RESEARCH ARTICLE

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Ungulate occurrence in forest harvest blocks is influenced by forage availability, surrounding habitat and silviculture practices

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Abstract

1. Forest harvesting causes habitat loss and alteration and can change predator–prey dynamics. In Canada, forest harvesting has shifted the distribution and abundance of ungulates (deer, elk and moose) that prefer early seral forest, resulting in unsustainable caribou predation by shared predators (bears, cougars and wolves). Long-term solutions for caribou recovery require management to reduce ungulate prey species within caribou ranges. Silviculture practices applied after forest harvesting directly affect the amount of forage available in harvested areas, and therefore influence ungulate distribution, but few studies have completed detailed assessments on how specific treatments of site preparation, planting and stand tending influence ungulate use of harvest blocks.

2. We used camera traps, silviculture data, GIS-derived habitat and disturbance data, and detailed vegetation data collected at field sites to investigate ungulate occurrence in harvest blocks in west-central Alberta, Canada. We compared seasonal ungulate occurrence and investigated how site-specific characteristics, the surrounding habitat and disturbance density, and fine-scale silviculture treatments influenced ungulate occurrence in blocks.

3. Deer, elk and moose occurrence was higher in summer compared to winter. Elk, moose and white-tailed deer occurrence was higher in blocks with greater availability of specific forage species. Moose occurrence was higher in blocks with a lower road density in the surrounding area, and white-tailed deer occurrence was higher in blocks further from seismic lines and with a lower proportion of harvest blocks in the surrounding area.

4. Deer, elk and moose occurrence was higher in younger harvest blocks. Mule deer and white-tailed deer occurrence was lower in blocks with higher planting densities of lodgepole pine, and mule deer occurrence was also lower in blocks that had been stand tended.

5. Our study provides detailed information on ungulate response to fine-scale silviculture methods used in Alberta, directly linking wildlife occurrence to forestry

practices, and providing practical scientific information to inform sustainable forestry. Translating this research into practical landscape management decisions could benefit boreal biodiversity, including threatened species like caribou, and culturally and economically important species like deer, elk and moose.

1 | INTRODUCTION

Human-caused habitat loss and alteration are among the main drivers of declining biodiversity and species extinctions (Maxwell et al., 2016; Young et al., 2016). Across the globe, forest harvesting causes habitat loss and alteration through the loss of forest cover and changes in forest structure, with profound impacts on biodiversity (Lindenmayer, 2009; Rocha-Santos et al., 2016). Moving forward, sustainable forest management that balances social, economic and ecological values has the potential to restore and maintain biodiversity and ecosystem function (Achim et al., 2022; Kremen & Merenlender, 2018; Spathelf et al., 2018).

In Canada, forest harvesting alters approximately 650,000 ha of boreal forest each year (Curtis et al., 2018; Komers & Stanojevic, 2013; White et al., 2017). Forest harvesting has had cascading impacts on the Canadian boreal ecosystem, as changes in the availability of forage result in changes in the density and distribution of ungulates like deer *Odocoileus virginianus* and *Odocoileus hemionus*, elk *Cervus elaphus* and moose *Alces alces*, and changes in these ungulate populations subsequently cause changes in the density and distribution of their predators like bears *Ursus americanus* and *Ursus arctos*, cougars *Puma concolor* and wolves *Canis lupus* (Laurent et al., 2020; Serrouya et al., 2021; Visscher & Merrill, 2009). Across Canada, forest harvesting within the ranges of threatened boreal and central mountain caribou *Rangifer tarandus* is associated with altered predator–prey dynamics and widespread declines in caribou populations due to apparent competition and unsustainable caribou mortality from shared predators (DeCesare et al., 2010; Hervieux et al., 2013; Latham et al., 2011). Long-term solutions for caribou recovery will require habitat restoration and adaptive management practices that reduce the density and distribution of the main apparent competitors of caribou (i.e. deer, elk and moose) within caribou ranges, in order to reduce predator populations and predation risk (Environment Canada, 2014; Ray et al., 2015; Serrouya et al., 2017).

In the province of Alberta in western Canada, clearcutting is the most common method of forest harvesting, with all or most of the merchantable trees in a block harvested at once (Alberta Sustainable Resource Development, 2006a). After trees are harvested, a range of silviculture methods are applied, including site preparation, tree planting and stand tending, with the goal of facilitating the establishment of commercial tree species (Alberta Sustainable Resource Development, 2006b; Lieffers et al., 2003; Wagner et al., 2006). These silviculture methods not only affect the regeneration rates of commercial tree species but also impact the diversity and abundance of understory species in harvest blocks (Bell et al., 1997; Boan et al., 2011; Haeussler et al., 1999). Wildlife use of harvest blocks therefore may be influenced by silviculture methods that affect the amount of forage available at the fine-scale, in addition to the effects of landscape-level characteristics such as the surrounding habitat and anthropogenic disturbance (Bowman et al., 2010; Kearney et al., 2019; Muhly et al., 2019).

With established links between forest harvesting, apparent competition and caribou population declines (DeCesare et al., 2010; Serrouya et al., 2019; Vors & Boyce, 2009), there is a body of research investigating how harvest blocks and silviculture methods affect lichen abundance, caribou habitat use, and caribou predation risk (Armleder & Stevenson, 1994; McNay, 2011; Stone et al., 2008). Previous research has also investigated the response of deer, elk and moose to forest harvesting, including the influence of harvest blocks on ungulate habitat use and reproductive success (Darlington et al., 2022; Dawe, 2011; Fisher et al., 2020; Fisher & Burton, 2021; Laurent et al., 2020), harvest block age and size (Fisher & Wilkinson, 2005; Lyon & Jensen, 1980; Visscher & Merrill, 2009), selective or partial harvesting methods (Nadeau Fortin et al., 2016; Vanderwel et al., 2009), response to herbicide-treated stands (Raymond et al., 1996; Thompson et al., 2003) and natural regeneration versus treated stands (Boan et al., 2011). Relationships between silviculture methods and available ungulate forage in harvest blocks (but not ungulate use of harvest blocks) have also been evaluated (Edwards et al., 2004; Lacascio et al., 1990; Lashley et al., 2011). Research within west-central Alberta has included analysis of pellet counts to investigate the response of ungulates to site preparation (scarification), block size and edge-to-area ratio (Stelfox et al., 1976; Tomm et al., 1981). However, to our knowledge, a comprehensive investigation of the response of deer, elk and moose to the multiple methods of site preparation, tree planting and stand tending currently applied in harvest blocks in west-central Alberta has not been previously completed. As such, our goal was to provide detailed and useful information for silviculture practices that could limit the distribution of deer, elk and moose in managed forests within caribou ranges.

We used camera traps, silviculture data, GIS-derived habitat and disturbance data, and detailed vegetation data collected at field sites to model the occurrence of elk, moose, mule deer and white-tailed deer (hereafter ungulates) in harvest blocks in west-central Alberta, Canada. We wanted to ensure that our results would be practical for forest management, so we consulted with forestry partners throughout the project, including project development, identifying

relevant covariates to include in our analysis and communication of results. Although we were interested in a general investigation of vegetation and landscape factors predicting occurrence of ungulates in harvest blocks, potential management actions in harvest blocks are directly related to silviculture practices. Therefore, our study objectives were to (i) investigate how site-specific characteristics (forage availability and forest stand characteristics) and characteristics of the surrounding area (habitat and anthropogenic disturbance) influence ungulate occurrence in harvest blocks, and (ii) investigate how site-specific silviculture treatments influence occurrence of ungulate species. Knowledge of how ungulates respond to current forest harvesting and silviculture practices could be used to inform future sustainable forest management in caribou ranges, benefiting caribou by limiting the distribution and abundance of ungulates and shared predators, contributing to long-term caribou conservation and boreal forest ecosystem function.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was within traditional and current lands of many Indigenous Peoples, including the Aseniwuche Winewak, Dane-zaa, Métis, Nehiyawak, Simpcw, Stoney and Tsuut'ina (best available information from Native-land.ca), and included the occupied ranges of the Narraway, Redrock Prairie Creek, A La Peche and Little Smoky caribou populations in west-central Alberta, buffered by 25 km (Figure 1). Caribou population estimates and 95% confidence limits (CLs) based on the most recently available information from the Government of Alberta include: A La Peche, 152 caribou (142–162); Narraway, 94 (38–75); Redrock Prairie Creek, 153 (CLs unavailable); and Little Smoky, 94 (69–129) (pers. comm. B. Nobert, July 28, 2022). The region is an intensively managed landscape with active natural resource extraction and includes areas of intact caribou habitat interspersed with large-scale natural disturbances (wildfires) and anthropogenic disturbances, including harvest blocks, below-ground pipelines, roads, seismic lines, and oil and gas wellsites. Forest management agreements in the region include ANC Timber Ltd., Canfor Corporation, Dunkley Lumber Ltd., Millar Western Forest Products Ltd., Norbord Inc., West Fraser Timber Co. Ltd. and Weyerhaeuser Company. 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). Ungulates within the study area include caribou, elk, moose, mule deer and white-tailed deer, with bighorn sheep *Ovis canadensis* and mountain goats *Oreamnos americanus* at higher elevations. Larger predators include black bears, cougars, coyotes *Canis latrans*, grizzly bears, lynx *Lynx canadensis*, wolverines *Gulo gulo* and wolves.

