and reviewed boxplots and variance inflation factors for categorical and binary covariates. We interpret occupancy as an index of habitat use, with harvest blocks as the resource units, and our models predict the probability of use of harvest blocks in relation to covariates (Gould et al., 2019; Mackenzie, 2006; Nagy-Reis et al., 2017).

3 | RESULTS

3.1 | Single-species detection and occupancy

We deployed camera traps during June 5, 2018 to August 29, 2020 with 37 survey occasions at 117 sites during summer and 22 survey occasions at 98 sites during winter, resulting in a total of 35,445 active trapping days. We did not detect caribou at any cameras during the study

TABLE 3 Number of 14-day survey occasions with detections of both species at a site (d_2), number of sites where both species were detected at least once (S_{D2}), observed co-occurrence (Obs), and mean estimates of probability of co-occurrence (Co) with lower (LCL) and upper (UCL) 90% confidence intervals for each species pair during summer at camera sites in harvest blocks in west-Central Alberta, Canada during 2018–2020.

Species pair	d_2	S_{D2}	Obs	Co	LCL	UCL
Black bear: Elk	**22**	**34**	**0.291**	**0.376**	**0.272**	**0.480**
Black bear: Moose	**94**	**73**	**0.624**	**0.699**	**0.620**	**0.777**
Black bear: Mule deer	**27**	**45**	**0.385**	**0.499**	**0.399**	**0.598**
Black bear: White-tailed deer	**114**	**79**	**0.675**	**0.740**	**0.652**	**0.827**
Grizzly bear: Elk	**3**	**13**	**0.111**	**0.175**	**0.089**	**0.261**
Grizzly bear: Moose	17	33	0.282	0.388	0.295	0.482
Grizzly bear: Mule deer	**10**	**27**	**0.231**	**0.329**	**0.241**	**0.417**
Grizzly bear: White-tailed deer	28	36	0.308	0.416	0.299	0.532
Wolf: Elk	0	9	0.077	0.259	0.033	0.486
Wolf: Moose	8	15	0.128	0.397	0.092	0.703
Wolf: Mule deer	0	10	0.085	0.298	0.047	0.549
Wolf: White-tailed deer	8	17	0.145	0.444	0.028	0.861

Note: Species pairs for which we built multi-species occupancy models are indicated in bold.

period. Detection and occupancy probability for all species was higher during summer than during winter, with significant differences in occupancy (i.e., nonoverlapping 90% CIs) between summer and winter for moose, mule deer and white-tailed deer (Table 2). There were too few detection events to build models with covariates for elk, mule deer, and wolves during winter and cougars during summer and winter, and winter detections of cougars were too low to estimate occupancy. Covariates retained in final detection probability models varied between species and seasons (Table S3).

Across species and seasons, between one and five covariates met our criteria (i.e., 90% CIs for coefficients did not include zero, ΔAIC ≤4 in univariate comparisons, Table S4) and were included in global models, for which we tested all possible combinations of the final covariates. During summer, elk and moose occupancy in harvest blocks increased with the percentage of deciduous forest within a 1 km radius of the harvest block, and moose occupancy increased with percent cover of *Cornus canadensis* (Table 4). Mule deer occupancy increased with elevation and mean forest age within a 1 km radius.

Species	Covariates	β	LCL	UCL
Summer				
Elk	Mean % deciduous (1 km)	2.165	0.910	3.420
Moose	Mean % deciduous (1 km)	4.603	0.671	8.534
	% cover *Cornus canadensis*	5.857	1.185	10.529
Mule deer	Elevation	0.688	0.135	1.241
	Mean forest age (1 km)	0.623	0.092	1.154
White-tailed deer	% cover *Chamerion angustifolium*	11.250	0.382	22.119
	Planted (0/1)	1.820	0.279	3.361
	Proportion harvest blocks (5 km)	−0.930	−1.776	−0.085
Black bear	% cover *Rosa asicularis*	1.723	0.129	3.317
	Planted (0/1)	1.844	0.821	2.867
Grizzly bear	% cover *Alnus* spp.	−0.883	−1.511	−0.255
	Proportion harvest blocks (1 km)	−0.674	−1.219	−0.130
Wolf	Road density (1 km)	−1.160	−2.178	−0.142
Winter				
Moose	Planted (0/1)	1.657	0.316	2.998
	Salix spp. biomass	0.658	0.255	1.061
White-tailed deer	Density of pine planted	−0.819	−1.571	0.067

Note: Distances (e.g., 1 km) indicate the radius within which the covariate was measured.

