

## ARTICLE

# Whose line is it anyway? Moose (*Alces alces*) response to linear features

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**Handling Editor:** Joseph D. Holbrook**Abstract**

Linear features are pervasive across the boreal forest of Canada, negatively impacting several wildlife species. Understanding how wildlife responds to different types and characteristics of linear features is necessary for coordinated landscape restoration. Currently, linear feature restoration is focused on recovering threatened woodland caribou (*Rangifer tarandus*) which may have unintended impacts on other boreal species like moose (*Alces alces*). Understanding how moose respond to different linear features can help ensure restoration is targeted and effective. We used GPS data from seven moose collected between 2008 and 2010 to investigate response to linear features and to determine how moose response was influenced by characteristics of linear features like the surrounding habitat and regeneration. At the landscape scale, moose selected areas closer to seismic lines when they were in areas with lower densities of seismic lines and higher densities of harvest blocks and wildfires. This response was stronger during winter. Moose selected areas closer to pipelines when they were in areas with lower densities of other linear features, harvest blocks, and wildfires and were indifferent to roads at the population-level. At the fine scale, during winter, moose selected areas closer to seismic lines regardless of vegetation height or the surrounding habitat, but were indifferent to seismic lines during summer, and were indifferent to roads and pipelines during summer and winter. Combined, our results suggest that there are characteristics of seismic lines which make them attractive to moose regardless of the regeneration height on the seismic lines, providing further evidence that effective linear feature restoration will need to address the fact that linear features increase landscape permeability and provide forage for multiple boreal wildlife species. Our results also further illustrate the importance of considering how linear feature restoration efforts focused on caribou may shift the distribution of other boreal wildlife species. Ultimately, conservation efforts for threatened species should recognize that conservation efforts focused on one species may have unintended consequences for interacting species.

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## KEYWORDS

boreal forest, caribou, habitat disturbance, LiDAR, linear features, moose, restoration

## INTRODUCTION

Linear features (roads, pipelines, seismic lines, powerlines, hydrolines, and railways) are some of the most pervasive disturbances across the boreal forest of Canada (Pasher et al., 2013). In comparison with polygonal disturbances created by wildfires and forestry, the geographic footprint of linear features is small; however, as they are widespread (>600,000 km; Pasher et al., 2013) and occur at high densities (up to 40 km/km<sup>2</sup>; Stern et al., 2018), they have significant effects on forest fragmentation, contributing to 80% of forest edges (Pattison et al., 2016). Linear features impact the distribution and abundance of lichens, nonvascular and vascular plants (Finnegan, MacNearney, et al., 2018; MacDonald et al., 2020), as well as the distribution and movements of invertebrates and vertebrates (Machtans, 2006; Riva et al., 2018). Notably, linear features have had significant effects on the distribution and movements of large boreal mammals (Dickie et al., 2020; Dyer et al., 2002; Finnegan, Pigeon, et al., 2018), causing cascading impacts on predator–prey dynamics (DeMars & Boutin, 2018; Mumma et al., 2018). Coordinated landscape planning and restoration of linear features that consider ecosystem processes and the ecological function of individual species are required to re-establish healthy ecosystems that support multiple boreal species (Akçakaya et al., 2020; Soulé et al., 2005).

Moose (*Alces alces*) occur across the Canadian boreal forest with fluctuating local populations (Kuzyk et al., 2018; Priadka et al., 2022; Timmermann & Rodgers, 2017). Localized population differences have been attributed to the interacting effects of habitat and climate change, which have changed moose distribution and density and also changed moose mortality risk from hunters, predators, and pathogens (Murray et al., 2006; Parlee et al., 2012; Timmermann & Rodgers, 2017). While moose generally benefit from early seral vegetation (e.g., abundant forbs and shrubs) produced after disturbance (i.e., forage; Rempel et al., 1997; Serrouya et al., 2021), their response to early seral habitat created by wildfires and forest harvesting is hierarchical, varies at broad scales relative to the surrounding habitat matrix, and at fine scales relative to the characteristics and age of disturbances (Francis et al., 2021; Maier et al., 2005; McKay & Finnegan, 2022; Mumma et al., 2021). Moose response to linear features is even more variable: linear features provide forage (Finnegan, MacNearney, et al., 2018; MacDonald et al., 2020; St-Pierre et al., 2022),

specifically they provide forage adjacent to mature forest with thermal shelter (van Beest et al., 2012), greater snow interception during winter (Droghini & Boutin, 2017), and refuge from predators (Kunkel & Pletscher, 2000). However, they may also act as ecological traps by increasing moose mortality risk via encounters with vehicles, human hunters, and predators (Eldegard et al., 2012; Francis et al., 2021; LeBlanc et al., 2011). Although moose response to roads has been the focus of previous research (e.g., Bartzke et al., 2015; Eldegard et al., 2012; Yost & Wright, 2001), there has been limited research on their response to pipelines and seismic lines. In British Columbia, moose had a weak response to seismic lines, although females selected seismic lines during summer, and males selected seismic lines during winter (Mumma et al., 2019). In Alberta, moose avoided seismic lines and pipelines during summer (Dickie et al., 2020). Because of differences in machinery and soil compaction during construction, differences in width (roads 20–30 m; pipelines 20 m; seismic lines 5–10 m), and differences in ongoing maintenance (roads are free of vegetation; pipelines are maintained with low vegetation; seismic lines are not maintained) (Alberta Energy Regulator, 2016; Pattison et al., 2016), the roads, pipelines, and seismic lines transecting the boreal forest are quite different from one another, with differing vegetation and wildlife responses (Dickie, Serrouya, McNay, et al., 2017; Finnegan, MacNearney, et al., 2018; MacDonald et al., 2020). Teasing out how moose respond to different linear features is relevant because pipelines and seismic lines are the most ubiquitous linear features in the boreal forest of western Canada, and they are the focus of ongoing restoration activities to conserve woodland caribou (*Rangifer tarandus*, hereafter caribou) (Dickie et al., 2021; Government of Alberta, 2017; Tattersall et al., 2020). Understanding the specifics of how moose respond to seismic lines and pipelines can help ensure restoration efforts are targeted and effective.

Caribou, moose, and linear features are linked through the positive impacts of linear features on shared predators of caribou and moose—primarily wolves (*Canis lupus*) (but also black bears [*Ursus americanus*] and grizzly bears [*Ursus arctos*]). The ultimate cause of caribou declines is habitat disturbance (Environment Canada, 2012)—early seral forage available after disturbance drives a numerical response in moose, deer (*Odocoileus virginianus* and *O. hemionus*), and elk (*Cervus elaphus*) and a numerical response in the shared predators of moose, deer, elk, and caribou. Linear

features also facilitate predator movement (Dickie, Serrouya, McNay, et al., 2017; Finnegan, Pigeon, et al., 2018), so disturbance increases overlap between caribou and predators, decreasing caribou survival (Mumma et al., 2017, 2018; Wittmer et al., 2005). Although the geographic footprint of linear features means that in comparison with polygonal disturbances, their contribution to the numerical response of moose is likely minimal, we know that moose use linear features to access forage and/or for movement (St-Pierre et al., 2022; Tattersall et al., 2023), and we know wolves follow their prey (Gasway et al., 1989). Correspondingly, caribou are at increased predation risk where they co-occur with moose (James et al., 2004; Peters et al., 2013) and when they are close to linear features (McKay et al., 2021; Mumma et al., 2017). Polygonal and linear disturbances combinedly contribute to caribou declines via apparent competition between caribou and moose, deer, and elk (DeCesare et al., 2010; Serrouya et al., 2021).

To address the impacts of habitat disturbance on caribou populations, caribou recovery efforts include addressing the proximate causes of declines by increasing calf survival and managing populations of predators and primary prey like moose (Hervieux et al., 2014; McNay et al., 2022; Serrouya et al., 2017) and addressing the ultimate cause of declines by restoring habitat, primarily linear features (Dickie et al., 2021; Lacerte et al., 2021; Tattersall et al., 2020). Predator and prey management can be controversial (Johnson et al., 2022), particularly when actions target culturally important species like moose which are themselves declining in some areas (Parlee et al., 2012; Timmermann & Rodgers, 2017). Long-term solutions for caribou conservation will require coordinated landscape planning and restoration, including restoration of linear features (Nagy-Reis et al., 2021). Recognizing the relationships between caribou, moose, and wolves and the need to recover caribou while maintaining moose populations, restoration efforts that reduce moose use of linear features and aim to re-establish spatial separation of caribou from moose and wolves could benefit caribou and moose. To achieve this, restoration of linear features will have to accomplish functional (predator movement) and structural (vegetation composition) restoration (Ray, 2014) and will need to consider the combined impacts of linear features, linear feature restoration, and the surrounding habitat matrix on habitat use by predators, caribou, and other wildlife species.