2.2 | Site selection and camera deployment

To select sites for camera deployment, we stratified harvest blocks within the study area by four age classes (0–10, 11–20, 21–30 and 31–50 years since harvest), ecosite type (three classes based on natural subregion, soil type and moisture regime), and the density of anthropogenic disturbance (harvest blocks, pipelines, roads, seismic lines and wellsites) surrounding each harvest block, defining three categories of disturbance density for stratification (low, medium and high) using natural breaks. We then randomly selected an equal number of study sites within each of the 36 age-ecosite-disturbance density strata. To increase the probability of independent detections (Tattersall et al., 2020; Tigner et al., 2014), we limited sites to harvest blocks ≥3 km apart, based on published mean daily movement rates and home ranges for elk and deer (D'eon & Serrouya, 2005; Fryxell et al., 2008; Webb et al., 2010).

Low wildlife detection rates at cameras can affect the sensitivity of camera studies, and many study designs include non-random placement of cameras on active wildlife trails to increase detections (Fisher & Burton, 2018; Rich et al., 2017; Shannon et al., 2014). However, the presence and quality of wildlife trails was inconsistent within harvest blocks in our study area, and non-random camera placement can bias results (Kolowski & Forrester, 2017). Consequently, we chose to generate study sites at harvest block centroids, setting up cameras (Browning Dark Ops HD Pro or Bushnell Trophy Cam) in clearings within 50 m of the centroid, using scent lure at camera sites to mitigate potentially low detection rates. Although the use of lure remains a topic of debate within camera trap research, lure can significantly improve detection rates for many wildlife species, and research suggests that landscape heterogeneity may have an equal or greater effect than lure on wildlife movement rates (Burton et al., 2015; Holinda et al., 2020; Stewart et al., 2019). We applied 28 g of O'Gorman's Long Distance Call scent lure in a tube secured 5 m in front of each camera and revisited each site within two to three months of set-up, at which time we reapplied 28 g of scent lure. Although the effect of the lure likely deteriorated over time, scent lure was applied consistently at all camera sites, and we consider the influence of lure on detection rates to be approximately equal across sites. Permission for use of scent lure at camera sites was granted by Alberta Environment and Parks (permits 19–526 and 20–114). We secured cameras onto trees or posts at a height of 1 m and programmed them 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) to monitor camera function. Most cameras 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
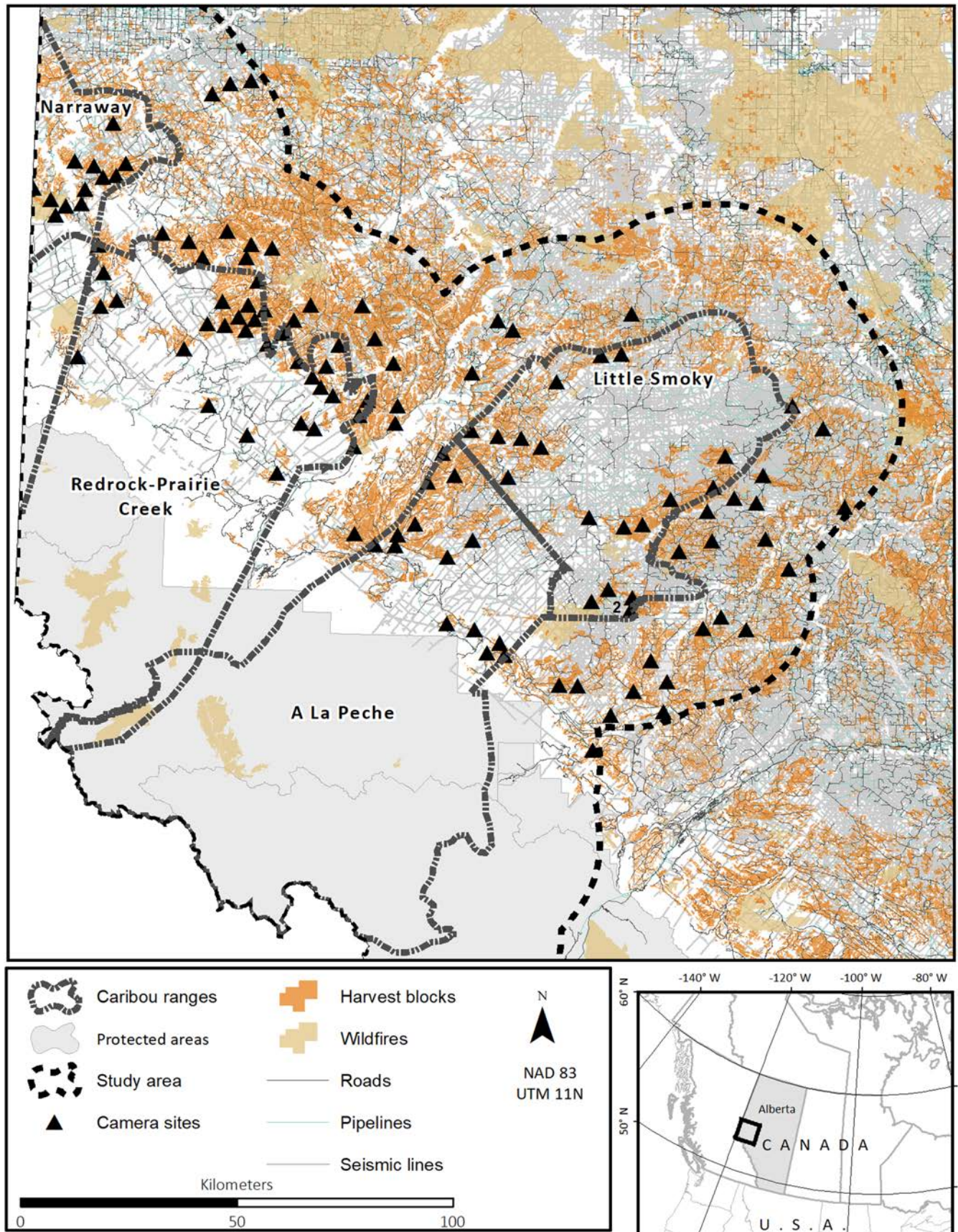
FIGURE 1 Map of study area in west-central Alberta, including study area boundary, caribou population ranges, harvest blocks, wildfires, linear features and locations of cameras deployed during 2018–2020. Inset indicates study area boundary within Alberta.

classified by trained personnel using TimeLapse2 Image Analyser software (Greenberg & Godin, 2013) following established guidelines to determine wildlife species.

2.3 | Field data collection

To measure forage, forest stand characteristics and hiding cover at each camera site, we established a 100m² vegetation sampling plot outside of each camera clearing, 5m due south of the camera location (Figure S1). Within 100m² plots, we measured diameter at breast height (DBH) for all trees present (Table S1), and recorded tree species composition and tree densities (stems/100m²) for trees ≥5cm DBH, and sapling species composition and sapling densities for trees <5cm DBH. We measured canopy cover using a spherical crown densiometer, and lateral (hiding) cover at two heights using a cover board (Coulombe et al., 2011). We established three 8m² subplots within each 100m² plot, within which we recorded percent cover of shrub species preferred by deer, elk and moose (Table S2; Stelfox et al., 1976; Strong & Gates, 2006; Visscher et al., 2006). We completed stem counts and basal diameter measurements of target shrub species, and we used these values to estimate available shrub biomass using equations from Visscher et al. (2006). Within each of the three 8m² plots, we established 1m² 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 72h and weighed to the nearest 0.01g.

2.4 | Covariates

Our analysis included covariates describing forest stand characteristics, forage, hiding cover, anthropogenic disturbance, surrounding habitat, terrain and silviculture characteristics (Tables 1 and 2). We obtained forest stand, forage and hiding cover data from field data collection as described in Section 2.3, calculating mean values across the three subplots at each site for shrub and herbaceous forage abundance and biomass. We derived anthropogenic disturbance densities from human footprint data obtained from the Alberta Biodiversity Monitoring Institute (ABMI, 2018) for harvest blocks, pipelines, roads, seismic lines and wellsites, and we calculated distances to the nearest pipeline, road and seismic line. For 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, 2017). We extracted elevation and slope values from a 30m×30m resolution digital elevation model (DEM). Wildlife responses to landscape characteristics are scale-dependent (DeCesare et al., 2012; D'eon & Serrouya, 2005; Kie et al., 2002), so we investigated the characteristics of the area surrounding each harvest block at two scales (1 and 5km radii) using a moving window analysis in ArcGIS. 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), including harvest block age (year of harvest), harvest block size and shape (i.e. area and perimeter to area ratio), site preparation, planting and stand tending data (Table 2).