TABLE 4 Covariates and standardized coefficients (β) with lower (LCL) and upper (UCL) 90% confidence intervals from top-ranked summer and winter occupancy probability models by species, based on detection data from camera sites in 117 and 98 harvest blocks in west-Central Alberta during 2018–2020.

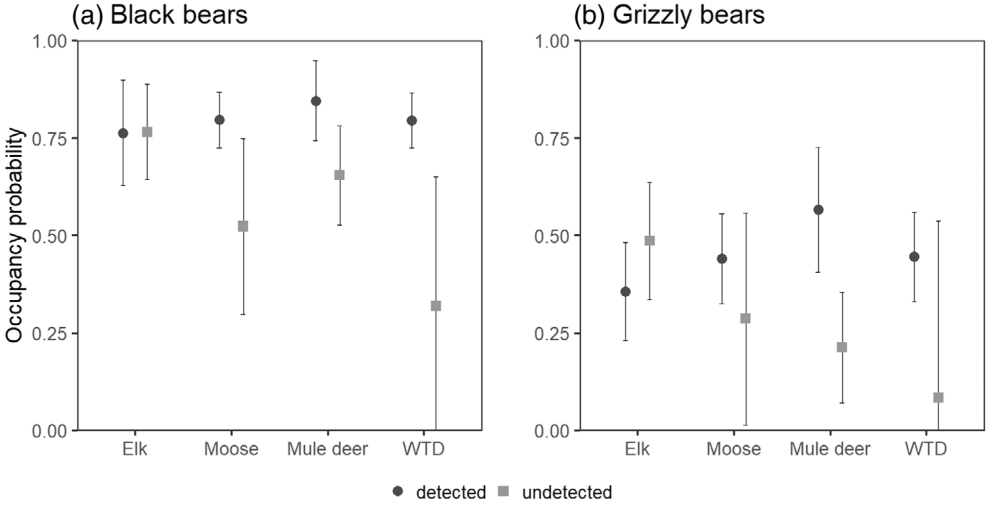

FIGURE 2 Mean predicted conditional occupancy probabilities and 90% confidence intervals for black bears (a), and grizzly bears (b) when elk, moose, mule deer, and white-tailed deer (WTD) were detected or undetected, predicted using data collected at cameras deployed in harvest blocks in west-Central Alberta, Canada, during 2018–2020.

TABLE 5 Covariates and standardized coefficients (β) with lower (LCL) and upper (UCL) 90% confidence intervals from top-ranked multispecies summer occupancy probability models by species pair, based on detection data from camera sites in 117 harvest blocks in west-Central Alberta during 2018–2020.

Species pair	Covariates	β	LCL	UCL
Black bear: Elk	Proportion harvest blocks (1 km)	−0.918	−1.448	−0.388
Black bear: Moose	Stand tending (0/1)	−2.190	−3.871	−0.509
Black bear: Mule deer	Density of pine planted	−0.667	−1.188	−0.145
	Site preparation (0/1)	−1.263	−2.206	−0.320
Black bear: White-tailed deer	Stand tending (0/1)	−1.797	−3.097	−0.497
	Harvest block area	−0.558	−1.043	−0.073
Grizzly bear: Elk	Proportion harvest blocks (5 km)	−0.894	−1.673	−0.114
Grizzly bear: Mule deer	Density of seismic (5 km)	−0.836	−1.509	−0.163

Note: Distances (e.g., 1 km) indicate the radius within which the covariate was measured. Species pairs with final models that did not include species dependence terms are not included.

