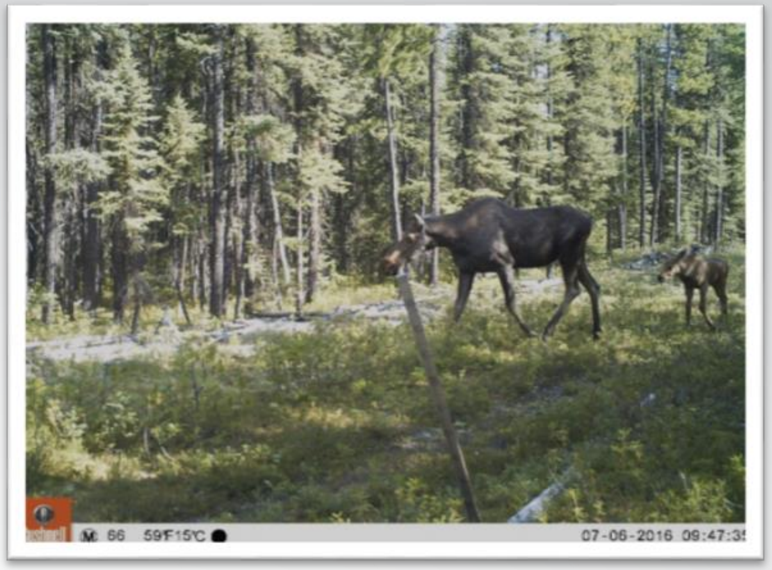

Targeting alternate prey to understand caribou and moose habitat management choices in west-central Alberta

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Alberta Upstream Research Petroleum Fund 18-ERPC-07

Final Report

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EXECUTIVE SUMMARY

Woodland caribou are declining across their range and decades of research show that habitat disturbance linked to industrial activities is the ultimate cause of caribou decline. The conversion of mature forests into early seral stands with abundant forage has resulted in more moose, deer, and elk in caribou ranges. Moose are a preferred prey of wolves and predation risk for caribou increases where moose and caribou overlap. The goals of this project were to i) assess moose response to attributes of habitat disturbances, and ii) build resource selection models that could be useful to forest managers. Identifying broad-scale landscape attributes and fine-scale habitat characteristics that are preferred by moose could help focus restoration activities within caribou ranges to efficiently reduce moose numbers, and wolf predation risk for caribou.

In year one, we built landscape-scale models to assess and map broad-scale habitat selection. We also assessed moose response to attributes of harvest blocks and seismic lines. At landscape scales, moose selected areas associated with forage and cover for thermoregulation. At fine-scales, moose selected harvest blocks with deciduous trees and shrubs, low vegetation heights, and fewer conifer trees, and in the lower foothills moose avoided herbicide-treated harvest blocks during summer. At fine-scales moose selected seismic lines with low vegetation during summer and wet seismic lines during winter. In year two (this report) we investigated landscape-scale functional responses of moose to habitat disturbance. At fine-scales, we assessed response of moose to regeneration and soil wetness of harvest blocks and seismic lines, and response of moose to attributes of roads, pipelines, and wellsites.

At landscape-scales moose response to canopy cover depended on forest densities. During summer, moose selected higher canopy cover when they were in areas with lower forest densities, but were ambivalent to canopy cover when they were in areas with higher forest densities. During winter, foothills moose selected lower canopy cover irrespective of forest densities. We also found a functional response of moose to disturbances with moose selecting seismic lines, harvest blocks, and wellsites when they were in areas with lower densities of seismic lines, but only selecting roads when they were in areas with higher road densities. At fine-scales, during winter moose selected wetter higher vegetation seismic lines and drier lower vegetation seismic lines, but generally avoided seismic lines during summer. Moose also selected roads in disturbances (winter) and forest (summer), selected pipelines in forest, and selected active wellsites. For harvest blocks, moose selected higher vegetation during winter and lower vegetation during summer.