2.5 | Data analysis

We treated wildlife detection events as independent when they occurred at least 30min apart (Murphy et al., 2021), and we used a 28-day survey occasion to generate detection histories for elk, moose, mule deer and white-tailed deer using 'detectionHistory' in camtrapR (Niedballa et al., 2016). For each survey occasion, we assigned each site a detection value of 1 if ≥1 photograph of the species was recorded during that survey occasion, and a detection value of 0 if the species was not recorded during that survey occasion. We defined two seasons (summer: 8 April–7 November, winter: 8 November–7 April) approximately equivalent to snow-free and snow periods in the study area, and summed detections by season and year for each site across survey occasions, with site-year as our sampling unit for each season. Camera malfunctions and changes in field of view (e.g. due to wildlife disturbing cameras) resulted in interruptions in deployment periods for several cameras and an unequal number of active camera trapping days across sites. We accounted for this by dividing the sum of detections for each site-season-year by the number of active camera days during that season-year at that site, and we used detections per 100 active camera days as our response variable (Burton et al., 2015; Caldwell & Klip, 2020). We define detections per 100 active camera days as the occurrence for each species-season, and we interpret occurrence as a measure of relative habitat use (Sun et al., 2021; Tattersall et al., 2020). We used Wilcoxon-rank-sum tests to compare detections per 100 active camera days in summer versus winter for each species.

Preliminary data exploration indicated that some habitat and disturbance covariates were closely related to silviculture covariates and could not be included in the same models in our analysis. For example, percent cover of vegetation species can be directly influenced by silviculture practices applied at a harvest block (Bell et al., 1997; Boan et al., 2011; Haeussler et al., 1999). The goal of this analysis was to relate vegetation, surrounding habitat and silviculture practices directly to wildlife use of harvest blocks, rather than to define the interrelationships of silviculture practices with vegetation and habitat, and forestry partners had previously identified several silviculture covariates as important for management decisions. To avoid eliminating these silviculture covariates during the model selection process and to allow for a detailed investigation of the relationships between silviculture practices and ungulate occurrence, we split our analysis into two parts: (1) ungulate occurrence in relation to habitat characteristics and anthropogenic disturbance at the harvest block and in the surrounding area, using the full dataset (n = 211 site-years; habitat models) and (2) ungulate occurrence in relation to site-specific silviculture characteristics and practices using

TABLE 1 Covariates considered in building habitat models assessing primary prey occurrence in harvest blocks in west-central Alberta, Canada during 2018–2020. Tree species and target shrub and herbaceous forage species measured are listed in Table S2.

Covariate group	Covariate	Range
Forest stand characteristics	Lodgepole pine (% of total)	0–100
	Spruce (black spruce + white spruce; % of total)	0–100
	Coniferous (% cover)	0–100
	Deciduous (% cover)	0–100
	Tree density, trees ≥5 cm DBH (stems/100 m^2)	0–0.70
	Canopy cover (%)	0–93
Forage: tree saplings	Total sapling density, saplings <5 cm DBH (stems/100 m^2)	0–7.99
	Total deciduous sapling density (stems/100 m^2)	0–6.72
	Deciduous saplings (%)	0–100
	Coniferous saplings (%)	0–100
Forage: shrubs	Target shrub species (% cover for each species)	0–80
	Other shrub species (% cover for all other species)	0–15
	Biomass of target shrub species (g/m^2)	0–304
Forage: herbaceous	Target forb species (% cover for each species)	0–73
	Carex spp. (% cover)	0–7
	Target grass species (% cover)	0–73
	All forbs (% cover)	0–98
	All grasses (% cover)	0–45
	Biomass (g/m^2)	0.6–279.6
Hiding cover	Lateral cover at 0–1 m height (%)	0.33–100
	Lateral cover at 1–2 m height (%)	0–100
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, 1 km radius (km/km^2)	0–3.34
	Density of pipelines, 5 km radius (km/km^2)	0–1.755
	Distance to nearest pipeline (m)	0–4276
	Density of roads, 1 km radius (km/km^2)	0–2.98
	Density of roads, 5 km radius (km/km^2)	0.207–1.220
	Distance to nearest road (m)	30–1284
	Density of seismic lines, 1 km radius (km/km^2)	0–6.268
	Density of seismic lines, 5 km radius (km/km^2)	0.241–5.362
	Distance to nearest seismic line (m)	0–2102
	Density of all linear features combined, 1 km radius (km/km^2)	0.243–8.437
	Density of all linear features combined, 5 km radius (km/km^2)	0.870–6.952
	Density of active wellsites, 1 km radius (wellsites/km^2)	0–0.757
	Density of active wellsites, 5 km radius (wellsites/km^2)	0–0.031
Surrounding habitat	Mean percent conifer within 1 km radius	11.2–10.0
	Mean percent conifer within 5 km radius	34.2–100
	Mean percent deciduous within 1 km radius	0–79.3
	Mean percent deciduous, 5 km radius	0–56.8
	Dominant derived ecosite phase within 1 and 5 km radius	Various
	Dominant nutrient regime, 1 and 5 km radius	Poor, medium, rich
	Mean forest stand age, 1 km radius (years)	36–196
	Mean forest stand age, 5 km radius (years)	58–179
Terrain	Elevation (m)	766–1590
	Slope (degrees)	0–25

TABLE 2 Covariates considered in building silviculture models assessing primary prey occurrence in harvest blocks in west-central Alberta, Canada during 2018–2020.

Category	Dataset	Covariates	Range
Harvest block age	Full dataset	Harvest block age (years since harvested)	3–48 years
	Full dataset	Harvest block ≤25 years	0 or 1
	Full dataset	Harvest block ≤10 years	0 or 1
Harvest block size and shape	Full dataset	Harvest block area	23,920–2,603,837 m^2
	Full dataset	Harvest block perimeter	1500–18,898 m
	Full dataset	Perimeter to area ratio	0.00009–0.03038 m/m^2
Site preparation	Full dataset	Site preparation after harvesting	0 or 1
	Site prep subset	Site preparation equipment/method	Various; see Table S3
	Site prep subset	Years since most recent site preparation	3–47 years
	Site prep subset	Area site prepped	0–181 ha
	Site prep subset	Number of site prep treatments	0–5 treatments
Planting	Full dataset	Block planted after harvesting	0 or 1
	Planting subset	Density of lodgepole pine planted	0–3205 stems/ha
	Planting subset	Density of black spruce planted	0–1747 stems/ha
	Planting subset	Density of white spruce planted	0–1962 stems/ha
	Planting subset	Total density of all trees planted	0–3456 stems/ha
	Planting subset	Years since most recent planting	2–45 years
	Planting subset	Number of times planted	0–5 planting dates
Stand tending	Full dataset	Stand tending after planting	0 or 1
	Tending subset	Mechanical stand tending	0 or 1
	Tending subset	Chemical stand tending	0 or 1
	Tending subset	Years since most recent stand tending	1 to 16 years
	Tending subset	Area stand tended	ha
	Tending subset	Number of stand tending applications	0–3 treatments
	Chemical subset	Herbicide application rate	0–6.02 L/ha
	Chemical subset	Chemical application method	Various, see below

data subsets (n=74–211 site-years, depending on the silviculture practice; silviculture models).

We fit generalized linear models in R using 'glm' from the LME4 package (Bates et al., 2015), completed model selection using 'dredge' and 'model.sel', standardized covariates in final models using 'stdize' from the MuMIn package (Barton, 2015) and tested covariates for correlation using Pearson's r and variance inflation factors (VIFs), setting a tolerance of $r < 0.5$ and VIF < 3.0. As we collected data across 3 years, interannual variation in local ungulate densities had the potential to influence the number of detections each year, and we compared models with and without year as a covariate for each species-season using Akaike's information criterion (AIC). For species-seasons where models with year had a better AIC ranking, we included year as a fixed effect in all models for that species-season.

2.5.1 | Habitat models

For habitat models, we investigated the influence of forest stand characteristics, forage, hiding cover and terrain at the site level, and anthropogenic disturbance and habitat in the surrounding area on occurrence of ungulate species (elk, moose, mule deer, white-tailed deer) by season (summer, winter). Our goal was to provide detailed results to forestry partners, and our dataset included field-collected vegetation data for multiple canopy layers (i.e. trees, shrubs and groundcover) and numerous individual plant species preferred by ungulates (Table S2) as well as GIS-derived habitat and disturbance data at multiple scales. As a result, our initial analysis considered many habitat covariates (>100) with the potential to influence ungulate occurrence in harvest blocks (Table 1). To reduce the initial list of covariates, we ran univariate models and screened out covariates if 90% confidence intervals for coefficients included zero. We then tested for correlation among remaining covariates, and if covariates were correlated, we compared univariate models using AIC and retained the covariate with the better AIC ranking. We included these final covariates in a global model, and we used dredge with models ranked by AIC to determine the final habitat model for each species and season, limiting the maximum number of covariates in final models to approximately

one covariate per ten detections for each species. We report coefficients from final models if 90% confidence intervals do not include zero.