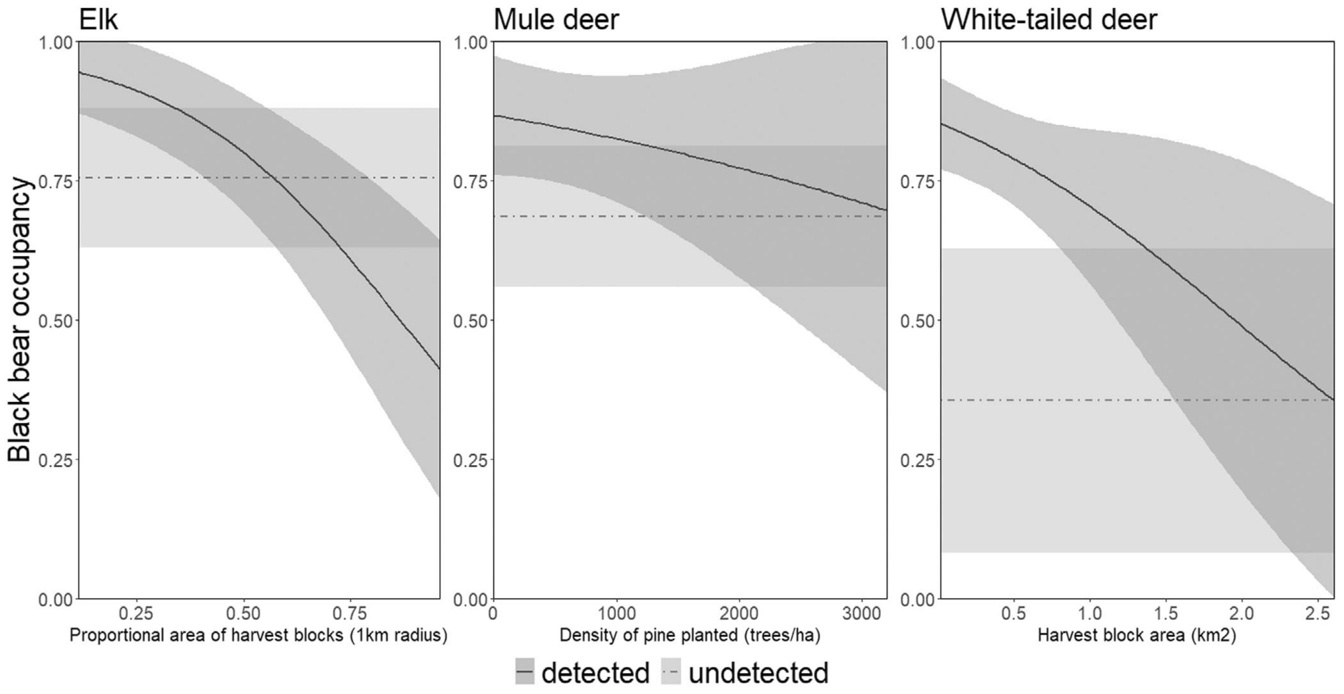

FIGURE 3 Probability of black bear occupancy when elk, mule deer, and white-tailed deer were detected or undetected, as predicted by covariates in top-ranked multispecies occupancy models using data collected at cameras deployed in harvest blocks in west-Central Alberta, Canada, during 2018–2020. Predicted black bear occupancy when elk, mule deer, and white-tailed deer are undetected does not change in response to changes in the covariates, as covariates in the multispecies models above were not retained in the top-ranked black bear single-species model, resulting in flat lines (zero slope).

White-tailed deer occupancy increased with percent cover of *Chamerion angustifolium*, was higher in harvest blocks that were planted versus those that were not, and decreased with an increasing proportion of harvest blocks within a 5 km radius. Black bear occupancy increased with percent cover of *Rosa acicularis* and was higher in harvest blocks that were planted. Grizzly bear occupancy decreased with increasing percent cover of *Alnus* spp. and increasing proportion of harvest blocks within a 1 km radius, and wolf occupancy decreased with increasing densities of roads within a 1 km radius. During winter, moose occupancy increased with higher *Salix* spp. biomass and was higher in blocks that had been planted, while white-tailed deer occupancy decreased with an increasing density of pine planted.