The goal of our study was to build upon previous research that provided insights into the relationships between characteristics of linear features, the surrounding habitat matrix, and wildlife response (Dickie, Serrouya, DeMars, et al., 2017; Finnegan, Pigeon, et al., 2018; Muhly et al., 2019; St-Pierre et al., 2022) and focus on providing

information that could be used to inform linear feature restoration looking beyond predator responses. We used GPS data from moose collected between 2008 and 2010 to investigate moose response to three different types of linear features (roads, pipelines, and seismic lines). At the landscape scale, our goal was to assess whether moose, like wolves (Pigeon et al., 2020), had a functional response to linear features in our study area. However, we were also interested in gaining a mechanistic understanding of the drivers behind moose response to linear features in our study area. Specifically, if moose are selecting linear features, are they likely using them for travel (i.e., only responding when there are low densities of linear features available to use as travel routes on the landscape), as a source of forage (i.e., only selecting linear features where there are low densities of polygonal disturbances preferred by moose for forage), or for other reasons (i.e., selecting linear features because of the characteristics of the linear features themselves—combined access to forage, travel, shelter, refuge from predators)? For this, we assessed proximity of moose to seismic lines, pipelines, and roads in relation to the surrounding (1) densities of seismic lines, pipelines, or roads, respectively, (2) densities of other linear features (i.e., within seismic line models “other” linear features included pipelines and roads), and (3) densities of polygonal disturbances (harvest blocks and wildfires <25 years old). As these models assessed habitat selection in relation to the changing availability of linear features and polygonal disturbances, we consider them functional response models (Mysterud & Ims, 1998), although we defined availability at a local scale (Malcolm et al., 2020; Pigeon et al., 2020), rather than at the home-range scale (Muhly et al., 2019). At a fine scale, our goal was to assess how moose proximity to linear features changed as a function of the characteristics of the linear feature like the surrounding habitat, depth to water under the linear feature (a proxy for vegetation growth), and vegetation height (seismic lines only). Understanding how moose response to linear features varies as function of the surrounding habitat matrix, regeneration, and depth to water at the disturbance, when combined with existing knowledge on predator response (Dickie, Serrouya, DeMars, et al., 2017; Finnegan, Pigeon, et al., 2018; Pigeon et al., 2020), will help prioritize linear feature restoration at fine and landscape scales, which considers the ecological needs of caribou and moose.

## METHODS

### Study area

The study area was within the homelands of several Indigenous peoples including the Aseniwuche Winewak,

Dane-zaa, Nehiyawak, Métis, Simpcw, Stoney, and Tsuut'ina (best available knowledge from [native-land.ca](http://native-land.ca)) in west-central Alberta, Canada (Figure 1). The study area included the ranges of one boreal caribou population (Little Smoky), three central mountain caribou populations (A La Pêche, Narraway, and Redrock-Prairie Creek), and intersected with the subalpine, upper foothills, and lower foothills natural subregions (Natural Regions Committee, 2006). Forests within the study area are primarily coniferous, with lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*) in uplands and black spruce (*Picea mariana*), larch (*Larix laricina*), and poorly drained muskeg in lowlands (Natural Regions Committee, 2006). Ungulates within the study area include caribou, moose, white-tailed deer, mule deer, and elk. The primary predators of caribou in this area are grizzly bears, black bears, cougars (*Puma concolor*), and wolves, and additional predators include lynx (*Lynx canadensis*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*). Anthropogenic disturbances within the study area include forest harvest blocks, well sites, below-ground pipelines, roads, and seismic lines, while natural disturbances include wildfires and mountain pine beetle kill. Disturbance densities differ across the study area but are generally higher in the east (Figure 1).

## Animal location data

We used GPS telemetry data collected from adult moose captured and collared by the Government of Alberta and the University of Montana (ATS G2000 GPS collars; Advanced Telemetry Systems, Isanti, MN, USA) between 2008 and 2010. Capture and handling protocols were approved by the University of Montana Animal Care and Use Protocol 056-56MHECS-010207 and 059-09MHWB-122109 and by Alberta Sustainable Resource Development licenses no. 21803, 27086, 27088, 27090. Collars were programmed to record positional fixes at 4-h intervals. To account for the seasonal importance of different resources, we partitioned GPS collar locations into “winter” (17 October–15 May) or “summer” (16 May–16 October) following Peters et al. (2013). Because the focus of our study was to understand moose response to anthropogenic habitat disturbance which is focused in the foothills of the study area (Figure 1), we only included moose that had >50% of their locations in the lower and/or upper foothills natural subregions (“foothills moose” as defined by Peters et al., 2013). The final dataset consisted of 20,911 locations (12,069 winter; 8842 summer) from 7 moose (3 female [winter: 6 individual-years; summer: 3 individual-years], 4 male [winter: 8 individual-years; summer: 4 individual-years]; Appendix S1: Table S1).

## Data analysis

For landscape-scale habitat selection analysis, we used individual generalized linear models (GLM) to build seasonal resource selection functions (RSFs) at the home-range scale which compared the habitat that moose used with that which was available to them (Manly et al., 2002). For fine-scale habitat selection analysis, we again compared habitat that moose used with that which was available to them but applied step selection functions (SSFs) instead of RSFs. SSFs constrain availability to locations that moose could have selected based on their location and the distance and directionality of actual moose steps (distance and direction between consecutive moose locations), rather than locations randomly disturbed across the entirety of the moose seasonal range (Fortin et al., 2005).

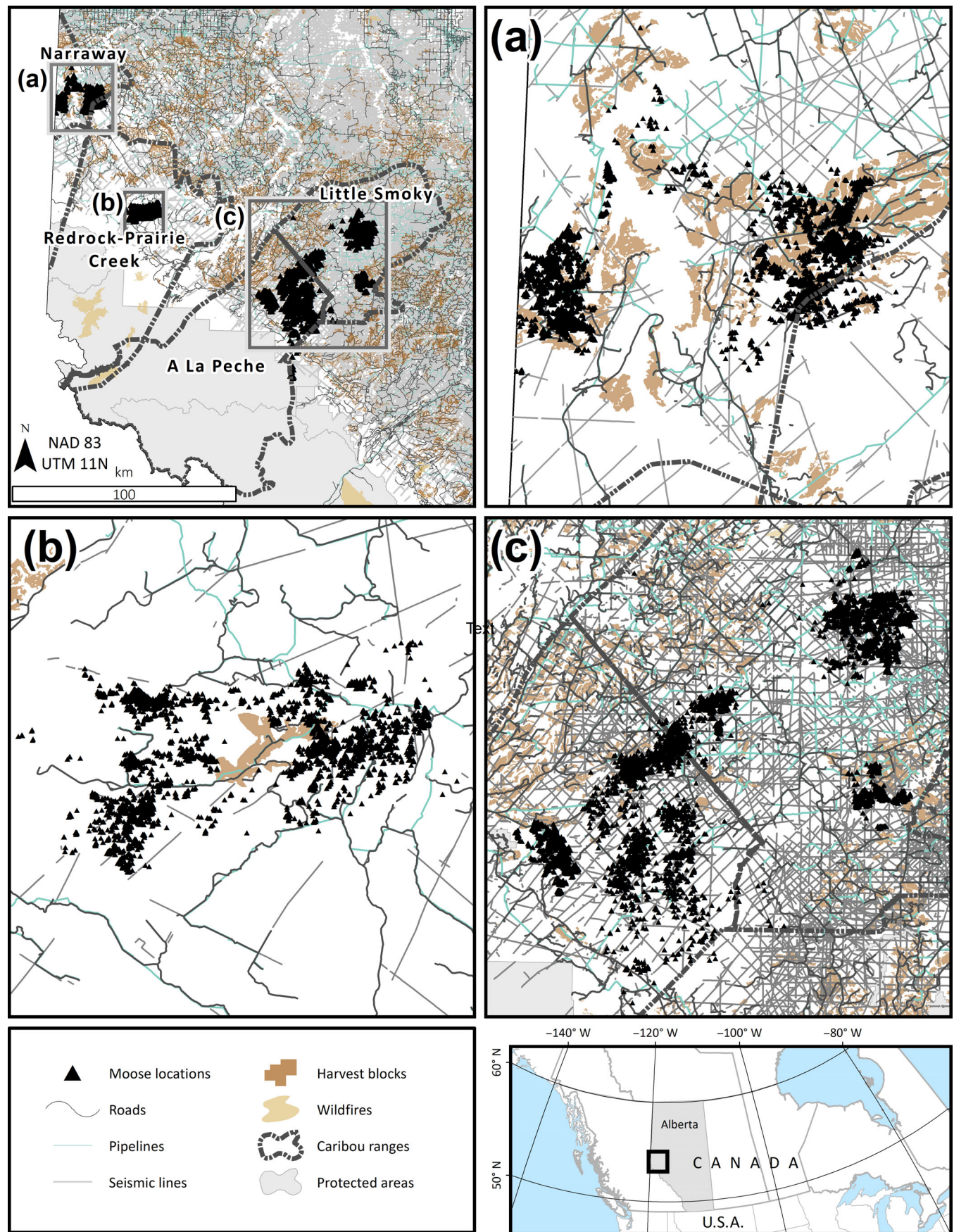
## Environmental data

Our primary objective was to investigate moose response to linear features. However, to account for other characteristics of the environment that influence an animal's location, we included additional variables that influenced habitat selection of moose in the study area (Peters et al., 2013). These variables included broad-scale attributes of the landscape related to “Terrain,” “Habitat,” “Forest” (Appendix S1: Table S2), and “Disturbance” (Table 1).