2.5.2 | Silviculture models

For silviculture models, we investigated the influence of harvest block age, harvest block size and shape, site preparation (prep), planting and stand tending (tending) on occurrence of ungulate species (elk, moose, mule deer, white-tailed deer) by season (summer, winter). We used the full dataset ($n = 211$ site-years) to investigate the influence of block age, size, shape and whether a block had been prepped, planted and/or tended (Table 2, Figure S2). To investigate covariates specific to each of these silviculture practices, we generated three subsets of data (Figure S2) to include only those sites that had been prepped ($n = 102$ site-years), planted ($n = 175$) or tended ($n = 89$). To specifically investigate chemical stand tending covariates (e.g. herbicide application rate, herbicide application method), we further subset the stand tending dataset to include only those sites that had been chemically tended ($n = 74$). For each dataset, we ran univariate models for all covariates, and if 90% confidence intervals for coefficients did not include zero, we combined these covariates into final (global) silviculture models specific to each dataset (i.e. full dataset and for each subset). Where covariates were correlated but the influence of both covariates was potentially important for management actions (e.g. density of pine planted and total density of trees planted), we ran models separately, and we report results for both covariates. We report coefficients from final models if 90% confidence intervals do not include zero. As site prep included 17 different methods, we grouped site prep data into five categories (blade/plough, disk, drag, mounder and spot treatments) based on the nature and amount of disturbance (Haeussler et al., 2002; Table S3). Chemical application methods at study sites included aerial broadcast methods (chemical-aerial-broadcast, Accu-flo© or TVB©), chemical-aerial-highlight, and chemical completion reduction). We completed pair-wise comparisons between all mechanical site prep and chemical stand tending methods for each ungulate species and season and we report differences between methods as significant where $p < 0.10$ in pair-wise comparisons.

3 | RESULTS

The camera trapping period was from 5 June 2018 to 29 August 2020, including 22,963 active camera trapping days at 117 camera sites (211 site-years) in summer and 12,408 days at 98 sites (190 site-years) in winter. We report the total number of sites, site-years and 28-day survey occasions (28 days) with species detections and total detections per 100 active camera days (occurrence) for each species and season-year (Table 3). Occurrences (detections per 100 active camera days) of elk, moose, mule deer and white-tailed deer were significantly higher in summer than in winter ($p < 0.001$ for all Wilcoxon-rank-sum comparisons).

3.1 | Habitat models

During summer, elk, moose and white-tailed deer occurrence was higher in blocks with higher percent cover of *Calamagrostis canadensis*, and elk and white-tailed deer occurrence was lower with higher percent cover of *Cornus canadensis* (Table 4). Elk occurrence was also higher in blocks with a higher overall density of saplings, higher percentage of deciduous saplings, and a higher linear feature density in the surrounding area (5 km radius). Moose occurrence was higher in harvest blocks with higher percent cover of *Equisetum* spp. and *Salix* spp. and lower road densities in the surrounding area. Mule deer occurrence was higher in blocks with lower tree densities and lower lateral cover (0–1 m height), at higher elevations, on steeper slopes and further from roads. White-tailed deer occurrence was higher in blocks further from seismic lines and with a lower proportion of harvest blocks in the surrounding area (1 km radius).

During winter, moose occurrence and white-tailed deer occurrence was higher in blocks with a higher deciduous sapling density or overall sapling density (Table 4), and moose occurrence was also higher in blocks with greater biomass of *Salix* spp. and *Viburnum* spp. There were not enough detection events (Table 3) to build habitat models for elk or mule deer in winter.

3.2 | Silviculture models

During summer, elk, mule deer and white-tailed deer occurrence was higher in harvest blocks that were ≤10 years old (Table 5). Moose

TABLE 3 Total number of sites, site-years and 28-day survey occasions (28 days) with ≥1 detection, and detections per 100 active camera days (occurrence) by species and season, based on detection data from camera sites in 117 harvest blocks during summer and 98 harvest blocks during winter in west-central Alberta during 2018–2020.

Species	Summer				Winter			
	Sites	Site-years	28 days	Occurrence	Sites	Site-years	28 days	Occurrence
Elk	46	54	78	0.340	8	9	9	0.073
Moose	98	140	323	1.407	49	61	76	0.613
Mule deer	57	67	113	0.492	2	2	2	0.016
White-tailed deer	107	158	405	1.764	22	22	23	0.185

occurrence was higher in harvest blocks that had been planted multiple times, while mule deer occurrence was higher in harvest blocks that had not been stand tended. Mule deer and white-tailed deer occurrence was lower in blocks with higher densities of total trees and/or lodgepole pine planted, while elk occurrence was higher with higher densities of total trees or white spruce planted.

During winter, moose occurrence was higher in harvest blocks that were ≤25 years old (Table 5). There were not enough detection events (Table 3) to build silviculture models for elk or mule deer in winter, and white-tailed deer winter occurrence in harvest blocks was not predicted by silviculture covariates.

4 | DISCUSSION

We found seasonal differences in ungulate occurrence in harvest blocks and found that occurrence was influenced by site-specific characteristics, characteristics of the surrounding area and silviculture practices used at the blocks. This information could be used to inform forest management practices to reduce the distribution of ungulate species in managed forests within caribou ranges and to mitigate the ecosystem-level impacts of forest harvesting across the boreal forest of Canada.

4.1 | Seasonal occurrence in harvest blocks

For all four ungulate species (elk, moose, mule deer and white-tailed deer), occurrence in harvest blocks was higher in summer compared to winter, suggesting seasonal use of the available herbaceous forage in harvest blocks, as well as use of hiding cover that deciduous species provide in summer (Hewitt, 2011; Moen, 1978; Stelfox et al., 1976). In addition, lower winter use may be related to the deeper snowpack associated with harvest blocks when compared to intact forest stands, reducing access to woody browse and increasing movement costs (Schwab et al., 1987; Telfer & Kelsall, 1979; Visscher et al., 2006). Low winter use of harvest blocks by deer, moose, and elk has been observed previously in our study area (Stelfox et al., 1976). Caribou are exposed to increased predation risk in areas where they overlap with ungulates and shared predators (Latham et al., 2011;

TABLE 4 Covariates, standardized coefficients (β) and lower and upper 90% confidence limits (90% CI) for final summer and winter habitat models assessing ungulate use of harvest blocks, based on detection data from camera sites in 117 harvest blocks during summer and 98 blocks during winter in west-central Alberta during 2018–2020. Distances (e.g. 1 km) indicate the radius within which the covariate was measured. Habitat covariates are described in detail in Table 1.

Season/species	Covariates	β	90% CI	
Summer				
Elk	Sapling density	0.095	0.013	0.177
	% deciduous saplings	0.128	0.039	0.217
	% cover *Calamagrostis canadensis*	0.472	0.377	0.567
	% cover *Cornus canadensis*	−0.091	−0.168	−0.015
	Linear feature density (5 km)	0.122	0.040	0.203
Moose	% cover *Salix* spp.	0.268	0.135	0.400
	% cover *Calamagrostis canadensis*	0.175	0.007	0.343
	% cover *Equisetum* spp.	0.290	0.155	0.425
	Road density (1 km)	−0.188	−0.320	−0.055
Mule deer	Tree density	−0.114	−0.195	−0.032
	Lateral cover (0–1 m)	−0.092	−0.179	−0.005
	Elevation	0.154	0.070	0.239
	Slope	0.132	0.048	0.216
	Distance to road	0.653	0.152	1.155
White-tailed deer	% cover *Calamagrostis canadensis*	0.906	0.729	1.084
	% cover *Cornus canadensis*	−0.175	−0.321	−0.028
	Proportion harvest blocks (1 km)	−0.156	−0.309	−0.004
	Distance to seismic line	0.718	0.080	1.357
Winter				
Moose	Deciduous sapling density	0.667	0.420	0.914
	Salix spp. biomass	0.179	0.051	0.307
	Viburnum spp. biomass	0.467	0.265	0.670
White-tailed deer	Sapling density	0.766	0.635	0.897

Season/species	Covariate	β	90% CI	
Summer				
Elk	Harvest block <10 years	0.264	0.059	0.469
	Density white spruce planted	0.134	0.032	0.236
	Total density of all trees planted	0.149	0.014	0.285
Moose	Number of times planted	0.272	0.100	0.443
Mule deer	Harvest block ≤10 years	0.394	0.209	0.579
	Stand tending (0/1)	−0.289	−0.462	−0.116
	Density lodgepole pine planted	−0.114	−0.215	−0.014
	Total density of all trees planted	−0.147	−0.264	−0.030
White-tailed deer	Harvest block ≤10 years	0.379	0.003	0.755
	Density lodgepole pine planted	−0.274	−0.465	−0.083
Winter				
Moose	Harvest block ≤25 years	0.649	0.170	1.129

TABLE 5 Covariates, standardized coefficients (β) and lower and upper 90% confidence limits (90% CI) for final summer and winter silviculture models assessing ungulate occurrence in harvest blocks, based on detection data from camera sites in 117 harvest blocks in summer and 98 blocks in winter in west-central Alberta during 2018–2020. Silviculture covariates are described in detail in Table 2.