To our knowledge, this is the first study to investigate functional responses of moose to habitat disturbance and demonstrates the insights that may be gained from assessing response of generalist herbivores to proximity of disturbances and densities of disturbances. Notably, our results i) complement previous work on wolves demonstrating that restoration efforts need to consider not only the feature being restored, but also the overall densities of disturbance on the landscape, and ii) demonstrate that restoration efforts that achieve structural and functional restoration are most likely to reduce moose use of disturbed habitat. Overall, the results of this project may be used prioritize recovery actions in a cost-effective manner that maximizes their benefit to caribou.

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1. INTRODUCTION

1.1. Project Background

Woodland caribou (*Rangifer tarandus*) are declining across their range (McLoughlin et al., 2003; Vors and Boyce, 2009). The causes of caribou population declines are complex, and include interactions between a number of species and landscape disturbances, with additional potential impacts of climate change. However, based on decades of research (DeCesare et al., 2014; Vors et al., 2007; Vors and Boyce, 2009), it is well established that habitat disturbance is the ultimate cause of caribou declines. As a result, one of the priorities of the federal caribou recovery strategy is to reduce habitat disturbance within caribou ranges below a threshold of 35% disturbed area (Environment Canada, 2012). Currently, habitat disturbance in many caribou ranges exceeds this threshold, with up to 97% disturbed area in some ranges (Environment Canada, 2011). To ensure that recovery efforts are cost efficient and effective for caribou conservation, a triage approach will likely be necessary to prioritize habitat restoration in areas that will most benefit caribou populations (Finnegan et al., 2018b; Noss et al., 2009).

Caribou have evolved to occupy nutrient-poor mature forests that are unattractive to moose, deer, and elk (i.e., primary prey species; Bergerud, 1988). Historically, this allowed caribou to avoid high densities of predators, as the low numbers of primary prey within caribou habitat sustained only low predator numbers (Bergerud, 1992; Bergerud et al., 1984). However, across caribou ranges, resource extraction activities have converted mature forests into early seral stands with abundant forage preferred by moose, deer, and elk (Finnegan et al., 2018a; Latham et al., 2013; Visscher and Merrill, 2009). As a result, the landscape can sustain more primary prey within caribou ranges, which in turn leads to more predators (i.e., more wolves; Serrouya et al., 2011; Street et al., 2015b). The consequences include increased predation risk for caribou, especially in areas with more linear disturbances (Mumma et al., 2018; Whittington et al., 2011), resulting in population-level declines of caribou (Hervieux et al., 2013; McLoughlin et al., 2003; Vors et al., 2007) through a process called apparent competition (DeCesare et al., 2010).

Moose are the primary prey of wolves in Alberta (Kojola et al., 2004; Serrouya et al., 2011), and in west-central Alberta, caribou are at greater risk where they co-occur with moose (Peters et al., 2013). By identifying habitat characteristics and specific landscape attributes preferred by moose, restoration activities could be better focused to efficiently reduce moose numbers, subsequently reducing wolf densities within caribou ranges and spatial overlap between caribou and moose (Pigeon et al., 2020; Serrouya et al., 2017). Forest harvesting practices alter characteristics of the landscape, and understanding which of these specific practices result in habitats preferred by moose (e.g., via forest harvesting methods such as harvest block size and mounding) could help managers choose specific harvesting practices that reduce the suitability of new disturbances for moose or prioritize remediation of existing disturbances. By addressing the issue of apparent competition, these approaches could decrease predation risk for caribou, with potential for population level effects.