### Terrain, forest, and habitat data

For terrain, we derived variables describing slope, aspect, elevation, topographic position index (TPI; Jenness, 2006), and compound topographic index (CTI; Gessler et al., 2000) from a 25 m digital elevation model. Using values obtained from the aspect raster, we generated a binary variable “Flat” for pixels with zero slope. Winds in the area are predominantly from the southwest; therefore, for pixels with slope greater than zero, we reclassified aspect into two binary categories related to predominant winds in the region: windward slopes (Wind) and leeward slopes (Lee). These categories were used as an index of snow accumulation and perceived temperature on the ground (i.e., windchill and solar radiation). For water and soil wetness, we used provincial data mapped at coarse (1:1,000,000) and fine (1:20,000) scales to calculate two distance-to-water variables, and we used wet areas mapping (WAM; White et al., 2012) as an indication of soil moisture (Appendix S1: Table S2). To represent the diminishing impact of depth to water on vegetation growth, we transformed WAM using an exponential decay





**FIGURE 1** Study area in west-central Alberta, Canada, indicating moose GPS locations (2008–2010), disturbance (roads, pipelines, seismic lines, harvest blocks and wildfires <25 years old in 2010), caribou population range boundaries, and protected areas.

**TABLE 1** Disturbance variables used to describe landscape- and fine-scale habitat selection of moose in west-central Alberta, Canada, between 2008 and 2010.

Variable	Description and units	Range	Landscape scale	Fine scale
dSeismic	Distance to seismic lines (m), exponential decay	0–1	x	x
Seismic1km	Density of seismic lines within a 1 km radius (km/km <sup>2</sup> )	0–8.7	x	
Seismic_veght	Vegetation height on seismic line, m	0–7.9		x
Seismic_veght <sup>2</sup>	Vegetation height on seismic line, squared	0–53		x
dPipe	Distance to pipelines (m), exponential decay	0–1	x	x
Pipeline1km	Density of pipelines within a 1 km radius (km/km <sup>2</sup> )	0–2	x	
dRoad	Distance to roads (m), exponential decay	0–1	x	x
Road1km	Density of roads within a 1 km radius (km/km <sup>2</sup> )	0–9.8	x	
Lin1km	Density of seismic lines, pipelines, and roads within a 1 km radius (km/km <sup>2</sup> )	0–11	x	
Non-lin1km	Density of wildfires and harvest blocks <25 years old within a 1 km radius (km <sup>2</sup> /km <sup>2</sup> )	0–1	x	
_%con	Mean percent conifer (%) within buffer surrounding seismic line, pipeline, or road segment	0–96		x
_eWam	Mean wetness of seismic lines, pipelines, and roads, depth to water (m), exponential decay	0–1		x

function  $(1 - \exp^{-1.55 \times \text{WAM}(m)})$  (Finnegan, Pigeon, et al., 2018)—this decay function caused the effect of depth to water to become constant at depths >3 m, which is the mean root depth of boreal forest vegetation (Canadell et al., 1996). Following Peters et al. (2013), we also included Moderate Resolution Imaging Spectroradiometer (MODIS)-derived snow cover (winter) and vegetation greenness (normalised difference vegetation index [NDVI]; summer) mapped at a 250 m resolution.

For habitat, we derived landcover variables from Earth Observation for Sustainable Development of Forests (EOSD) (Natural Resources Canada, 2009) mapped at a 30 m resolution. We used annual maps of landscape disturbance (MacNearney et al., 2016) to annually update the EOSD, classifying new disturbances by year as a new landcover type “disturbance.” From landcover data, we calculated forest cover as a binary variable indicating forested (1) versus nonforested (0) and used a 1 km circular moving window average in ArcGIS 10.2 (Environmental Systems Research Institute [ESRI], 2015) to calculate percent forest. We used a combination of MODIS and Landsat imagery mapped at a 30 m resolution (McDermid et al., 2009) to extract percent canopy cover by year.

## Disturbance data

For landscape-scale analysis, we calculated the distance to and density of pipelines, seismic lines, and roads, and

the density of wildfires, harvest blocks, linear disturbance (pipelines, seismic lines, and roads combined), and nonlinear disturbance (wildfires and harvest blocks combined). For density variables, consistent with Peters et al. (2013), we used a 1 km circular moving window average calculated in ArcGIS 10.2 (ESRI, 2015). Pipeline, seismic line, road, and wildfire data were provided by the Government of Alberta under the open government license. Harvest block data were provided by Forest Management Agreement holders within the study area. Since we were interested in the influence of early seral stage on moose habitat selection, we considered wildfires and harvest blocks for analyses if they had been burned or harvested <25 years prior to collection of animal data (Table 1).

For fine-scale analysis, we included additional variables describing attributes of disturbances, including regeneration height, site wetness, and the habitat surrounding the disturbance. First, we partitioned linear features (seismic lines, pipelines, and roads) into 100 m segments. For seismic lines, we attributed each 100 m segment with LiDAR-derived mean vegetation heights and WAM (described in Finnegan, Pigeon, et al., 2018) and with mean percent conifer intersecting the seismic line. For wider linear features (i.e., pipelines and roads) that are captured in 30-m resolution raster canopy cover data, we buffered each 100 m segment by 60 m on either side and determined mean percent conifer within each buffered road and pipeline segment. We attributed each 100 m segment with the mean WAM intersecting



each segment and transformed mean WAM values using the previously described exponential decay (eWam). There was insufficient variation in disturbance age for inclusion in models. For disturbance variables and associated attributes, we used annual disturbance data (2008–2010) matched to the year the moose data were collected, except for LiDAR-derived data (vegetation heights for seismic lines), which were collected circa 2007 (see Finnegan, Pigeon, et al., 2018).

## Modeling

### Landscape-scale

We generated 20 random locations per moose GPS location within individual-year-seasonal 100% minimum convex polygons (MCP) and used ArcGIS (ESRI, 2015) and the package “raster” (Hijmans, 2022) to assign environmental data to used and available moose locations. We used a 100% MCP because our goal was to delineate the habitat disturbance available to each moose during each season rather than determine home ranges, and because the 4-h GPS data available to us were likely to underestimate the true availability for each moose. Because the influence of a habitat type or disturbance variable is likely to decrease at increasing distances from that feature, for distance variables, we calculated two decay functions that caused the influence of disturbances to decrease after 2 or 1 km ( $1 - \exp^{(-0.002 \times \text{distance(m)})}$ ,  $1 - \exp^{(-0.004 \times \text{distance(m)})}$ ). We used GLM and Akaike information criterion (AIC; Akaike, 1983; Burnham & Anderson, 2002) to identify the most parsimonious decay function (we carried out AIC model selection and calculated  $\omega_i$  for each individual-year and identified the most parsimonious decay as the decay function with the highest mean model weight [ $\omega_i$ ] across all individual-years) to use in seasonal models.