Mumma et al., 2018; Whittington et al., 2011), specifically during the summer (Seip, 1992; Serrouya et al., 2011; Wittmer et al., 2005) and fall migration periods (Blagdon & Johnson, 2021). Recent research in our study area found an increased probability of bear occupancy in harvest blocks that were occupied by deer, suggesting that harvest blocks may directly influence predator–prey dynamics (McKay & Finnegan, 2022). The seasonal differences in occurrence we observed in this study could indicate seasonal differences in the spatial overlap of ungulates, caribou, and predators in areas with harvest blocks, with an associated increased caribou predation risk during the summer. These results could have particular significance in the context of white-tailed deer range and population expansion in Alberta (Dawe & Boutin, 2016; Fisher & Burton, 2021).

4.2 | Habitat models

For habitat models, covariates predicting summer and winter occurrence in harvest blocks varied among ungulate species and included both site-specific forage availability and anthropogenic disturbance in the surrounding area. Specifically, we found that summer occurrence of elk, moose, and white-tailed deer was higher in harvest blocks with greater availability of *Calamagrostis canadensis*, and both elk and white-tailed deer occurrence was lower with higher percent cover of *Cornus canadensis*, while moose occurrence was higher with greater availability of *Equisetum* spp. and *Salix* spp. Summer occurrence of elk and winter occurrence of moose and white-tailed deer was also higher in blocks with greater availability of saplings, and winter moose occurrence was higher with greater biomass of *Salix* and *Viburnum* spp. These plant species are previously documented as preferred forage species for elk, moose and deer (Månsson et al., 2007; Strong & Gates, 2006; Visscher et al., 2006). While not surprising, this direct relationship between the amount of specific forage species and elk, moose and white-tailed deer occurrence in harvest blocks suggests that managing the abundance of specific vegetation species within blocks

could directly impact the use of harvest blocks by ungulates. In addition, these results confirm the importance of collecting detailed vegetation data at field sites to better understand links between wildlife use of disturbances and specific vegetation species (Serrouya & D'Eon, 2008).

White-tailed deer occurrence was lower in harvest blocks with higher harvest block densities in the surrounding area. 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 in west-central Alberta, Nielsen et al. (2017) reported that white-tailed deer abundance decreased with increasing harvest block density. While ungulate species generally select for early seral stands (Fisher & Wilkinson, 2005; Toews et al., 2018), our results suggest that at the landscape scale, ungulate occurrence in harvest blocks may be dependent on the availability of both old and young forest, consistent with previous findings that uneven-aged forests and large-scale habitat heterogeneity are important for predicting deer habitat selection and distribution (Kie et al., 2002; Nielsen et al., 2017; Wallmo & Schoen, 1980). These results indicate that forest stand age distribution at the landscape-scale has an influence on ungulate habitat use, an important consideration for land management and long-term forestry planning.

The influence of anthropogenic disturbance on occurrence in harvest blocks varied among ungulate species. While elk occurrence was higher in blocks with higher linear feature densities in the surrounding area, moose occurrence was lower in blocks with higher road densities, mule deer occurrence was higher further from roads and white-tailed deer occurrence was higher further from seismic lines. Our results are similar to previous research indicating moose avoid areas with higher road densities, mule deer avoid roads, and white-tailed deer avoid seismic lines (D'eon & Serrouya, 2005; Mumma et al., 2019; Toews et al., 2018). Again, these results further indicate the importance of the surrounding area in influencing ungulate use of harvest blocks at the site level and highlight that

local anthropogenic disturbance densities may be a relevant consideration in forestry planning.

4.3 | Silviculture models

We found that elk, mule deer, moose and white-tailed deer occurrence was higher in younger harvest blocks, consistent with results previously reported for moose and deer (Bowman et al., 2010; Fisher & Wilkinson, 2005; Toews et al., 2018), and likely related to greater forage availability in younger seral stands (Hewitt, 2011; Moen, 1978; Stelfox et al., 1976). Specifically, elk, mule deer and white-tailed deer summer occurrence was higher in blocks harvested within the previous 10 years, consistent with results previously reported for deer (Toews et al., 2018). These results are further indication that younger harvest blocks have more of an influence than older harvest blocks on altering local prey distribution and predator–prey dynamics, with likely cascading impacts on caribou predation risk in recently harvested areas (Boucher et al., 2022; Latham et al., 2011).

We also found that mule deer and white-tailed deer occurrence was lower in harvest blocks with higher planting densities of lodgepole pine. These results are likely explained by higher tree densities providing more canopy cover, resulting in less transmission of light to the understory and decreased abundance of herbaceous forage species (Hart & Chen, 2008; Lieffers et al., 1999; Lieffers & Stadt, 1994). We also found that mule deer occurrence was higher in harvest blocks that had not been stand tended. Stand tending involves the removal of competing vegetation, and harvest blocks that are tended have reduced availability of forage and browse species such as grasses, deciduous saplings, and shrubs (Ehrentraut & Branter, 1990; Pekin et al., 2014). Both planting and stand tending accelerate succession away from the deciduous habitat preferred by ungulates towards a conifer-dominated forest with less understory forage species (Boan et al., 2011), and our results suggest that silviculture methods resulting in higher pine densities with less competing vegetation could result in reduced use of harvest blocks by deer, moose and elk, due to the decreased forage availability.

4.4 | Study limitations

We recognize that our study had limitations. As our goal was to compare ungulate occurrence between harvest blocks, we did not employ a grid cell design across the study area but set up all camera sites within harvest blocks. As a result, we could not assess the relative use of harvest blocks by ungulates compared to other habitat types in our study area, and as such, we could not determine whether ungulate species selected or avoided harvest blocks. We experienced a high number of camera failures in winter due to extremely cold temperatures, and as occurrences were lower across species in the winter, we did not have enough data to model occurrences for elk or mule deer in winter. In addition, it is likely that the effect of lure was reduced in winter due to snow cover, and this may have contributed

to the lower detection rates we observed in winter. Finally, our study design did not allow for estimation of ungulate abundance or density. Particularly in the context of caribou conservation, ungulate densities would provide more direct information about the status of wildlife populations in the study area and how forestry practices influence predator–prey dynamics through changes in ungulate populations. Continuing advances in camera data analysis (e.g. Becker et al., 2022; Moeller et al., 2018) may allow for abundance or density estimations in the future.

5 | CONCLUSIONS

It is worth noting that we did not detect caribou at any of our harvest block camera sites during 2018–2020. Our results do not provide direct conclusions regarding caribou selection or avoidance of harvest blocks, but the lack of caribou occurrence in harvest blocks in our study further supports previous evidence that caribou avoid younger (i.e. <50 years since harvest) harvest blocks (Mumma et al., 2018; Peters et al., 2012; Smith et al., 2000).

Different silviculture treatments affect the abundance of specific forage species in regenerating harvest blocks (Bell et al., 1997; Cardoso et al., 2020; Wiensczyk et al., 2011), and we found that several forage species had a direct positive influence on the occurrence of elk, moose and white-tailed deer. These results suggest that using site preparation and stand tending methods to control specific vegetation species could decrease the occurrence of ungulate species in harvest blocks. Although not in the scope of our current study, future analysis of the direct relationships between silviculture treatments and vegetation abundance in our study area could provide useful information for management. We also found that higher planting densities of lodgepole pine decreased occurrence of mule deer and white-tailed deer in harvest blocks. The general goal of site preparation, planting and stand tending methods is to remove competing species, many of which are also ungulate forage, and to accelerate the establishment of commercial tree species (i.e. conifers) at adequate stocking densities (Government of Alberta, 2018). Caribou in the Narraway, Redrock Prairie Creek, A La Peche and Little Smoky populations select for conifer forests, including closed canopy lodgepole pine stands (DeCesare, 2012; Rudolph et al., 2019). Silviculture practices aimed at reducing specific ungulate forage species and establishing high densities of pine could meet forestry goals and reduce ungulate densities while restoring forests towards becoming functional caribou habitat. However, this management strategy would need to be balanced against other values on the landscape, including reducing the spread of mountain pine beetle and maintaining populations of culturally important species like moose (Government of Alberta, 2007; Popp et al., 2020).

Mitigating the impacts of habitat loss and alteration is essential to arrest global biodiversity loss (IPBES, 2019; United Nations, 2015). In a quickly changing boreal forest ecosystem (Curtis et al., 2018; Komers & Stanojevic, 2013; White et al., 2017), our study provides

detailed information on ungulate response to specific silviculture practices used in Alberta, Canada, directly linking wildlife occurrence to forestry practices. Translating this research into practical landscape management decisions could inform effective and forward-thinking sustainable forest management to benefit boreal biodiversity, including threatened species like caribou as well as culturally and economically important species like deer, moose and elk. Providing practical scientific information to inform forestry practices could help decision makers and land managers restore forest ecosystem function and increase the resilience of forest ecosystems and biodiversity to future change, including climate change (IPBES, 2019; United Nations, 2015).