In this study, we used GPS data from moose collared in west-central Alberta between 2008 and 2010 to assess moose response to i) habitat disturbance and habitat characteristics at a broad-scale, and ii) attributes of habitat disturbances at a fine-scale, including forest harvest blocks and seismic lines. These GPS data have been previously used to describe moose response to habitat disturbance in west-central Alberta (Peters, 2010; Peters et al., 2013), and moose habitat use within caribou ranges has been investigated elsewhere (Mumma et al., 2018; Nielson and Boutin, 2017). However, to our knowledge no studies in western Canada have considered the functional response of moose to habitat disturbance. Functional responses occur when selection or avoidance response relative to a feature varies as a function of the availability of the feature on the landscape. For example, wolves are more likely to select linear features when they are in areas with lower densities of those features (Houle et al., 2010; Pigeon et al., 2020). These studies suggest that when restoring linear features, restoration plans should consider the density of seismic lines in the surrounding landscape to avoid causing an increase in wolf use of unrestored seismic lines (Pigeon et al., 2020). For moose, a functional response relative to food availability and cover has been assessed (Bjørneraas et al., 2012; Mabille et al., 2012), but considering caribou conservation, understanding functional responses of predators (wolves; Pigeon et al., 2020) and their primary prey (moose; this study) to specific habitat disturbances (and restoration) will be the most informative when planning restoration activities.

There is increasing evidence that fine-scale characteristics like vegetation height and human activity levels influence animal response to specific disturbance features (Finnegan et al., 2018b; McKay et al., 2014; Northrup et al., 2012), including moose response (Belovsky, 1981; Melin et al., 2016; Tomm et al., 2007). Understanding how moose response to disturbance varies as function of the surrounding habitat matrix, regeneration, and human activity levels at the disturbance may help prioritize restoration at the fine-scale, and could be used to mitigate the impacts of future disturbances within caribou ranges.

1.2. Objectives

The goal of our project was to assess moose response to regeneration and other attributes of habitat disturbances in west-central Alberta, and to build habitat selection models that considered habitat categories used by forest managers in their forest management plans (i.e., ecosites and natural subregions). Specifically, our objectives for this project were to:

1. Assess moose broad-scale response to habitat, topography, and disturbance (‘landscape-scale’), (years one and two).
2. Assess moose fine-scale response to characteristics of disturbances (years one and two).
3. Apply results from objectives 1 and 2 to create spatially explicit probability maps of moose habitat use of regenerating anthropogenic features in west-central Alberta (year one).
4. Integrate these results into an interactive GIS tool that can be used by land managers to inform habitat restoration within caribou ranges (in progress).

2. METHODS

2.1. Study area

The study area included the ranges of one boreal caribou herd (Little Smoky) and three central mountain caribou herds (A La Peche, Narraway, and Redrock-Prairie Creek) in west-central Alberta. Within the study area, there are five natural subregions: alpine, subalpine, upper foothills, lower foothills, and montane (Natural Regions Committee, 2006). Forests are primarily coniferous, characterized by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*) in upland areas, and by black spruce (*Picea mariana*), larch (*Larix laricina*), and poorly drained muskeg in lowland areas (Saher and Schmiegelow, 2005; Smith et al., 2000). Ungulates within the study area include caribou, moose (*Alces alces*), whitetail and mule deer (*Odocoileus virginianus* and *O. humionus*), and elk (*Cervus elaphus*). The primary predators of caribou in this area are grizzly bears (*Ursus arctos*), cougars (*Felis concolor*), and wolves (*Canis lupus*), and additional predators include black bears (*Ursus americanus*), lynx (*Lynx canadensis*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*) (Stevenson et al., 2001; Stotyn et al., 2007; Wittmer et al., 2005).