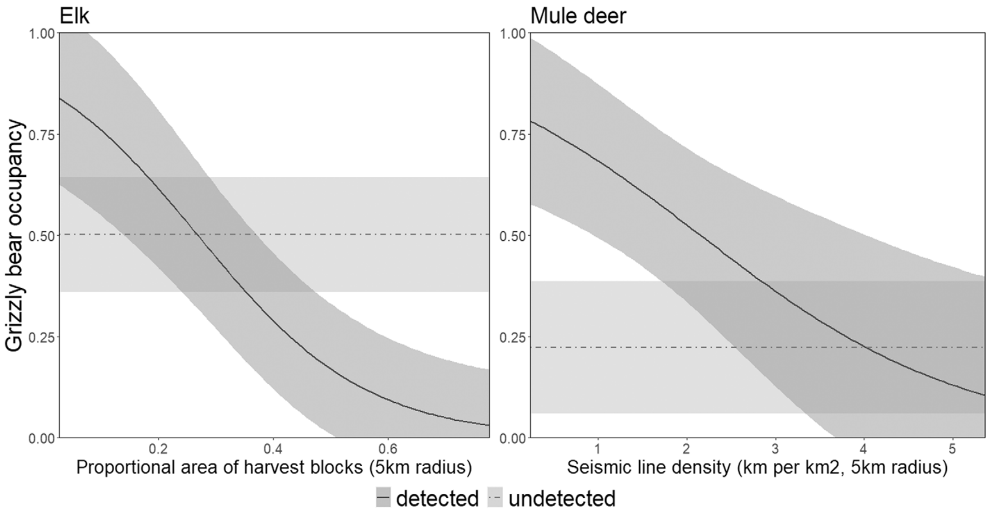

FIGURE 4 Probability of grizzly bear occupancy when elk and mule deer were detected or undetected, as predicted by covariates in top-ranked multispecies occupancy models using data collected at cameras deployed in harvest blocks in west-Central Alberta, Canada, during 2018–2020. Predicted grizzly bear occupancy when elk and mule deer are undetected does not change in response to changes in the covariates, as covariates in the multispecies models above were not retained in the top-ranked grizzly bear single-species model, resulting in flat lines (zero slope).

3.2 | Multispecies occupancy

Observed co-occurrence of species pairs ranged from 0.077 (Wolf: Elk) to 0.675 of sites (Black bear: White-tailed deer) (Table 3). There were too few detection events to include cougars and wolves in multispecies models, and detections of cougars were too low to estimate co-occurrence (Tables 2 and 3). Conditional occupancy probabilities indicated that black bear occupancy was higher when white-tailed deer were detected as compared to when they were undetected (i.e., nonoverlapping 90% CIs), and grizzly bear occupancy was higher when mule deer were detected as compared to when they were undetected (Figure 2).

Based on model comparisons for each bear-primary prey species pair (Table S5), co-occurrence of grizzly bears and moose was not influenced by anthropogenic features or silviculture practices, and there was no evidence of species dependence for grizzly bears and white-tailed deer. Co-occurrence of black bears with elk decreased with an increasing proportion of harvest blocks within a 1 km radius, and co-occurrence of black bears with mule deer decreased with an increasing density of pine planted and was lower in blocks that had been site prepped prior to planting (Table 5; Figure 3). Co-occurrence of black bears with moose and white-tailed deer was lower in blocks that had been stand tended, and co-occurrence of black bears with white-tailed deer decreased with increasing block area (Figure 3). Co-occurrence of grizzly bears and elk decreased with an increasing proportion of harvest blocks within a 5 km radius, and co-occurrence of grizzly bears and mule deer decreased with increasing seismic line density within a 5 km radius (Figure 4).

4 | DISCUSSION

4.1 | Single-species occupancy

Moose, mule deer, and white-tailed deer occupancy in harvest blocks was higher during summer than in winter. Lower winter use of harvest blocks by deer and moose has been previously reported in our study area, and may be driven by deer preference for the summer forage provided by deciduous species in harvest blocks (Hewitt, 2011; Moen, 1978; Stelfox et al., 1976), or could be related to the deeper snowpack in harvest blocks compared to intact forest stands, reducing access to woody browse and increasing movement costs for ungulates (Telfer & Kelsall, 1979; Visscher et al., 2006). Caribou are exposed to increased predation risk in areas where they overlap with primary prey and shared predators (Latham et al., 2011; Mumma et al., 2018; Whittington et al., 2011), specifically during the summer and fall migration (Blagdon & Johnson, 2021; Wittmer et al., 2005). The seasonal differences in occupancy we observed could have implications for the spatiotemporal distribution of predators and prey within caribou ranges, with corresponding seasonal changes in caribou predation risk.