Before building models, we standardised continuous variables to improve model convergence. Then we identified base models for each season using terrain, forest, and habitat variables (Appendix S1: Table S2). If variables were correlated (i.e.,  $r \geq 0.4$  or variance inflation factors  $\geq 3$ ), we used univariate models and mean  $\omega_i$  to identify which of the correlated variables to use in base models (Zuur et al., 2010). Because our goal was to assess moose response to linear features, we excluded terrain, forest, or habitat variables that were correlated with linear feature variables. After identifying base models for each season, we added variables describing functional responses to linear features. As we were interested in providing information that could be used to prioritize areas for restoration based on the distribution of linear features at local

scales, and because of the heterogeneous distribution of disturbance across the study area (Figure 1), we used densities of disturbances measured at each used and available location to assess functional responses (Malcolm et al., 2020; Pigeon et al., 2020), rather than a single metric describing mean density of linear features within each moose home range (Northrup et al., 2022). For each linear feature, we considered multiple functional response models including distance to the linear feature, and interactions with (1) density of the linear feature of interest, (2) density of other linear features, and (3) density of non-linear features (Table 2). We considered that there was a functional response when there was a significant interaction (95% confidence intervals [CI] not overlapping zero), indicating that moose selection for linear features was influenced by changes in the local availability of linear features or polygonal disturbances (Mysterud & Ims, 1998). Because some linear features did not occur within moose MCPs or occurred too infrequently to include in models, we fit models using different subsets of individual-years for each linear feature type and interaction (seismic lines: 7–11 individual-years, pipelines: 6–7 individual-years, roads: 7–12 individual-years). We then identified the most parsimonious model for each linear feature using AIC-based model selection fit to each individual-year, where we calculated  $\omega_i$  for each model for each individual-year and identified the most parsimonious model as the model with the highest mean  $\omega_i$  across all individual-years. Where the number of individual-years available for analysis differed, we carried out model selection using the smallest subset of individual-years across the three models. We fit final models to each individual-year and calculated population-level coefficients for each season using inverse-weighting (Murtaugh, 2007). We conducted analyses and model selection using the packages “lattice” (Deepayan, 2008), “MuMin” (Bartón, 2022), and “lme4” (Bates et al., 2015), and visualized results using “ggplot2” (Wickham, 2016), within R (R Development Core Team, 2022).

We present results as mean inverse-weighted coefficients ( $\beta$ ) and lower (LCL) and upper (UCL) 95% confidence limits for each season. Also, because moose habitat selection differs between males and females (Marchand et al., 2015; Mumma et al., 2019), and we were interested in teasing out potential sex-based differences in response to linear features, we also present results as the number of individual female and male moose with positive, negative, and nonsignificant (95% CIs include zero) coefficients for each model and season. We evaluated the fit of final seasonal models using fivefold cross validation (Boyce et al., 2002) with 100 iterations applied to each individual-year. We report observed (Obs) and random (Rand) minimum, mean, and maximum  $r_s$  values across

**TABLE 2** Generalized linear logistic regression models used to assess seasonal (winter, summer) landscape-scale functional response of moose to linear features in west-central Alberta, between 2008 and 2010.

Linear feature	Model ID	Model structure	Mean $\omega_i$	
			Winter	Summer
Seismic lines	L_S1	~Base + dSeismic $\times$ Seismic1km	<b>0.334</b>	<b>0.857</b>
	L_S2	~Base + dSeismic $\times$ Lin1km <sup>a</sup>	<b>0.333</b>	0
	L_S3	~Base + dSeismic $\times$ NonLin1km	<b>0.333</b>	0.143
Pipelines	L_P1	~Base + dPipe $\times$ Pipe1km	0.286	0
	L_P2	~Base + dPipe $\times$ Lin1km <sup>b</sup>	<b>0.639</b>	0.418
	L_P3	~Base + dPipe $\times$ NonLin1km	0.075	<b>0.582</b>
Roads	L_R1	~Base + dRoad $\times$ Road1km	<b>0.454</b>	0.114
	L_R2	~Base + dRoad $\times$ Lin1km <sup>c</sup>	0.252	<b>0.571</b>
	L_R3	~Base + dRoad $\times$ NonLin1km	0.295	0.314

Note: The best models are indicated in boldface. Variables are described in Table 1.

<sup>a</sup>Density of pipelines + roads.

<sup>b</sup>Density of seismic lines + roads.

<sup>c</sup>Density of seismic lines + pipelines.

all individual-years for each season. Obs  $r_s$  values should be greater than Rand  $r_s$  values, and Obs  $r_s$  values closer to 1 indicate better model fit.

## Fine scale

For fine-scale habitat selection analysis, for each used (actual) step (straight-line distance between consecutive locations), we generated 10 available steps, randomly sampling steps from a gamma distribution and turn angles from a von Mises distribution (Duchesne et al., 2015), based on used steps specific to each individual and season (package “amt”; Signer et al., 2019). We then used ArcGIS (ESRI, 2015) to attribute the end of each used and available step with environmental data (Table 1; Appendix S1: Table S2). We fit SSF models using conditional logistic regression; conducted analyses and model selection using the packages “lattice” (Deepayan, 2008), “MuMin” (Bartón, 2022), and “survival” (Therneau, 2022; Therneau & Grambsch, 2000); and visualized results using “ggplot2” (Wickham, 2016), within R (R Development Core Team, 2022). Similar to the landscape-scale analysis, before building models, we standardized all continuous variables and checked for correlation. If variables were correlated, we used univariate models and the quasi-likelihood information criterion (QIC) (Pan, 2001) to identify which of the correlated variables to use in final models. We used QIC as a conservative model selection criterion given our small sample size (Pan, 2001).

To investigate moose habitat selection in relation to attributes of disturbances, we started with the base models from the landscape-scale analysis and then used SSF to

assess moose response to each linear feature type and its associated attributes in turn (i.e., separate models with seismic lines, pipelines, and roads for each season). We fit separate models because we wanted to include interactions within models (e.g., moose response to seismic lines relative to vegetation height and soil wetness) and models would not converge when we fit multiple interactions for different disturbances within the same model. For each linear feature, we considered multiple models including distance to the disturbance, attributes of the disturbance, and interactions (Table 3). For seismic line models, we also considered a squared term for vegetation height as moose may select intermediate vegetation heights over low and high vegetation heights (Melin et al., 2013; Mumma et al., 2021). Like at the landscape scale, some linear features did not occur within moose home ranges, or moose were too far from linear features to include in models, so we fit models and carried out model selection using different subsets of individual-years (seismic lines: 6–10, pipelines: 5–7, roads: 3–6). Where the number of individual-years available for analysis differed, we carried out model selection using the smallest subset of individual-years across the three models. We identified the most parsimonious model for each disturbance type using QIC-based model selection fit to each individual-year; the most parsimonious model was the model with the highest mean  $\omega_i$  across all individual-years. We fit final models to each individual-year using conditional logistic regression and calculated population-level coefficients for each season using inverse-weighting (Murtaugh, 2007).

We present results as mean inverse-weighted coefficients ( $\beta$ ) and LCL and UCL 95% confidence limits for each season and as the number of individual female and



**TABLE 3** Conditional logistic regression models used to assess seasonal (winter, summer) fine-scale functional response of moose to characteristics of linear features in west-central Alberta, between 2008 and 2010.

Linear feature	Model ID	Model structure	Mean $\omega_i$	
			Winter	Summer
Seismic lines	F_S1	~Base + dSeismic $\times$ Seismic_veght	0.117	0.073
	F_S2	~Base + dSeismic $\times$ Seismic_eWAM	0.161	0.155
	F_S3	~Base + dSeismic $\times$ Seismic_%con	0.154	0.175
	F_S4	~Base + dSeismic $\times$ Seismic_veght $\times$ Seismic_eWAM	0.120	0.039
	F_S5	~Base + dSeismic $\times$ Seismic_veght $\times$ Seismic_%con	<b>0.260</b>	<b>0.290</b>
	F_S6	~Base + dSeismic $\times$ Seismic_eWAM $\times$ Seismic_%con	0.189	<b>0.268</b>
Pipelines	F_P1	~Base + dPipe	0.082	0.150
	F_P2	~Base + dPipe $\times$ Pipe_eWAM	<b>0.448</b>	0.166
	F_P3	~Base + dPipe $\times$ Pipe_%con	0.182	<b>0.334</b>
	F_P4	~Base + dPipe $\times$ Pipe_eWAM $\times$ Pipe_%con	0.288	<b>0.350</b>
Roads	F_R1	~Base + dRoad	0.332	0.211
	F_R2	~Base + dRoad $\times$ Road_eWAM	0.088	0.050
	F_R3	~Base + dRoad $\times$ Road_%con	<b>0.405</b>	0.329
	F_R4	~Base + dRoad $\times$ Road_eWAM $\times$ Road_%con	0.175	<b>0.411</b>

Note: Quasi-likelihood information criterion model selection was applied to each individual-year and the most parsimonious model for each season was identified based on the highest mean model weight ( $\omega_i$ ) across all individual-years. The best models are indicated in boldface. Variables are described in Table 1 and Appendix S1: Table S2.

male moose with positive, negative, and non-significant coefficients for each model and season. We evaluated the fit of final seasonal model(s) using 5-fold cross validation (Boyce et al., 2002) code from the package “hab” (Basilie, 2015) applied to each individual-year. We report minimum, mean, and maximum observed (Obs) and random (Rand)  $r_s$  values across all individual-years for each season as we do for the landscape scale analysis.