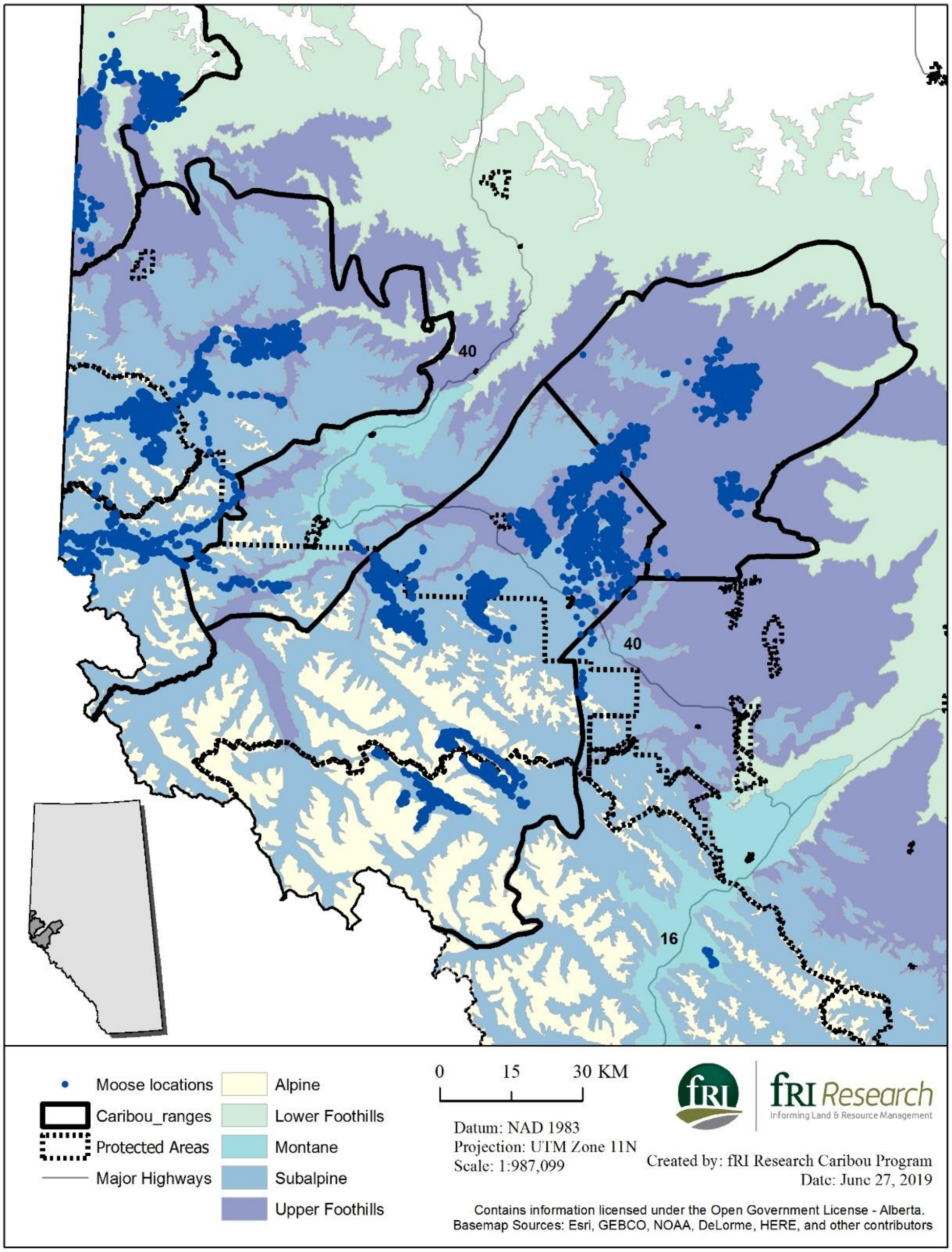

Figure 2.1. Study area showing moose GPS locations collected between 2008 and 2010 within west-central caribou herd ranges and natural subregions, Alberta, Canada.

2.2. Animal location Data

We used GPS telemetry data collected from 17 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 hour-intervals, resulting in 6 potential fixes per day per animal.

To account for the seasonal importance of different resources, we partitioned GPS collar locations into ‘winter’ or ‘summer’ based on seasons previously defined for moose in the same study area (winter: 17 October to 15 May; summer: 16 May to 16 October; Peters et al., 2013). We generated individual Minimum Convex Polygons (MCPs) for winter and summer for each year of data for each moose. We removed GPS locations and seasonal MCPs for individual-season-years with less than 100 GPS locations. The final dataset included 31 seasonal MCPs from 12 individual moose. We also partitioned GPS collar locations into natural subregions (Natural Regions Committee, 2006) and following Peters et al. (2013), we classified individuals as ‘foothills’ moose if > 50% of their locations were in the lower and/or upper foothills natural subregions, and as ‘mountain’ moose if > 50% of their locations were in the montane, subalpine and/or alpine natural subregions. The final dataset consisted of 38,230 locations (Table 2.1).