Occupancy was predicted directly by site-specific forage availability as well as by landscape-level characteristics linked to forage. We found that moose and white-tailed deer occupancy increased with the site-specific availability of preferred forage species (*C. canadensis*, *C. angustifolium*, and *Salix* spp.; Strong & Gates, 2006; Visscher et al., 2006), and black bear occupancy of harvest blocks was also influenced by forage preferred by black bears (*R. acicularis*; Costello et al., 2016). At the landscape-level, elk and moose summer occupancy increased with the percentage of deciduous forest in the surrounding area, consistent with previous research suggesting that elk and moose prefer deciduous or mixedwood forest, likely due to the increased availability of woody browse (Gillingham & Parker, 2008; van Beest et al., 2014; Visscher et al., 2006). These results suggest that use of harvest blocks by both primary prey and black bears could be reduced by site-specific silviculture practices aimed at reducing forage species preferred by primary prey and bears, combined with landscape-scale planning to consider surrounding forest stand types.

During summer, white-tailed deer occupancy was higher in blocks that had been planted, but during winter, occupancy decreased with increasing density of pine planted. Occupancy of black bears in summer and moose in winter was also higher in blocks that had been planted compared to those that were not. These differences may be driven by seasonal differences in forage availability and hiding cover, differences in availability of forage due to changes in canopy cover at different stages of succession, variation in understory and forage due to local soil and moisture conditions, or complex interactions between local site conditions and silviculture practices (Hart & Chen, 2006; Lieffers et al., 2003). Further research directly linking forage abundance to specific silviculture practices and assessing differences in forage availability during summer versus winter might help to explain these findings.

Occupancy of harvest blocks was also impacted by the surrounding forest age. Mule deer summer occupancy of harvest blocks increased with increasing forest age in the surrounding area, and both white-tailed deer and grizzly bear occupancy increased as the amount of young forest (i.e., harvest blocks <50 years old) in the surrounding area decreased. These results contrast with research in northern Alberta, where the total amount of harvest blocks increased the probability of white-tailed deer presence (Dawe, 2011) and white-tailed deer selected areas closer to harvest blocks (Darlington et al., 2022), but complement research in west-central Alberta, where there was a negative relationship between white-tailed deer abundance and harvest blocks (Nielsen et al., 2017). While we found occupancy of harvest blocks was influenced by the age of the forest surrounding the harvest block, our results did not suggest that occupancy was directly related to the site-specific age of the harvest block. Successional stages and timing of succession can vary with local conditions like soil moisture, acidity, and topography (Brulisauer et al., 1996; Hart & Chen, 2006), and harvest block age alone may not be an accurate indicator of available ungulate forage in our study area. While it is frequently suggested that deer select for early seral stands (Darlington et al., 2022; Fisher & Wilkinson, 2005; Toews et al., 2018), our results indicate that use of harvest blocks may be dependent on the availability of forest across a range of successional stages. Others have reported that deer select for uneven-aged mature forest and large-scale habitat heterogeneity (Kie et al., 2002; Nielsen et al., 2017; Wallmo & Schoen, 1980), and grizzly bear use of harvest blocks depends on the landscape-level forest composition (Kearney et al., 2019; Nielsen et al., 2004; Stewart et al., 2012). Again, these results further indicate the importance of the surrounding habitat in influencing wildlife use of harvest blocks at the site level.

4.2 | Multispecies occupancy

The focus of our investigation of multispecies occupancy was to examine how disturbance characteristics may affect predator–prey dynamics in harvest blocks, and we found that anthropogenic disturbance and/or silviculture practices influenced black bear co-occurrence with elk, moose, mule deer and white-tailed deer, and grizzly bear co-occurrence with elk and mule deer. We found no evidence of species dependence for co-occurrence of grizzly bears with white-tailed deer, rather, the co-occurrence of these species was best predicted by the marginal occupancy of each species in the pair (Rota et al., 2016), and co-occurrence of grizzly bears and moose was not influenced by anthropogenic features or silviculture practices. These results suggest that disturbance characteristics do not influence the co-occurrence of grizzly bears with moose or white-tailed deer within harvest blocks in our study area.