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

DATA AVAILABILITY STATEMENT

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REFERENCES

ABMI. (2018). *Explore the status and trend of human footprint status by Alberta's natural regions*. https://abmi.ca/home/reports/2018/human-footprint/Natural-Regions

Achim, A., Moreau, G., Coops, N. C., Axelson, J. N., Barrette, J., Bédard, S., Byrne, K. E., Caspersen, J., Dick, A. R., D'Orangeville, L., Drolet, G., Eskelson, B. N. I., Filipescu, C. N., Flamand-Hubert, M., Goodbody, T. R. H., Griess, V. C., Hagerman, S. M., Keys, K., Lafleur, B., ... White, J. C. (2022). The changing culture of silviculture. *Forestry: An International Journal of Forest Research*, 95(2), 143–152. https://doi.org/10.1093/forestry/cpab047

Alberta Sustainable Resource Development. (2006a). *Alberta forest management planning standard version 4.1* (p. 114). https://open.alberta.ca/publications/3491799

Alberta Sustainable Resource Development. (2006b). *Appendix 9A-silviculture, C5 forest management plan 2006-2026* (p. 12). https://www1.agric.gov.ab.ca/$department/deptdocs.nsf/ba3468a2a8681f69872569d60073fde1/01d6ffc28fdeecac87257f6500003236/$FILE/Appendix9A-Silviculture.pdf

Armleder, H. M., & Stevenson, S. K. (1994). Using alternative silvicultural systems to integrate mountain caribou and timber management in British Columbia. *Rangifer*, 9, 141–148.

Barton, K. (2015). *MuMIn: Multi-model inference version*. 1.13.4. http://cran.r-project.org/package=MuMIn

Bates, D., Machler, M., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.

Becker, M., Huggard, D. J., Dickie, M., Warbington, C., Schieck, J., Herdman, E., Serrouya, R., & Boutin, S. (2022). Applying and testing a novel method to estimate animal density from motion-triggered cameras. *Ecosphere*, 13(4), 1–14. https://doi.org/10.1002/ecs2.4005

Bell, F. W., Lautenschlager, R. A., Wagner, R. G., Pitt, D. G., Hawkins, J. W. P., & Ride, K. R. (1997). Motor-manual, mechanical, and herbicide release affect early successional vegetation in northwestern Ontario. *The Forestry Chronicle*, 73(1), 61–68.

Blagdon, D., & Johnson, C. J. (2021). Short term, but high risk of predation for endangered mountain caribou during seasonal migration. *Biodiversity and Conservation*, 30(3), 719–739. https://doi.org/10.1007/s10531-021-02114-w

Boan, J. J., McLaren, B. E., & Malcolm, J. R. (2011). Influence of post-harvest silviculture on understory vegetation: Implications for forage in a multi-ungulate system. *Forest Ecology and Management*, 262(9), 1704–1712. https://doi.org/10.1016/j.foreco.2011.07.022

Boucher, N. P., Anderson, M., Ladle, A., Procter, C., Marshall, S., Kuzyk, G., Starzomski, B. M., & Fisher, J. T. (2022). Cumulative effects of widespread landscape change alter predator–prey dynamics. *Scientific Reports*, 12(1), 11692. https://doi.org/10.1038/s41598-022-15001-3

Bowman, J., Ray, J. C., Magoun, A. J., Johnson, D. S., & Dawson, F. N. (2010). Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. *Canadian Journal of Zoology*, *88*(5), 454–467. https://doi.org/10.1139/z10-019

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675–685. https://doi.org/10.1111/1365-2664.12432

Caldwell, M. R., & Klip, J. M. K. (2020). Wildlife interactions within highway underpasses. *The Journal of Wildlife Management*, *84*(2), 227–236. https://doi.org/10.1002/jwmg.21801

Cardoso, J. C., Burton, P. J., & Elkin, C. M. (2020). A disturbance ecology perspective on silvicultural site preparation. *Forests*, *11*(12), 1–12. https://doi.org/10.3390/f11121278

Coulombe, M. L., Huot, J., Massé, A., & Côté, S. D. (2011). Influence of forage biomass and cover on deer space use at a fine scale: A controlled-density experiment. *Ecoscience*, *18*(3), 262–272. https://doi.org/10.2980/18-3-3445

Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest loss. *Forest Ecology*, *361*, 1108–1111.

Darlington, S., Ladle, A., Burton, A. C., Volpe, J. P., & Fisher, J. T. (2022). Cumulative effects of human footprint, natural features and predation risk best predict seasonal resource selection by white-tailed deer. *Scientific Reports*, *12*(1), 1072. https://doi.org/10.1038/s41598-022-05018-z

Dawe, K. L. (2011). *Factors driving range expansion of white-tailed deer, Odocoileus virginianus, in the boreal forest of northern Alberta, Canada* [PhD dissertation]. University of Alberta.

Dawe, K. L., & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution*, *6*(18), 6435–6451. https://doi.org/10.1002/ece3.2316

DeCesare, N. J. (2012). *Resource selection, predation risk, and population dynamics of woodland caribou* [PhD dissertation]. University of Montana.

DeCesare, N. J., Hebblewhite, M., Robinson, H. S., & Musiani, M. (2010). Endangered, apparently: The role of apparent competition in endangered species conservation. *Animal Conservation*, *13*(4), 353–362. https://doi.org/10.1111/j.1469-1795.2009.00328.x

DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., Bradley, M., Whittington, J., Smith, K. G., Morgantini, L. E., Wheatley, M., & Musiani, M. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, *22*(4), 1068–1083.

D'eon, R. G., & Serrouya, R. (2005). Mule deer seasonal movements and multiscale resource selection using global positioning system radio-telemetry. *Journal of Mammalogy*, *86*(4), 736–744.

Edwards, S. L., Demarais, S., Watkins, B., & Strickland, B. K. (2004). White-tailed deer forage production in managed and unmanaged pine stands and summer food plots in Mississippi. *Wildlife Society Bulletin*, *32*(3), 739–745. https://doi.org/10.2193/0091-7648(2004)032[0739:WDFPIM]2.0.CO;2

Ehrentraut, G., & Branter, K. (1990). *Vegetation management by manual and mechanical means in Alberta boreal forests* (pp. 366–368). The Forestry Chronicle.

Environment Canada. (2014). *Recovery strategy for the woodland caribou, southern mountain population (Rangifer tarandus caribou) in Canada* (pp. 1–113). Environment Canada, Ottawa.

Fisher, J. T., & Burton, A. C. (2018). Wildlife winners and losers in an oil sands landscape. *Frontiers in Ecology and the Environment*, *16*(6), 323–328. https://doi.org/10.1002/fee.1807

Fisher, J. T., & Burton, A. C. (2021). Spatial structure of reproductive success infers mechanisms of ungulate invasion in Nearctic boreal landscapes. *Ecology and Evolution*, *11*(2), 900–911. https://doi.org/10.1002/ece3.7103

Fisher, J. T., Burton, A. C., Nolan, L., & Roy, L. (2020). Influences of landscape change and winter severity on invasive ungulate persistence in the Nearctic boreal forest. *Scientific Reports*, *10*(1), 8742. https://doi.org/10.1038/s41598-020-65385-3

Fisher, J. T., & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the north American boreal forest. *Mammal Review*, *35*(1), 51–81.

Fryxell, J. M., Hazell, M., Bö Rger A. L., Dalziel, B. D., Haydon, D. T., Morales, J. M., Mcintosh, T., & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19114–19119. www.pnas.org/cgi/doi/10.1073/pnas.0801737105

Government of Alberta. (2007). *Mountain pine beetle management strategy* (p. 20). https://open.alberta.ca/publications/9780778565468

Government of Alberta. (2017). *Derived ecosite phase* (*DEP*). https://open.alberta.ca/dataset/derived-ecosite-phase

Government of Alberta. (2018). *Reforestation standard of Alberta.* https://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/formain15749/$FILE/reforestation-standard-alberta-may1-2018.pdf

Greenberg, S., & Godin, T. (2013). *A tool supporting the extraction of angling effort data from remote camera images* (pp. 1–14). University of Calgary. https://doi.org/10.11575/PRISM/30646

Haeussler, S., Bedford, L., Boateng, J. O., & Mackinnon, A. (1999). Plant community responses to mechanical site preparation in northern interior British Columbia. *Canadian Journal of Forest Research*, *29*, 1084–1100.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., & Kranabetter, M. J. (2002). Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fennica*, *36*(1), 307–327.

Hart, S. A., & Chen, H. Y. H. (2008). Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. *Ecological Monographs*, *78*(1), 123–140. https://doi.org/10.1890/06-2140.1

Hervieux, D., Hebblewhite, M., DeCesare, N. J., Russell, M., Smith, K., Robertson, S., & Boutin, S. (2013). Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology*, *91*(12), 872–882. https://doi.org/10.1139/cjz-2013-0123

Hewitt, D. G. (2011). Nutrition. In *Biology and management of white-tailed deer* (pp. 75–106). CRC Press, Taylor & Francis Group.

Holinda, D., Burgar, J. M., & Burton, A. C. (2020). Effects of scent lure on camera trap detections vary across mammalian predator and prey species. *PLoS ONE*, *15*(5), e0229055. https://doi.org/10.1371/journal.pone.0229055

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem servcies of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (p. 60). IPBES.