Table 2.1. Sample size of GPS locations and the number of collared individuals by year and season for adult moose with home ranges within west-central caribou herd ranges in Alberta, Canada, between 2008 and 2010.

	Foothills				Mountains			
	Summer		Winter		Summer		Winter	
	Individuals	Locations	Individuals	Locations	Individuals	Locations	Individuals	Locations
2008	2	1,159	2	1,671	2	1,063	6	1,450
2009	5	7,683	7	7,689	6	5,709	8	7,180
2010	-	-	5	2,709	-	0	6	1,917
Total	7	8,842	7	12,069	8	6,772	8	10,547

2.3. Landscape variables

Our primary objective was to investigate disturbance-specific resource selection of moose. However, to account for broad selection patterns that influence an animal's general location (DeCesare et al., 2012; Johnson et al., 2004), we included additional variables that were previously found to influence habitat selection of moose in the study area (Peters et al. 2013). Variables included broad-scale attributes of the landscape related to 'Terrain', 'Habitat', and 'Disturbance' (see Tables 2.2 and 2.3). We used ArcGIS (Environmental Systems Research Institute (ESRI), 2015) and the R package raster (Hijmans, 2014) to extract variables to used and available moose locations.

2.3.1 Terrain

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 25m 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 re-classified 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 (Table 2.2.). To represent the diminishing impact of depth to water on vegetation growth we transformed WAM using an exponential decay function (eWAM: $1- \exp^{-1.55*WAM(m)}$; Finnegan et al., 2018b). See Table 2.2 for details.

2.3.2 Habitat

For habitat, we derived landcover variables from an Earth Observation for Sustainable Development of Forests (EOSD) (Natural Resources Canada, 2009) mapped at a 30m resolution. We used annual maps of landscape disturbance 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 non-forested (0), and used a 1km circular moving window average in ArcGIS 10.2 (Environmental Systems Research Institute (ESRI), 2015) to calculate forest density. We used a combination of Moderate Resolution Imaging Spectroradiometer (MODIS) and Landsat imagery mapped at a 30m resolution (Franklin et al., 2002a, 2002b; McDermid et al., 2009) to extract percent canopy cover by year. See Table 2.2 for details.

Table 2.2. Environmental variables used to describe landscape-scale habitat selection of moose within four west-central caribou herd ranges in Alberta, Canada, between 2008 and 2010.

Variables	Description and units
Terrain	
Elev	Elevation based on 25m resolution digital elevation model (m)
Slope	Slope, derived from digital elevation model (°)
Flat	Binary variable describing flatness, zero slope (1) or slope greater than 0 (0)
Lee	Binary variable: northeast aspects as leeward slopes (1) and southwest aspects as windward slopes (0)
CTI	Compound topographic index built from a 250m moving window average (unitless)
TPI	Topographic index built from a 1km-radius moving window average (unitless)
eWam	Wet areas mapping, depth to water (m) represented as exponential decay
Forest	
Forest1km	Percent of area covered by forest, 1km-radius moving window average (%)
ForestYN	Forest (conifer, broadleaf, or mixed); binary
Conifer.pct	Percent conifer within 30m pixels (%)
Canopy	Percent canopy cover within 30m pixels (%)
Habitat	
Water	Lakes, reservoirs, rivers, streams; binary
Barren	Rock, rubble, exposed land; binary
Shrub	≥20% ground cover, ≥33% shrub; binary
Herb	≥20% ground cover/≥33% herb; binary
Wet treed	Land with wetland/aquatic processes; majority vegetation conifer, broadleaf, mixed wood; binary
Wet shrub	Land with wetland/aquatic processes; majority vegetation shrub; binary
Wet herb	Land with wetland/aquatic processes; majority vegetation herb; binary
Con den	≥60% crown closure, ≥75% conifer by basal area; binary
Con open	26-60% crown closure, ≥75% conifer by basal area; binary
Broad den	≥60% crown closure, ≥75% broadleaf by basal area; binary
Broad open	26-60% crown closure, ≥75% broadleaf by basal area; binary
Mixed	≥60% crown closure, <75% conifer/broadleaf by basal area; binary
dWater_20K	Streams at 1:20,000 (1:20K), distance to (m) represented as exponential decay
dWater_1M	Streams at 1:1,000,000 (1:1M), distance to (m) represented as exponential decay