## RESULTS

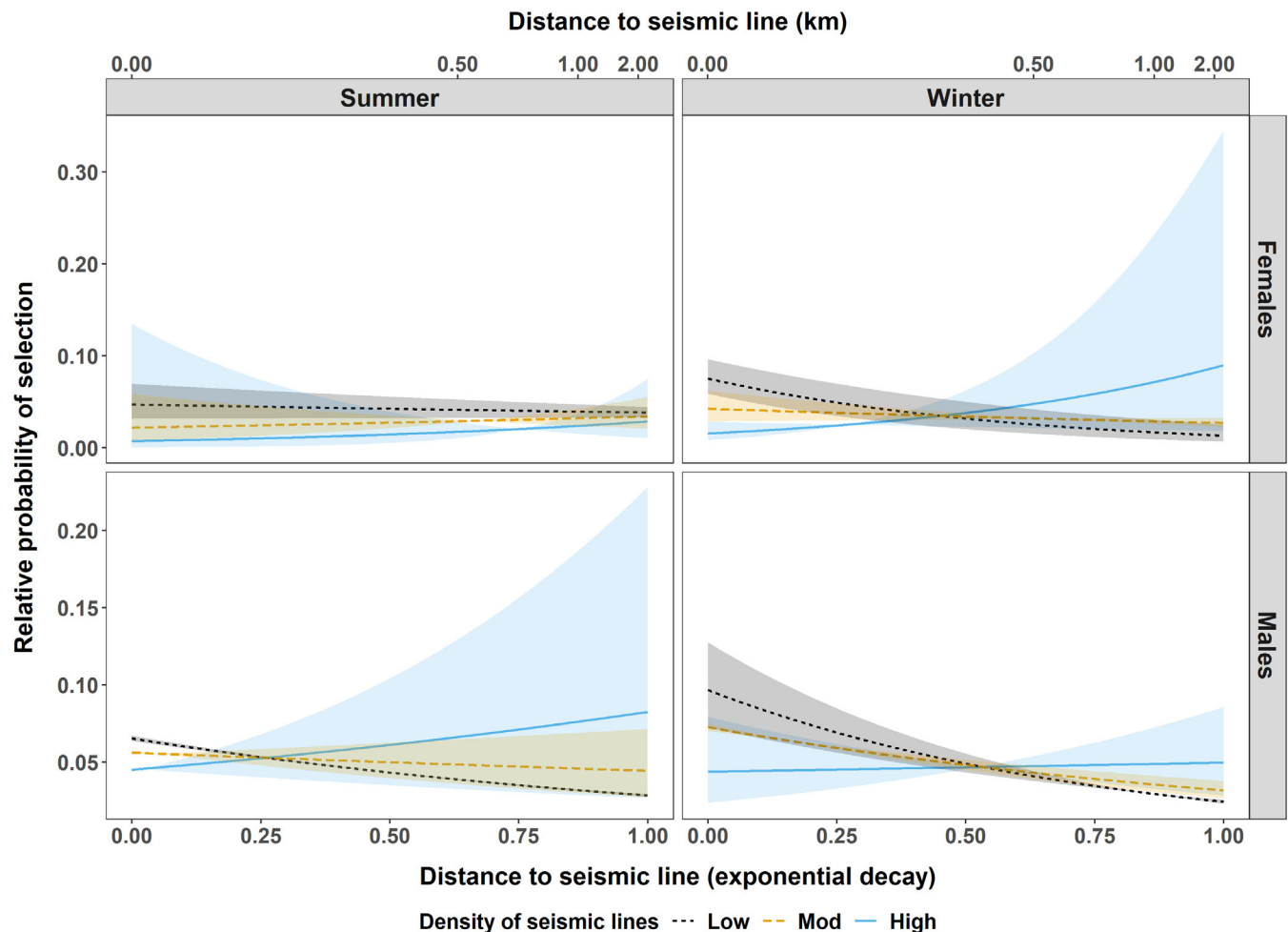
During summer, 0.7%, 3%, and 13% of moose locations were <50 m from pipelines, roads, and seismic lines, respectively, while during winter, 0.8%, 5%, and 17% of moose locations were <50 m from pipelines, roads, and seismic lines, respectively (Appendix S1: Figure S1). Base models included habitat, terrain, snow cover during winter, and NDVI during summer. These models indicated that moose generally selected wet areas, wet shrub habitat, and forest with lower percent conifer (Appendix S2).

### Landscape-scale

During summer, the best seismic line model included an interaction with density of seismic lines, while during winter all models had similar mean  $\omega_i$  (Table 2). These

models indicated that moose selected areas closer to seismic lines when they were in areas with lower densities of seismic lines regardless of season (summer, 7 individual-years: dSeismic  $\beta$  = 0.006 [LCL -0.150, UCL 0.163], Seismic1km  $\beta$  = 0.297 [LCL -0.098, UCL 0.692], dSeismic  $\times$  Seismic1km  $\beta$  = 0.172 [LCL 0.037, UCL 0.308]; winter, 11 individual-years: dSeismic  $\beta$  = -0.134 [LCL -0.219, UCL -0.049], Seismic1km  $\beta$  = 0.353 [LCL 0.078, UCL 0.629], dSeismic  $\times$  Seismic1km  $\beta$  = 0.204 [LCL 0.049, UCL 0.359]; Figure 2; Appendix S2: Tables S1 and S2). These functional responses of moose to seismic lines were driven by male moose and were stronger during winter (Figure 2). These models also indicated that during winter, moose selected areas closer to seismic lines when they were in areas with higher densities of non-linear disturbances (9 individual-years, dSeismic  $\beta$  = 0.014 [LCL -0.110, UCL 0.139], NonLin1km  $\beta$  = 0.109 [LCL -0.361, UCL 0.578], dSeismic  $\times$  NonLin1km  $\beta$  = -0.138 [LCL -0.253, UCL -0.024]; Appendix S2: Table S3), but there was no impact of the density of other linear disturbances on moose response to seismic lines (8 individual-years, Appendix S2: Table S4). K-fold validation indicated good model fit (mean Obs  $r_s$  = 0.858–0.900; mean Rand  $r_s$  = -0.011 to 0.014; Appendix S2: Section S1).

During winter, the best pipeline model included an interaction between distance to pipelines and the density of other linear features, while during summer, the best pipeline model included an interaction between distance



**FIGURE 2** Relative probability of selection by male and female moose during summer and winter in west-central Alberta, Canada, between 2008 and 2010, at the landscape-scale, in relation to distance to seismic lines (exponential decay at 2 km) and densities of seismic lines (mean of the lower [low], middle [Mod], and upper [High] quantiles; Table 2: L\_S1). Other variables were kept at their mean for prediction. Shaded areas are 95% CIs.