Kearney, S. P., Coops, N. C., Stenhouse, G. B., Nielsen, S. E., Hermosilla, T., White, J. C., & Wulder, M. A. (2019). Grizzly bear selection of recently harvested forests is dependent on forest recovery rate and landscape composition. *Forest Ecology and Management*, *449*, 117459. https://doi.org/10.1016/j.foreco.2019.117459

Kie, J. G., Bowyer, R. T., Nicholson, M. C., Boroski, B. B., & Loft, E. R. (2002). Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology*, *83*(2), 530–544. https://doi.org/10.2307/2680033

Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PLoS ONE*, *12*(10), e0186679. https://doi.org/10.1371/journal.pone.0186679

Komers, P. E., & Stanojevic, Z. (2013). Rates of disturbance vary by data resolution: Implications for conservation schedules using the Alberta boreal forest as a case study. *Global Change Biology*, *19*(9), 2916–2928. https://doi.org/10.1111/gcb.12266

Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for bio-diversity and people. *Science, 362*(6412), eaau6020. https://doi.org/10.1126/science.aau6020

Lacascio, C. G., Lockaby, B. G., Caulfied, J. P., Edwards, M. B., & Causey, M. K. (1990). Influence of mechanical site preparation on deer forage in the Georgia Piedmont. *Southern Journal of Applied Forestry, 14*(2), 77–80. https://doi.org/10.1093/sjaf/14.2.77

Lashley, M. A., Harper, C. A., Bates, G. E., & Keyser, P. D. (2011). Forage availability for white-tailed deer following silvicultural treatments in hardwood forests. *The Journal of Wildlife Management, 75*(6), 1467–1476. https://doi.org/10.1002/jwmg.176

Latham, A. D. M., Latham, M. C., McCutchen, N. A., & Boutin, S. (2011). Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management, 75*(1), 204–212. https://doi.org/10.1002/jwmg.28

Laurent, M., Dickie, M., Becker, M., Serrouya, R., & Boutin, S. (2020). Evaluating the mechanisms of landscape change on white-tailed deer populations. *The Journal of Wildlife Management, 85*(2), 1–14. https://doi.org/10.1002/jwmg.21979

Lieffers, V. J., Messier, C., Burton, P. J., Ruel, J.-C., & Grover, B. E. (2003). *Nature-based silviculture for sustaining a variety of boreal forest values.* https://www.researchgate.net/publication/270342072

Lieffers, V. J., Messier, C., Stadt, K. J., Gendron, F., & Comeau, P. G. (1999). Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research, 29*, 796–811.

Lieffers, V. J., & Stadt, K. J. (1994). Growth of understory *Picea glauca, Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. *Canadian Journal of Forest Research, 24*(6), 1193–1198.

Lindenmayer, D. B. (2009). Forest wildlife management and conservation. *Annals of the New York Academy of Sciences, 1162*(1), 284–310.

Lyon, L. J., & Jensen, C. E. (1980). Management implications of elk and deer use of clear-cuts in Montana. *The Journal of Wildlife Management, 44*(2), 352. https://doi.org/10.2307/3807965

Månsson, J., Andrén, H., Pehrson, Å., & Bergstrom, R. (2007). Moose browsing and forage availability: A scale-dependent relationship? *Canadian Journal of Zoology, 85*(3), 372–380.

Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). The ravages of guns, nets, and bulldozers. *Nature, 536*, 143–145.

McKay, T. L., & Finnegan, L. A. (2022). Predator–prey co-occurrence in harvest blocks: Implications for caribou and forestry. *Conservation Science and Practice, 4*, 1–19. https://doi.org/10.1111/csp2.12847

McKay, T. L., & Finnegan, L. A. (2023). Data from: Ungulate occurrence in forest harvest blocks is influenced by forage availability, surrounding habitat, and silviculture practices. *Dryad Digital Repository.* https://doi.org/10.5061/dryad.vdncjsz03

McNay, R. S. (2011). Silviculture options for use in ranges designated for the conservation of northern caribou in British Columbia. *BC Journal of Ecosystems and Management, 12*(2), 55–73.

Moeller, A. K., Lukacs, P. M., & Horne, J. S. (2018). Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere, 9*(8), e02331. https://doi.org/10.1002/ecs2.2331

Moen, A. N. (1978). Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *The Journal of Wildlife Management, 42*(4), 715–738.

Muhly, T. B., Johnson, C. A., Hebblewhite, M., Neilson, E. W., Fortin, D., Fryxell, J. M., Latham, A. D. M., Latham, M. C., McLoughlin, P. D., Merrill, E., Paquet, P. C., Patterson, B. R., Schmiegelow, F., Scurrah, F., & Musiani, M. (2019). Functional response of wolves to human development across boreal North America. *Ecology and Evolution, 9*(18), 10801–10815. https://doi.org/10.1002/ece3.5600

Mumma, M. A., Gillingham, M. P., Johnson, C. J., & Parker, K. L. (2019). Functional responses to anthropogenic linear features in a complex predator-multi-prey system. *Landscape Ecology, 34*(11), 2575–2597. https://doi.org/10.1007/s10980-019-00905-9

Mumma, M. A., Gillingham, M. P., Parker, K. L., Johnson, C. J., & Watters, M. (2018). Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. *Biological Conservation, 228*, 215–223. https://doi.org/10.1016/j.biocon.2018.09.015

Murphy, A., Diefenbach, D. R., Ternent, M., & Lovallo, M. (2021). Threading the needle: How humans influence predator-prey spatiotemporal interactions in a multiple-predator system. *Journal of Animal Ecology, 90*, 2377–2390. https://doi.org/10.1111/1365-2656.13548

Nadeau Fortin, M. A., Sirois, L., & St-Laurent, M. H. (2016). Extensive forest management contributes to maintain suitable habitat characteristics for the endangered Atlantic-Gaspésie caribou. *Canadian Journal of Forest Research, 46*(7), 933–942. https://doi.org/10.1139/cjfr-2016-0038

Natural Regions Committee. (2006). *Natural regions and subregions of Alberta.* Government of Alberta.

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). CamtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution, 7*(12), 1457–1462.

Nielsen, S. E., Larsen, T. A., Stenhouse, G. B., & Coogan, S. C. P. (2017). Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore. *Oikos, 126*(3), 369–380. https://doi.org/10.1111/oik.03144

Pekin, B. K., Wisdom, M. J., Endress, B. A., Naylor, B. J., & Parks, C. G. (2014). Ungulate browsing maintains shrub diversity in the absence of episodic disturbance in seasonally-arid conifer forest. *PLoS ONE, 9*(1), e86288. https://doi.org/10.1371/journal.pone.0086288

Peters, W., Hebblewhite, M., Decesare, N., Cagnacci, F., & Musiani, M. (2012). Resource separation analysis with moose indicates threats to caribou in human altered landscapes. *Ecography, 35*, 1–12.

Popp, J. N., Priadka, P., Young, M., & Koch, K. (2020). Indigenous guardianship and moose monitoring: Weaving indigenous and western ways of knowing. *Human-Wildlife Interactions, 14*(2), 296–308.

Ray, J. C., Cichowski, D. B., St-Laurent, M.-H., Johnson, C. J., Petersen, S. D., & Thompson, I. D. (2015). Conservation status of caribou in the western mountains of Canada: Protections under the species at risk act, 2002–2014. *Rangifer, 35*(23), 49–80. https://doi.org/10.7557/2.35.2.3647

Raymond, K. S., Servello, F. A., Griffith, B., & Eschholz, W. E. (1996). Winter foraging ecology of moose on glyphosate-treated clearcuts in Maine. *The Journal of Wildlife Management, 60*(4), 753. https://doi.org/10.2307/3802374

Rich, L. N., Davis, C. L., Farris, Z. J., Miller, D. A. W., Tucker, J. M., Hamel, S., Farhadinia, M. S., Steenweg, R., Di Bitetti, M. S., Thapa, K., Kane, M. D., Sunarto, S., Robinson, N. P., Paviolo, A., Cruz, P., Martins, Q., Gholikhani, N., Taktehrani, A., Whittington, J., … Kelly, M. J. (2017). Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. *Global Ecology and Biogeography, 26*(8), 918–929. https://doi.org/10.1111/geb.12600

Rocha-Santos, L., Pessoa, M. S., Cassano, C. R., Talora, D. C., Orihuela, R. L. L., Mariano-Neto, E., Morante-Filho, J. C., Faria, D., & Cazetta, E. (2016). The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. *Biological Conservation, 196*, 1–9. https://doi.org/10.1016/j.biocon.2016.01.028

Rudolph, T. D., MacNearney, D., & Finnegan, L. (2019). Lost in translation? Insights into caribou habitat selection from forest inventory data. *Facets, 2019*(4), 531–550. https://doi.org/10.1139/facets-2018-0050

Schwab, F., Pitt, M. D., & Schwab, S. W. (1987). Browse burial related to snow depth and canopy cover in northcentral British Columbia. *The Journal of Wildlife Management, 51*(2), 337–342.

Seip, D. (1992). Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology, 70*, 1494–1503.