2.3.3. Disturbance variables

For landscape-scale analysis, we calculated the density of pipelines, seismic lines, roads, wellsites, and harvest blocks using a 1km circular moving window average in ArcGIS 10.2 (Environmental Systems Research Institute (ESRI), 2015), and investigated density variables as well as distance-to variables for each disturbance type. For pipelines, seismic lines and roads, we used data provided by the Government of Alberta. For wellsites, we used locations and activity information provided by the Alberta Energy Regulator (AER) and the Alberta Biodiversity Monitoring Institute (ABMI, 2018). For harvest blocks, we used data provided by Forest Management Agreement (FMA) holders within the study area. Since we were interested in the influence of early seral stage on moose habitat selection, we considered harvest blocks for analyses if they had been cut < 25 years prior to collection of animal data (Table 2.3).

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 all linear features (seismic lines, pipelines, roads) into 100m segments. For seismic lines we attributed each 100m segment with LiDAR-derived mean vegetation heights and WAM (described fully in Finnegan et al. 2018b), and with the landcover class intersecting the majority of the seismic line segment. For wider linear features (i.e., pipelines and roads), we buffered each 100m segment by 60m on either side and determined the dominant landcover intersecting each buffered road and pipeline segment. We attributed each 100m segment of pipelines and roads with mean WAM values. We generated a 60m buffer around each harvest block and wellsite polygon, and calculated the dominant landcover intersecting each buffered harvest block and wellsite. For harvest blocks, we attributed each harvest block with mean WAM values and with LiDAR-derived vegetation height, accounting for higher vegetation height in retention patches by using the 95th percentile of vegetation height within each harvest block. For wellsites, we attributed each wellsite with mean WAM values, and used wellsite activity data to classify each wellsite as active or abandoned (ABMI, 2018). To facilitate model fit we re-classified landcover intersecting disturbances as forest (con_den, con_open, broad_den, broad_open, mixed), non-forest (other landcover; see Table 2.2), or disturbance (Table 2.3). We also transformed mean WAM values interesting disturbances using the previously described exponential decay (eWam). Initially, we considered the age of disturbances in models, however there was insufficient variation in disturbance age for inclusion in final models.

All variables are further described in Table 2.3. For disturbance variables and associated attributes we used annual disturbance data (2008 – 2010) matched to the year the moose data were collected, with the exception of LiDAR-derived data (vegetation heights for seismic lines and harvest blocks), which were collected circa 2007 (see Finnegan et al. 2018b).

Table 2.3. Disturbance variables used to describe landscape- and fine-scale habitat selection of moose within four west-central caribou herd ranges in Alberta, Canada, between 2008 and 2010.

Variable	Description and units	Landscape-scale	Fine-scale
dSeismic	Distance to seismic lines(m) represented as exponential decay	x	x
Seismic1km	Density of seismic lines within a 1km radius (km/km^2)	x	
Seismic_veght	Vegetation height on seismic line measured with LiDAR, m		x
dPipe	Distance to pipelines (m) represented as exponential decay	x	x
Pipeline1km	Density of pipelines within a 1km radius (km/km^2)	x	
dRoad	Distance to roads (m) represented as exponential decay	x	x
Road1km	Density of roads within a 1km radius (km/km^2)	x	
dCut	Distance to harvest blocks (m) represented as exponential decay	x	x
Cuts1km	Density of harvest blocks < 25 years old within a 1km radius (km^2/km^2)	x	
Cut_veght	Vegetation height within harvest block measured with LiDAR, m		x
dWell	Distance to wells (m) represented as exponential decay	x	x
Well1km	Density of well sites within a 1km radius (km^2/km^2)	x	
Well_activity	Active or abandoned		x
_forest	Landcover intersecting or surrounding the majority of the seismic line, pipeline, or road segment, or harvest block and wellsite classified as forest (1) or non-forest (0) [see Table 2.2]		x
_disturb	Landcover intersecting or surrounding the majority of the seismic line, pipeline, or road segment, or harvest block and wellsite classified as disturbance (1) or non-disturbance (0) [see Table 2.2]		
_eWam	Wetness of seismic lines, pipelines, harvest blocks, roads, and wellsites, depth to water (m) represented as exponential decay		x