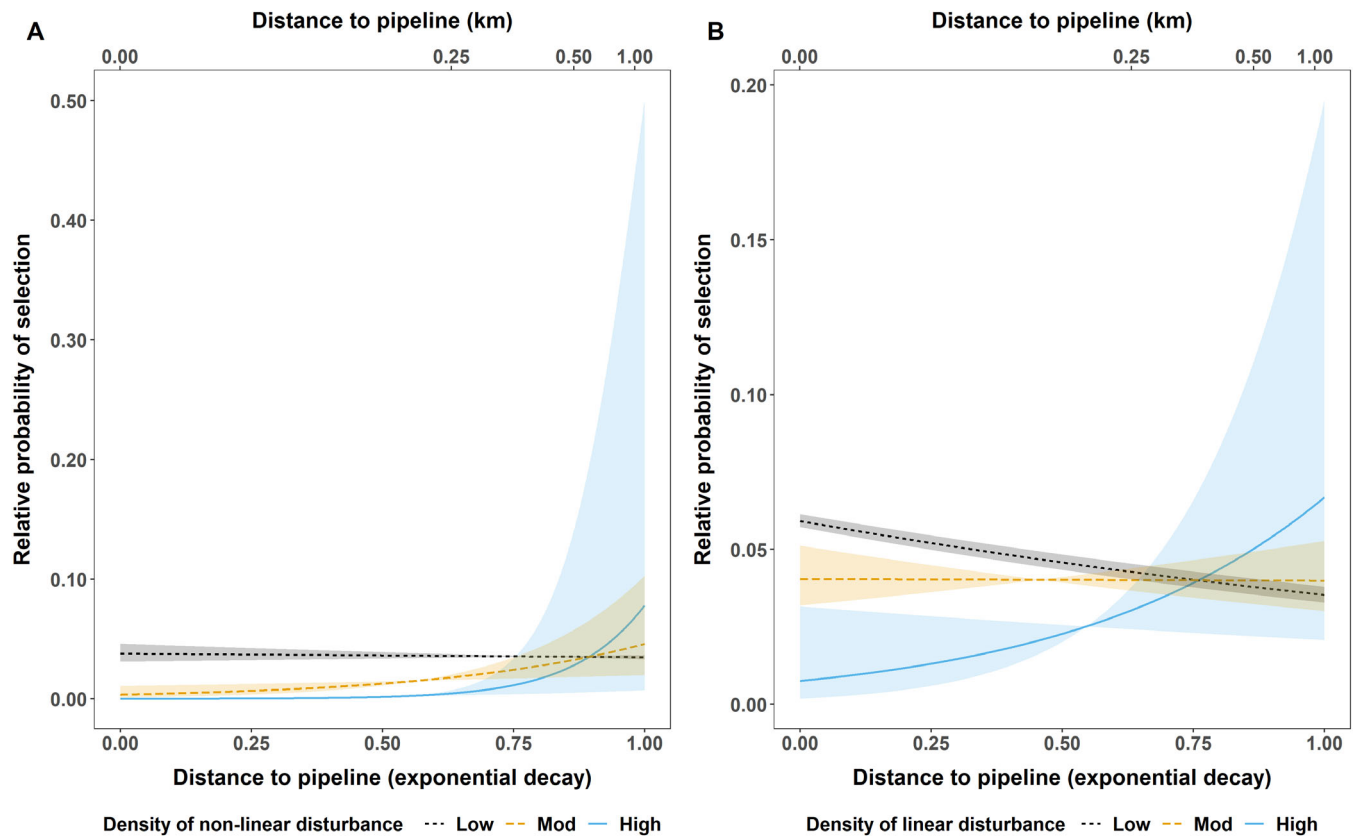
to pipelines and the density of non-linear features (Table 2). These models indicated that moose selected areas closer to pipelines when they were in areas with lower densities of other linear features and non-linear features (summer, 6 individual-years: dPipe  $\beta = 0.119$  [LCL  $-0.003$ , UCL  $0.240$ ], NonLin1km  $\beta = 0.079$  [LCL  $-0.329$ , UCL  $0.487$ ], dPipe  $\times$  NonLin1km  $\beta = 0.222$  [LCL  $0.079$ , UCL  $0.365$ ]; winter, 7 individual-years: dPipe  $\beta = 0.095$  [LCL  $-0.088$ , UCL  $0.278$ ], Lin1km  $\beta = 0.246$  [LCL  $-0.250$ , UCL  $0.742$ ], dPipe  $\times$  Lin1km  $\beta = 0.243$  [LCL  $0.013$ , UCL  $0.474$ ]; Figure 3; Appendix S2: Section S2). K-fold validation indicated good model fit (mean Obs  $r_s$   $0.878$ – $0.885$ ; mean Rand  $r_s$   $-0.018$  to  $-0.019$ ; Appendix S2: Section S2).

During winter, the best road model included an interaction between distance to roads and the density of roads, while during summer, the best road model included an interaction between distance to roads and the density of

other linear features (Table 2). These models indicated that moose response to roads was inconsistent, with some individuals selecting areas closer to roads, and some selecting areas farther from roads (summer 7 individual-years, winter 12 individual-years, Appendix S2: Section S3).

## Fine scale

During winter, the best seismic line model included an interaction between distance to seismic lines, seismic line vegetation height, and the percent conifer surrounding the seismic line (Table 3). This model indicated that moose selected areas closer to seismic lines irrespective of the vegetation height on the seismic line or the percent conifer forest surrounding the seismic line (10 individual-years, Table 4; Figure 4). During summer, the best seismic line models included an interaction between distance to



**FIGURE 3** Relative probability of selection by moose during (A) summer and (B) winter in west-central Alberta, Canada, between 2008 and 2010, at the landscape-scale, in relation to distance to pipelines (exponential decay at 1 km) and densities of non-linear (Table 2: L\_P3) or linear (Table 2: L\_P2) disturbances (mean of the lower [low], middle [Mod], and upper [High] quantiles). Other variables were kept at their mean or null for prediction. Shaded areas are 95% CIs.

seismic lines, depth to water under the seismic line, and either vegetation height or the percent conifer forest surrounding the seismic line (6 individual-years, Table 3). These models indicated that during summer, moose were indifferent to seismic lines, although there was individual variation (Table 4; Appendix S3: Section S1). K-fold validation indicated moderate predictive ability of models (mean Obs  $r_s$  0.568–0.641; mean Rand  $r_s$  0.007–0.009; Table 4; Appendix S3: Section S1).

During winter, the best pipeline model included an interaction between distance to pipelines and the percent conifer surrounding the pipeline, and the best summer models also included depth to water under the pipeline (winter 7 individual-years, summer 5 individual-years, Table 3). During winter, the best road model included distance to roads and the percent conifer surrounding the road, and the best summer model also included the depth to water under the road (winter 6 individual-years, summer 3 individual-years, Table 3). These models indicated that moose were largely indifferent to pipelines and roads, although again there was variation among individuals (Appendix S3: Sections S2 and S3). K-fold validation

indicated moderate predictive ability of models (mean Obs  $r_s$  0.521–0.630; mean Rand  $r_s$  –0.018 to 0.017; Appendix S3: Sections S2 and S3).

## DISCUSSION

We found evidence of landscape-scale functional responses in moose habitat selection of seismic lines and pipelines, but no response to roads. At the fine scale, moose generally selected areas closer to seismic lines regardless of their characteristics but were indifferent to pipelines and roads, although responses varied among individuals. These results derived from GPS data collected from seven moose exposed to a wide gradient in availability of linear features, together with previous research (Dickie, Serrouya, DeMars, et al., 2017; Finnegan, Pigeon, et al., 2018; Pigeon et al., 2020; Tattersall et al., 2020), provide further evidence that (1) seismic lines will likely need functional and structural restoration to restore ecosystem function, and (2) linear feature restoration efforts should consider the densities of



**TABLE 4** Inverse-weighted population-averaged standardized coefficients ( $\beta$ ) and lower and upper 95% CIs (LCL, UCL) for conditional logistic regression models assessing response of moose in west-central Alberta, Canada, to seismic lines and characteristics of seismic lines during winter and summer between 2008 and 2010.

Model and variables	Population			Individual-year <sup>a</sup>		
	$\beta$	LCL	UCL	+	–	NS
Winter—Model F_S5						
dSeismic <sup>b</sup>	<b>−0.148</b>	<b>−0.243</b>	<b>−0.054</b>	1M	1F, 4M	1F, 3M
Seismic_veght <sup>2</sup>	−0.015	−0.060	0.029	1M	2M	2F, 5M
Seismic_%con	−0.076	−0.161	0.009	1F	2M	1F, 6M
dSeismic <sup>b</sup> × Seismic_veght <sup>2</sup>	0.002	−0.031	0.035	1M	0	2F, 7M
dSeismic <sup>b</sup> × Seismic_%con	−0.007	−0.073	0.058	1F, 1M	2M	1F, 5M
Seismic_veght <sup>2</sup> × Seismic_%con	0.022	−0.008	0.052	1M	0	2F, 7M
dSeismic <sup>b</sup> × Seismic_veght <sup>2</sup> × Seismic_%con	0.005	−0.033	0.043	0	1M	2F, 7M
Summer—Model F_S5						
dSeismic <sup>b</sup>	0.016	−0.064	0.096	1F, 1M	0	1F, 3M
Seismic_veght	0.024	−0.037	0.086	0	0	2F, 4M
Seismic_%con	−0.071	−0.153	0.011	0	1 M	2F, 3M
dSeismic <sup>b</sup> × Seismic_veght	0.000	−0.054	0.053	0	0	2F, 4M
dSeismic <sup>b</sup> × Seismic_%con	0.011	−0.044	0.066	0	0	2F, 4M
Seismic_veght × Seismic_%con	−0.002	−0.081	0.077	1F	0	1F, 4M
dSeismic <sup>b</sup> :Seismic_veght × Seismic_%con	0.014	−0.044	0.072	1F, 1M	0	1F, 3M

Note: Coefficients with CIs not overlapping zero are in bold. Models are described in Table 3. Variables are described in Table 1 and Appendix S1: Table S2. Complete model results are in Appendix S3: Section S1. For each variable the number of female (F) and male (M) individual-years with positive (+), negative (−) or non-significant (NS) 95% CIs are indicated.

<sup>a</sup>For winter,  $n = 10$ : 2F, 8M; for summer,  $n = 6$ : 2F, 4M.