Black bear occupancy was higher in harvest blocks where white-tailed deer were detected compared to blocks where white-tailed deer were not detected, and grizzly bear occupancy was higher in blocks where mule deer were detected compared to blocks where mule deer were not detected. Although co-occurrence cannot be directly interpreted as species interactions (Blanchet et al., 2020), the increased probability of bear occupancy in harvest blocks occupied by deer suggests that harvest blocks may directly influence predator–prey dynamics within our study area. Black bear predation of white-tailed deer has been reported in other areas (Mathews & Porter, 1988; Popp et al., 2018; Svoboda et al., 2011), and it is well established that ungulates are important in predicting abundance of grizzly bears in our study area (Munro et al., 2006; Nielsen et al., 2017), but to our knowledge, these bear–deer conditional occupancy patterns have not been previously reported in west-central Alberta caribou ranges. Our results suggest that in addition to the vegetative forage provided by harvest blocks, bears may also be attracted to blocks because of the presence of deer, potentially increasing the local overlap of bears and deer within caribou ranges in areas with harvest blocks, with possible consequences for apparent competition and predation risk for caribou. These results may have particular significance in the context of white-tailed deer range and population expansion in Alberta, as white-tailed deer could eventually replace moose as the main apparent competitor within some caribou ranges (Dawe et al., 2014; Fisher & Burton, 2021; Latham et al., 2011).

In interpreting results of multispecies occupancy models, it is important to note that habitat covariates predicting the marginal occupancy of each species of the pair are accounted for by the incorporation of single-species detection and occupancy models within the nested structure of multispecies models, and any covariates predicting co-occurrence are directly related to species dependence (Estevo et al., 2017; Ladle et al., 2018). We found that silviculture practices and harvest block characteristics influenced the co-occurrence of black bears with moose, mule deer, and white-tailed deer. Black bears were less likely to co-occur with moose and white-tailed deer in harvest blocks that had been stand tended, and co-occurrence of black bears and mule deer was lower in blocks that had been prepped prior to planting and decreased with an increasing density of pine planted. These results are likely related to the removal of competing vegetation during site preparation and stand tending and the decreased light transmission associated with higher tree densities, resulting in reduced availability of forage and browse species (Ehrentraut & Branter, 1990; Hart & Chen, 2008; Pekin et al., 2014). Co-occurrence of black bears with white-tailed deer also decreased with increasing harvest block area, indicating that block size may influence predator–prey dynamics. Previous research suggests that forest edges are important for bears, primary prey species and predator–prey interactions (Fortin et al., 2015; Murphy et al., 2021; Vanlandeghem et al., 2021), and the open spaces distant from forest cover created by larger harvest blocks may deter use of these blocks by deer and bears. In addition, seismic line density in the surrounding area influenced the co-occurrence of grizzly bears with mule deer, while harvest block density in the surrounding area influenced co-occurrence of black bears and grizzly bears with elk, providing further evidence that the surrounding anthropogenic disturbance also influences co-occurrence and wildlife use of harvest blocks at the site level. Overall, our multispecies results are consistent with results from single-species models suggesting that silviculture practices aimed at reducing forage species combined with landscape-scale planning could help reduce predator–prey overlap in harvest blocks.

4.3 | Limitations and future research

We recognize that this study had limitations. We experienced a high number of camera failures in winter due to extremely cold temperatures, and as detection rates were lower across species in the winter, we did not have enough data to model winter occupancy for most species. In addition, because of the low number of detections of cougars and wolves, we were unable to model cougar occupancy or include wolves in multispecies occupancy models. Low levels of detections for wolves in our study area may be confounded by the ongoing Government of Alberta wolf population reduction program (Hervieux et al., 2014). Cougars and wolves are important caribou predators in our study area (McKay et al., 2021), and a lack of knowledge regarding how forest harvesting influences the occupancy of these large predators and their co-occurrence with primary prey may have implications for the effectiveness of management actions.