2.4. Data analysis

2.4.1. Landscape-scale habitat selection analyses

For landscape-scale habitat selection analysis we generated 20 random locations per moose GPS location within each individual-year-seasonal MCP within the study area and used resource selection functions (RSFs) to compare the habitat that moose used to that which was available to them. We used generalized linear models (GLM) and mixed models (GLMM) to assess habitat selection, conducted analyses and model selection using the R packages lattice (Deepayan, 2008), MuMin (Bartón, 2015), and lme4 (Bates et al., 2015), and visualised results using ggplot2 (Wickham, 2009), all within R and RStudio (R Development Core Team, 2015; RStudio Team, 2016). 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 (1-exp $^{(-0.002 \times \text{distance (m)})}$, 1-exp $^{(-0.001 \times \text{distance (m)})}$). For each region, we then used GLMM and Akaike's Information Criterion (AIC; Akaike, 1983; Burnham and Anderson, 2002) to identify the most parsimonious decay function for each region to use as the distance-to- variable in final models.

Before building models, we standardized all continuous variables to improve model convergence. Because moderate collinearity can be problematic when investigating ecological signals, if variables were correlated (i.e., $r \geq 0.5$ or Variance Inflation Factors ≥ 3) we used univariate models and AIC to identify which of the correlated variables to use in model building (Zuur et al., 2010). We used a multi-step approach to optimize models. First, to identify a base model, we built separate 'Terrain' and 'Habitat' models using variables associated with each of these categories (see Table 2.2). We then used GLMM and the 'drop1' function (R Development Core Team, 2015) to retain only influential variables within each category in the base model. Second, we built 'Forest' models including combinations of the forest variables and models for each of the disturbance variables and again used GLMM and AIC to identify the most parsimonious combinations of variables, including interactions, to include within final models. Finally, we added the forest and disturbance variables to the base model, fit these final models to each individual moose-season-year-region using GLM, and calculated population-level coefficients for each region and season using inverse-weighting (Murtaugh, 2007).

A number of forest and disturbance variables were correlated. Our primary goal was to assess the impacts of all disturbance features on moose habitat selection; therefore, when disturbance variables were correlated with one another, we fit final models including each of those variables in turn. Where we fit >1 model to a region-season we present results in the main text as mean coefficients (β) and 95% confidence intervals (LCL, UCL) across all models fit to that region-season. We evaluated the predictive ability of our final model(s) using k-fold cross validation (Boyce et al., 2002) applied to each moose-year. We report observed [Obs] and random [Rand] mean r_s values across all moose-years for each season and region. Obs r_s values should be greater than Rand r_s values, and Obs r_s values closer to 1 indicate better model fit.

2.4.2. Fine-scale habitat selection analyses

For fine-scale habitat selection analysis we again compared habitat that moose used to that which was available to them, but we applied step selection functions (SSFs) instead of RSFs and constrained availability to potential locations that moose could have selected based on their location 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. 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 between $-\pi$ and π, based on used steps specific to each individual and season (R package amt; Signer et al., 2019). We then used ArcGIS

(Environmental Systems Research Institute (ESRI), 2015) to extract habitat and disturbance characteristics at the end of each used and available step (Tables 2.2 and 2.3). We fit SSF models using conditional logistic regression, conducting analyses and model selection using the R packages lattice (Deepayan, 2008), MuMin (Bartón, 2015), and survival (Therneau, 2015), and visualising results using ggplot2 (Wickham, 2009), all within R and RStudio (R Development Core Team, 2015; RStudio Team, 2016). Similar to the landscape-scale analysis, before building models, we standardized all continuous variables and checked for correlation, and if variables were correlated (i.e., $r \geq 0.4$ or Variance Inflation Factors ≥ 3) we used univariate models and the quasi-likelihood under the independence model criterion (QIC; Pan, 2001) to identify which of the correlated variables to use in model building (Zuur et al., 2010).