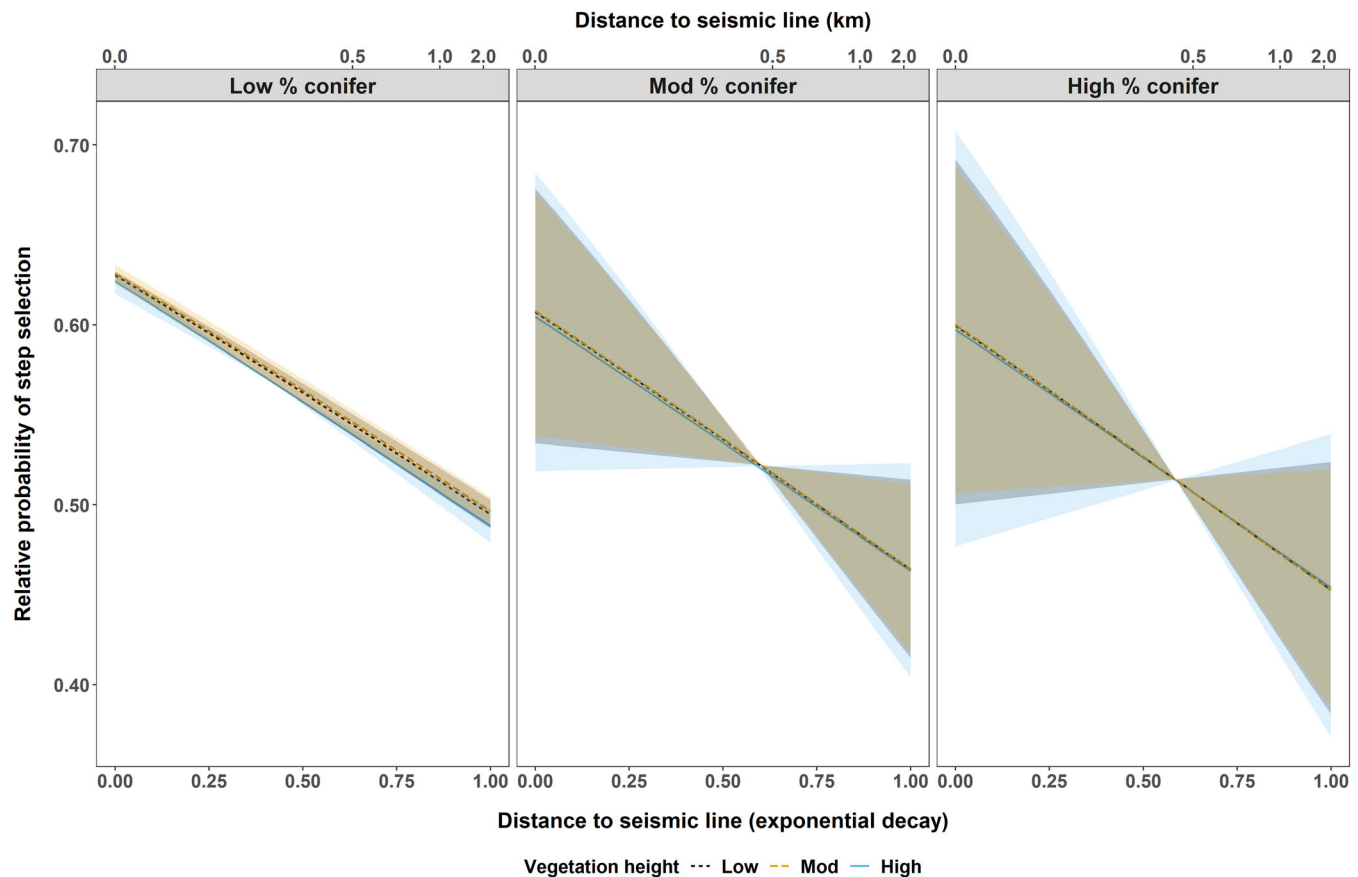
<sup>b</sup>Exponential decay at 2 km.

disturbances at landscape-scales and how restoration and landscape management may shift the distribution of boreal wildlife species.

Moose were more likely to select areas closer to seismic lines when there were less seismic lines in the surrounding area, and this response was more consistent among individuals during winter. During winter, we also found that moose were more likely to select areas closer to seismic lines when there were more harvest blocks and wildfires in the surrounding area. This functional response in selection of seismic lines has also been observed in wolves (Houle et al., 2010; Muhly et al., 2019; Pigeon et al., 2020) and moose (Mumma et al., 2019), but to our knowledge, ours is the first study to assess the interacting effects between moose response to seismic lines and different types of disturbances. We found that moose were more likely to be closer to seismic lines when there were less seismic lines in the surrounding area, but more polygonal disturbances in the surrounding area, and we also found that moose response to seismic lines was not influenced by other linear features. These results suggest that during winter, in particular, there are characteristics of the seismic lines themselves that make them

attractive to moose rather than moose selection of seismic lines being driven by a paucity of alternate travel routes (other linear features) or early seral forage (harvest blocks, wildfires). In comparison to wider and maintained linear features like roads and pipelines, it is possible that seismic lines are attractive to moose during winter because they provide a combination of forage, travel routes, shelter (thermal, snow interception), and security (proximity to mature forest) (Finnegan, MacNearney, et al., 2018; Kunkel & Pletscher, 2000; Tattersall et al., 2023; van Beest et al., 2012). Although roads and pipelines also provide forage and travel routes, forage is predominately at the edge of those features (MacDonald et al., 2020; Roever et al., 2008), and because roads and pipelines are wider than seismic lines, they likely have less thermal shelter, and lower snow interception. Roads and pipelines also have more human activity, which are generally avoided by moose (Bartzke et al., 2015; Bowman et al., 2010; Yost & Wright, 2001).

At the fine scale, moose selected areas closer to seismic lines regardless of the vegetation height on the seismic line or the habitat surrounding the seismic line. These results, like those at the landscape-scale, suggest



**FIGURE 4** Relative probability of step selection by moose during winter in west-central Alberta, Canada, between 2008 and 2010, at the fine scale, in relation to distance to seismic lines (exponential decay at 2 km), vegetation height on seismic lines (mean of the lower [Low], middle [Mod], and upper [High] quantiles), and the percent conifer within forest surrounding seismic lines (mean of the lower [Low], middle [Mod], and upper [High] quantiles; Table 3: F\_S5). Other variables were kept at their mean for prediction. Shaded areas are 95% CIs.

that there are multiple characteristics of seismic lines that make them attractive to moose during winter. The lack of response to vegetation height on seismic lines agrees with previous research on wolves and bears (Dickie, Serrouya, DeMars, et al., 2017; Finnegan, Pigeon, et al., 2018) and may be driven by moose selecting seismic lines with high vegetation during winter because they have abundant browse like willow (*Salix* spp.) and alder (*Alnus* spp.) (Finnegan, MacNearney, et al., 2018; Melin et al., 2013; Tattersall et al., 2023), as well as moose selecting seismic lines with lower vegetation for travel (Dickie, Serrouya, McNay, et al., 2017; Finnegan, Pigeon, et al., 2018). A parallel study in the same area which used field data (tracks and signs and vegetation cover) found that moose use of seismic lines was linked to the availability of specific forage species and the availability of game trails (Tattersall et al., 2023). It was curious that we found no links between the percent conifer surrounding seismic lines and moose response because moose generally select areas with higher availability of broadleaf trees (Courtois et al., 1998; Gagné et al., 2016; McKay & Finnegan, 2022). It is

possible that the scale we measured percent conifer surrounding seismic lines (30 m) was too fine to capture moose response to stand-level tree species. It is also possible that moose select seismic lines in stands with different percentages of conifer trees according to different ecological needs. For example, moose might select seismic lines surrounded by more conifer cover for refuge from predators, thermal shelter, and increased snow interception (Kunkel & Pletscher, 2000; Telfer, 1978; van Beest et al., 2012) and might select seismic lines in stands with less conifer cover because of access to forage adjacent to, as well as within, seismic lines (Courtois et al., 1998; Street et al., 2015). Overall, our fine-scale results support previous work that found vegetation height on seismic lines was insufficient to change wildlife habitat selection (Dickie, Serrouya, DeMars, et al., 2017; Finnegan, Pigeon, et al., 2018; Pigeon et al., 2020) and that understanding wildlife response to vegetation composition and vegetation height is needed to inform functional and ecological restoration of seismic lines to benefit caribou.