Serrouya, R., & D'Eon, R. G. (2008). The influence of forest cover on mule deer habitat selection, diet, and nutrition during winter in a deep-snow ecosystem. *Forest Ecology and Management*, *256*(3), 452–461. https://doi.org/10.1016/j.foreco.2008.04.048

Serrouya, R., Dickie, M., Lamb, C., Van Oort, H., Kelly, A. P., Demars, C., McLoughlin, P. D., Larter, N. C., Hervieux, D., Ford, A. T., & Boutin, S. (2021). Trophic consequences of terrestrial eutrophication for a threatened ungulate. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1943), 20202811. https://doi.org/10.1098/rspb.2020.2811

Serrouya, R., McLellan, B. N., Boutin, S., Seip, D. R., & Nielsen, S. E. (2011). Developing a population target for an overabundant ungulate for ecosystem restoration: Restoring a predator-prey system. *Journal of Applied Ecology*, *48*(4), 935–942. https://doi.org/10.1111/j.1365-2664.2011.01998.x

Serrouya, R., McLellan, B. N., van Oort, H., Mowat, G., & Boutin, S. (2017). Experimental moose reduction lowers wolf density and stops decline of endangered caribou. *PeerJ*, *8*, e3736. https://doi.org/10.7717/peerj.3736

Serrouya, R., Seip, D. R., Hervieux, D., McLellan, B. N., McNay, R. S., Steenweg, R., Heard, D. C., Hebblewhite, M., Gillingham, M., & Boutin, S. (2019). Saving endangered species using adaptive management. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(13), 6181–6186. https://doi.org/10.1073/pnas.1816923116

Shannon, G., Lewis, J. S., & Gerber, B. D. (2014). Recommended survey designs for occupancy modelling using motion-activated cameras: Insights from empirical wildlife data. *PeerJ*, *2014*(1), e532. https://doi.org/10.7717/peerj.532

Smith, K. G., Ficht, E. J., Hobson, D., Sorensen, T. C., & Hervieux, D. (2000). Winter distribution of woodland caribou in relation to clearcut logging in west-central Alberta. *Canadian Journal of Zoology*, *78*, 1433–1440.

Spathelf, P., Stanturf, J., Kleine, M., Jandl, R., Chiatante, D., & Bolte, A. (2018). Adaptive measures: Integrating adaptive forest management and forest landscape restoration. *Annals of Forest Science*, *75*(2), 55. https://doi.org/10.1007/s13595-018-0736-4

Stelfox, J. G., Lynch, G. M., & McGillis, J. R. (1976). *Effects of clearcut logging on wild ungulates in the central Albertan foothills* (pp. 65–70). The Forestry Chronicle.

Stewart, F. E. C., Volpe, J. P., & Fisher, J. T. (2019). The debate about bait: A red herring in wildlife research. *The Journal of Wildlife Management*, *83*(4), 985–992. https://doi.org/10.1002/jwmg.21657

Stone, I., Ouellet, J. P., Sirois, L., Arseneau, M. J., & St-Laurent, M. H. (2008). Impacts of silvicultural treatments on arboreal lichen biomass in balsam fir stands on Québec's Gaspé Peninsula: Implications for a relict caribou herd. *Forest Ecology and Management*, *255*(7), 2733–2742. https://doi.org/10.1016/j.foreco.2008.01.040

Strong, W. L., & Gates, C. C. (2006). Herbicide-induced changes to ungulate forage habitat in western Alberta, Canada. *Forest Ecology and Management*, *222*(1–3), 469–475. https://doi.org/10.1016/j.foreco.2005.10.036

Sun, C., Beirne, C., Burgar, J. M., Howey, T., Fisher, J. T., & Burton, A. C. (2021). Simultaneous monitoring of vegetation dynamics and wildlife activity with camera traps to assess habitat change. *Remote Sensing in Ecology and Conservation*, *7*(4), 666–684. https://doi.org/10.1002/rse2.222

Tattersall, E. R., Burgar, J. M., Fisher, J. T., & Burton, A. C. (2020). Boreal predator co-occurrences reveal shared use of seismic lines in a working landscape. *Ecology and Evolution*, *10*(3), 1678–1691. https://doi.org/10.1002/ece3.6028

Telfer, E. S., & Kelsall, J. P. (1979). Studies of morphological parameters affecting ungulate locomotion in snow. *Canadian Journal of Zoology*, *57*, 2153–2159.

Thompson, I. D., Baker, J. A., & Ter-Mikaelian, M. (2003). A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. *Forest Ecology and Management*, *177*, 441–469.

Tigner, J., Bayne, E. M., & Boutin, S. (2014). Black bear use of seismic lines in northern Canada. *The Journal of Wildlife Management*, *78*(2), 282–292. https://doi.org/10.1002/jwmg.664

Toews, M., Juanes, F., & Burton, A. C. (2018). Mammal responses to the human footprint vary across species and stressors. *Journal of Environmental Management*, *217*, 690–699. https://doi.org/10.1016/j.jenvman.2018.04.009

Tomm, H. O., Beck, J. A., Jr., & Hudson, R. J. (1981). Responses of wild ungulates to logging practices in Alberta. *Canadian Journal of Forestry Research*, *11*, 606–614.

United Nations. (2015). *Transforming our world: The 2030 agenda for sustainable development* (A/RES/70/1).

Vanderwel, M. C., Mills, S. C., & Malcolm, J. R. (2009). Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. *The Forestry Chronicle*, *85*(1), 91–104. https://doi.org/10.5558/tfc85091-1

Visscher, D. R., & Merrill, E. H. (2009). Temporal dynamics of forage succession for elk at two scales: Implications of forest management. *Forest Ecology and Management*, *257*(1), 96–106. https://doi.org/10.1016/j.foreco.2008.08.018

Visscher, D. R., Merrill, E. H., Fortin, D., & Frair, J. L. (2006). Estimating woody browse availability for ungulates at increasing snow depths. *Forest Ecology and Management*, *222*(1–3), 348–354. https://doi.org/10.1016/j.foreco.2005.10.035

Vors, L. S., & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global Change Biology*, *15*(11), 2626–2633. https://doi.org/10.1111/j.1365-2486.2009.01974.x

Wagner, R. G., Little, K. M., Richardson, B., & McNabb, K. (2006). The role of vegetation management for enhancing productivity of the world's forests. *Forestry*, *79*(1 Spec. Iss), 57–79. https://doi.org/10.1093/forestry/cpi057

Wallmo, O. C., & Schoen, J. W. (1980). Response of deer to secondary forest succession in Southeast Alaska. *Forest Science*, *26*(3), 448–462.

Webb, S. L., Gee, K. L., Strickland, B. K., Demarais, S., & Deyoung, R. W. (2010). Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. *International Journal of Ecology.*, *2010*, 1–12. https://doi.org/10.1155/2010/459610

White, J. C., Wulder, M. A., Hermosilla, T., Coops, N. C., & Hobart, G. W. (2017). A nationwide annual characterization of 25 years of forest disturbance and recovery for Canada using Landsat time series. *Remote Sensing of Environment*, *194*, 303–321. https://doi.org/10.1016/j.rse.2017.03.035

Whittington, J., Hebblewhite, M., DeCesare, N. J., Neufeld, L., Bradley, M., Wilmshurst, J., & Musiani, M. (2011). Caribou encounters with wolves increase near roads and trails: A time-to-event approach: Wolf-caribou encounter rates. *Journal of Applied Ecology*, *48*(6), 1535–1542. https://doi.org/10.1111/j.1365-2664.2011.02043.x

Wiensczyk, A., Swift, K., Morneault, A., Thiffault, N., Szuba, K., & Bell, F. W. (2011). An overview of the efficacy of vegetation management alternatives for conifer regeneration in boreal forests. *The Forestry Chronicle*, *87*(2), 175–200.

Wittmer, H. U., McLellan, B. N., Seip, D. R., Young, J. A., Kinley, T. A., Watts, G. S., & Hamilton, D. (2005). Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology*, *83*(3), 407–418. https://doi.org/10.1139/z05-034

Young, H. S., McCauley, D. J., Galetti, M., & Dirzo, R. (2016). Patterns, causes, and consequences of Anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics*, *47*, 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142

SUPPORTING INFORMATION

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

Figure S1. 100 m^2 vegetation sampling plot and 8 and 1 m^2 subplots used to measure forest stand characteristics, hiding cover, and available forage at camera sites, 5 m due south of each camera location. Within 100 m^2 plots, we measured diameter at breast height (DBH) for all trees (≥5 cm DBH) present, recorded tree species composition and tree densities (stems/100 m^2), and sapling species composition and sapling densities for tree species <5 cm DBH. Within 8 m^2 subplots we recorded percent cover, stem counts, and basal diameters of target shrub species (Table S2). Within 1m^2 subplots we recorded percent cover of target herbaceous species (Table S2) and collected herbaceous biomass samples.

Figure S2. Datasets and subsets included in analysis of habitat and silviculture covariates.

Table S1. Tree species recorded at vegetation plots in 117 harvest blocks in west-central Alberta, Canada during 2018–2020. For the purposes of analysis, Tamarack (*Larix laricina*) were considered as coniferous species.

Table S2. Target forage species preferred by deer, elk and moose, recorded at vegetation plots in 117 harvest blocks in west-central Alberta, Canada during 2018–2020.

Table S3. Mechanical site prep equipment and methods used at study sites in harvest blocks in west-central Alberta, Canada during 2018–2020. Methods were grouped into categories based on the nature and amount of disturbance of each method.