We were unable to include snow depth and temperature as covariates in our analysis. Future modeling including snow depth and temperature data will help to assess the relative roles of season, harvest block characteristics, and microclimate on the use of harvest blocks by predator and prey species. Future modeling will also include investigation of how silviculture methods directly influence abundance of specific forage species, and this information could be incorporated into silviculture prescriptions, providing practical information to reduce preferred forage species in harvest blocks in caribou ranges. Finally, the focus of this research was on predators of caribou and their primary prey species, and as such, this analysis was limited to occupancy and co-occurrence for predator-primary prey pairs, but future analysis could include additional species such as meso-carnivores (e.g., coyote, lynx) and investigation of intraguild co-occurrence.

4.4 | Management implications

Although an investigation of caribou habitat use was not the objective of our study, it is worth noting that we did not detect caribou at any of our harvest block camera sites across 35,445 active trapping days during 2018–2020. As we did not deploy cameras in other habitat types for comparison, our results do not provide direct conclusions regarding caribou selection or avoidance of harvest blocks, but the lack of caribou detections is consistent with previous research suggesting that caribou generally avoid harvest blocks (DeCesare et al., 2012; Mumma et al., 2018; Peters et al., 2013).

Provincial and federal caribou recovery plans prescribe restoration and management to make habitat less suitable for primary prey species (Environment Canada, 2012, 2014; Government of Alberta, 2017). Our results indicate that within the context of landscape-level planning, silviculture practices used to control forage availability could reduce the use of harvest blocks by primary prey, with the potential to influence the distribution of primary prey and predators within caribou ranges. However, management strategies will need to be balanced against other values on the landscape, including maintaining populations of culturally important species like moose, reducing the spread of mountain pine beetle (*Dendroctonus ponderosae*), and limiting the use of herbicides (Government of Alberta, 2007; Popp et al., 2020).

Our results demonstrated that black bear and grizzly bear occupancy was directly influenced by the presence of deer, highlighting the importance of considering a range of predator–prey dynamics in systems with multiple predator and prey species. Moose are often identified as the main apparent competitor for caribou, and federal caribou recovery plans and provincial predator control efforts are currently focused on maintaining low wolf densities (<3.0 wolves/1000 km^2) (Environment Canada, 2014; Hervieux et al., 2014; Serrouya et al., 2019), but future recovery efforts may need to consider the roles of deer, black bears, and grizzly bears in caribou predation risk, particularly in the context of white-tailed deer population and range expansion and recent grizzly bear population increases in Alberta (Dawe et al., 2014; Stenhouse et al., 2015, 2020).

Finally, our results show it is important to include both the characteristics of harvest blocks as well as the surrounding area when considering predator and prey distribution, and that for harvest blocks, disturbance age may not be the best indicator of when disturbances are no longer impacting predator–prey dynamics. Our results also indicate that silviculture practices are only part of the picture in predicting wildlife use of harvest blocks, and forestry planning within caribou ranges should consider both site-specific silviculture practices and landscape-level planning to best reduce use of harvest blocks by primary prey and predator species.

In a rapidly changing boreal forest ecosystem (Curtis et al., 2018; White et al., 2017), our study provides the first detailed insights into the impacts of forestry and silviculture on boreal forest predator–prey co-occurrence. Our research directly links wildlife response to forestry practices, and the application of these results in forestry best management practices and caribou recovery planning could help mitigate the impacts of forestry on boreal species in the future. Translating research into practical landscape management decisions could benefit threatened species like caribou as well as culturally and economically important species like deer, elk, moose, and bears. Overall, our results further demonstrate the impacts of forest harvesting on boreal forest predator–prey dynamics and illustrate the importance of multispecies studies for mitigating the impacts of anthropogenic landscape change on wildlife and boreal forest ecosystem function across Canada (Finnegan et al., 2021; Fisher & Ladle, 2022; Muhly et al., 2019).

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DATA AVAILABILITY STATEMENT

Data for this study are available at https://doi.org/10.5061/dryad.3n5tb2rmn.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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