Moose response to seismic lines differed between seasons; during winter, moose generally selected seismic lines, but during summer, individuals selected or avoided seismic lines at the landscape-scale or were indifferent to seismic lines at the fine scale. These seasonal differences in response to seismic lines have been reported elsewhere. In northwestern British Columbia, moose were indifferent to seismic lines during early summer, female moose selected seismic lines during late summer but avoided them during winter, and male moose selected seismic lines during winter (Mumma et al., 2019). Similarly, in northeastern Alberta, moose avoided seismic lines during summer (Dickie et al., 2020). It is likely that these seasonal differences in response to seismic lines are driven by seasonal differences in access to forage, travel efficiency, and cover on seismic lines. It is also worth noting that at both landscape and fine scales, the response to seismic lines we observed was driven by male moose. Mumma et al. (2019) also found that only male moose selected seismic lines during winter. Differences in seasonal habitat preferences of male and female moose are driven by differences in resource needs, reproductive status, and exposure to risk. Females with calves trade off access to forage against security and survival of their calves through the year, which drives more variable habitat selection patterns in females when compared with males (Francis et al., 2021; Mumma et al., 2019). It is also possible that narrow seismic lines with shallower/more compacted snow are more attractive to the larger males during winter (Droghini & Boutin, 2017; Telfer & Kelsall, 1984), driving the more consistent response we observed during that season for males. Therefore, even though seismic lines are used by predators for travel (Dickie, Serrouya, McNay, et al., 2017; McKenzie et al., 2012), and moose may associate seismic lines with predation risk (Dickie et al., 2020), our results at landscape and fine scales suggest that they may still be attractive to moose, particularly during winter when wolf use of seismic lines is lower than that during summer (Finnegan, Pigeon, et al., 2018; Pigeon et al., 2020) and when wolf movement can be limited by snow (Droghini & Boutin, 2017; Telfer & Kelsall, 1984).

Generally, at the population-scale, moose were indifferent to pipelines at the landscape and fine scale, with moose only selecting areas closer to pipelines when there was a paucity of harvest blocks and wildfires (summer) or roads and seismic lines (winter) in the surrounding area. However, sample sizes for pipeline models were smaller than those of seismic lines, so these results should be interpreted with caution. During summer, the width of pipelines combined with ongoing vegetation management may result in pipelines having similar thermal cover, but less forage availability than harvest blocks and wildfires,

making pipelines less attractive to moose when harvest blocks and wildfires are available. Moose use of harvest blocks and pipelines during summer is linked to the availability of shrubs and lateral cover (McKay & Finnegan, 2023; Tattersall et al., 2023); pipelines are periodically cleared to maintain line-of-sight (Alberta Energy Regulator, 2016; MacDonald et al., 2020), while with the exception of mechanical or chemical stand tending a few years after planting, harvest blocks are left to regenerate. Therefore, harvest blocks and areas that are naturally regenerating after wildfires are likely more attractive sources of shrub and sapling moose forage than maintained pipelines with graminoids and clover less preferred by moose (MacDonald et al., 2020; McKay & Finnegan, 2023; Tattersall et al., 2023). During winter, as previously mentioned, pipelines likely offer less shelter, cover, and forage available above the snowpack than seismic lines, which is likely driving winter moose selection for pipelines only when other linear features are not available to them. At the fine scale, we found that moose were indifferent to pipelines regardless of the surrounding habitat or underlying soil wetness but that there were differences among individuals, and therefore, like seismic lines and harvest blocks, moose use of pipelines is most likely linked to finer scale characteristics like vegetation composition, lateral cover, and the presence of game trails (McKay & Finnegan, 2023; Tattersall et al., 2023).

We found no response of moose to roads, although again the sample size for the road models was small, and there was also considerable variation among individuals. The lack of population-level response to roads could be driven by some moose avoiding areas with human activity, and others selecting road edges for wildlife forage (Roever et al., 2008; Yost & Wright, 2001). The lack of response could also be driven by the variety of road types within our study area; including two-lane gravel roads with high levels of activity, single-lane gravel roads, truck trails, and winter roads (Alberta Biodiversity Monitoring Institute and Alberta Human Footprint Monitoring Program, 2019). Because of our small sample size, we were unable to include road type within our models, and future research incorporating road type, traffic levels, and vegetation composition along road edges may yield more conclusive results (Tattersall et al., 2023; Yost & Wright, 2001).

We recognize that our study had limitations. First, because of the heterogenous distribution of anthropogenic disturbance across our study area, we had a limited number of individual moose to fit some of the pipeline and road models, so those models need to be interpreted with caution. Also, the small number of female-years ( $n = 2$ ) in some models meant that we could not present those model results separately for males and females. Second, although moose prefer early seral habitat



available 20–30 years after disturbance, research has shown that moose specifically prefer disturbed areas 10–30 years after disturbance (Maier et al., 2005; Mumma et al., 2021). Additional analysis with larger datasets that facilitates partitioning harvest blocks and wildfires further by age since disturbance could provide further insights into the relationships between moose response to linear features and the availability of polygonal disturbances in the surrounding area. Third, seismic lines were the predominant linear feature within our study area (Figure 1). In areas where seismic lines occur at low densities, or do not occur at all, it is possible that pipelines, roads, or other linear features like hydrolines will have a stronger impact on moose habitat use; understanding how moose not only respond to different linear features, but also how this response varies across different areas, will be important to inform effective linear feature restoration across the boreal forest. Fourth, SSF models had poorer model fit than RSF models, which is likely driven by fine-scale characteristics like vegetation composition, hiding cover, snow cover, and localized predation risk, which we were unable to include in models (Droghini & Boutin, 2017; Finnegan, MacNearney, et al., 2018; Finnegan, Pigeon, et al., 2018). Finally, the fix rate of the moose GPS data we used in this study meant that we were only able to assess links between linear feature characteristics and moose habitat selection as a function of *distance to* linear features, rather than when moose were *on* linear features. Future work using more frequent GPS fix rates (Dickie et al., 2020; Dickie, Serrouya, DeMars, et al., 2017) (although using 15-min fix rates, only ~1% of steps were on linear features; Dickie et al., 2020), or that assess moose use of linear features using cameras or tracks and signs (Dickie et al., 2023; Tattersall et al., 2020, 2023), will likely provide more detailed information on the links between fine-scale linear feature characteristics and moose use of linear features.

## CONCLUSIONS

Caribou and moose are vitally important to the boreal ecosystem, including Indigenous peoples who have been intertwined with the boreal ecosystem for millennia. Integrated recovery and habitat restoration efforts focused on caribou should also consider impacts to moose. Our results indicate that moose response to seismic lines is likely driven by several nonexclusive factors including the densities of other disturbances on the landscape, and fine-scale food availability, predation risk, and movement efficacy associated with individual seismic lines. From a landscape perspective, our results, combined with previous research (Muhly et al., 2019;

Mumma et al., 2019; Pigeon et al., 2020), suggest that seismic line restoration efforts and changing harvesting practices (e.g., aggregated harvesting; Government of Alberta, 2017) could change the distribution of both moose and wolves; increasing their use of seismic lines in areas where there are fewer seismic lines, increasing their use of pipelines where there is less harvest in the surrounding area and creating pockets of elevated predation risk for both caribou and moose as wolves are funneled to the remaining linear features in an area. Therefore, landscape-level restoration planning that creates large areas of fully restored and eventually intact habitat, rather than piecemeal efforts where only one type of disturbance in an area is restored, is likely to benefit caribou and moose, helping to reestablish the spatial separation between caribou and moose, a natural part of the boreal ecosystem (James et al., 2004). Considering seismic lines, our results provide further support to the proposal that effective restoration will need to address the role that seismic lines play in increasing landscape permeability for predators and other wildlife species like moose, and the role that seismic lines play as a source of wildlife forage (Ray, 2014). Although higher vegetation height on seismic lines does impede predator travel (Dickie, Serrouya, McNay, et al., 2017; Finnegan, Pigeon, et al., 2018), vegetation height alone does not completely change wildlife response (Dickie et al., 2023; Dickie, Serrouya, DeMars, et al., 2017; Pigeon et al., 2020). In the short term, seismic line restoration efforts focusing on reducing predator movement could help mitigate the impacts of linear features on predator–prey dynamics to benefit caribou (Dickie et al., 2023), but long-term efforts should aim to both block predator movement and reduce attractive wildlife forage.

Habitat disturbance is increasing across the boreal forest, and habitat restoration is urgently needed to re-establish ecosystem function (Nagy-Reis et al., 2021). Conservation efforts for threatened species like caribou are increasingly looking beyond single species, recognizing that threatened species are not separate from the ecosystem they inhabit, and that conservation efforts focused on one species may have unintended consequences for interacting species (Akçakaya et al., 2020; Soulé et al., 2005). With a focus on providing information that could be used to prioritize linear feature restoration, our study is one of the first to directly assess moose functional response to habitat disturbance and different linear features at the landscape-scale and moose response to attributes of linear features at a fine scale, providing valuable information that could be used for boreal conservation and restoration planning to benefit caribou and moose. Ultimately, for linear feature restoration to be effective, it needs to address the nuanced changes in landscape

permeability, forage availability, species interactions, and mortality risk created by different types of linear features for multiple boreal wildlife species.

## ACKNOWLEDGMENTS

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data are available from Movebank: [https://www.movebank.org/cms/webapp?gwt\\_fragment=page=studies,path=study178994931](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study178994931).

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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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