To investigate moose habitat selection in relation to attributes of specific disturbances, we started with the base models identified from the landscape-scale analysis and then used SSF to assess moose response to each disturbance type (‘focal disturbance’) and its associated attributes in turn (i.e., separate models with seismic lines, pipelines, roads, harvest blocks, and wellsites as the focal disturbance for each region and 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. However, when variables for focal disturbances for a particular model were not correlated with those of other disturbances, we accounted for the impact of other disturbances on moose habitat selection by including distance-to variables for those disturbances within models (see Table 2.4). For each disturbance type we considered multiple models including distance to the disturbance, attributes of the disturbance, and interactions (Table 2.4). 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 model weight across all individual-years. We fit final models to each individual moose-season-year-region using conditional logistic regression and calculated population-level coefficients for each region and season using inverse-weighting (Murtaugh, 2007).

We present results as mean coefficients (β) and 95% confidence intervals (LCL, UCL). We evaluated the predictive ability of our final model(s) using k-fold cross validation (Boyce et al., 2002) using the R package hab (Basille, 2015) applied to each individual moose-season-year-region. We report mean observed [Obs] and random [Rand] r_s values across all individual moose-years for each season and region.

Table 2.4. Models used to assess fine-scale response of moose to habitat disturbance within four west-central caribou herd ranges in Alberta between 2008 and 2010. The most parsimonious model for each region and season was identified using the Quasi-likelihood under the independence model criterion (QIC). QIC model selection was applied to each individual and the most parsimonious model was identified based on the highest mean model weight (ω_i) across all individuals. The best model is indicated in bold. Mountain moose were in areas with little disturbance during summer so we were unable to fit disturbance models for that season and region.

Focal disturbance	Model	Mean ω_i		
		Foothills		Mountains
		Winter	Summer	Winter
Seismic lines	~Base + dSeismic* Seismic_veght + other[1]	0.342	**0.359**	0.442
	~Base + dSeismic* Seismic_veght*Seismic_eWAM + other[1]	**0.483**	0.316	**0.491**
	~Base + dSeismic* Seismic_veght*Seismic_forest + other[1]	0.176	0.325	0.067
Pipelines	~Base + dPipe*Pipe_eWAM + other[1]	0.354	0.382	-
	~Base + dPipe*Pipe_forest + other[1]	**0.646**[2]	**0.618**	-
Roads	~Base + dRoad*Road_eWAM + other[1]	0.169	0.350	-
	~Base + dRoad*Road_disturbance + other[1]	**0.566**	-	-
	~Base + dRoad*Road_forest + other[1]	0.265	**0.377**	-
	~Base + dRoad*Road_eWAM*Road_disturbance + other[1]	-	-	-
	~Base + dRoad*Road_eWAM*Road_forest + other[1]	-	0.274	-
Harvest blocks	~Base + dCut*Cut_veght + other[1]	0.350	1[3]	-
	~Base + dCut*Cut_forest + other[1]	0.650	-	-
Wellsites	~Base + dWell*Well_eWAM + other[1]	**0.724**	0.207	-
	~Base + dWell*Well_activity + other[1]	0.147	**0.489**	-
	~Base + dWell*Well_forest + other[1]	0.129	0.304	-

[1] other included distance-to disturbance variables for disturbance types that were not correlated with the focal disturbance; [2] we could only include Pipe_forest as an additive term; [3] we could only fit harvest block model in the foothills during summer

3. RESULTS

3.1. Landscape-scale habitat selection

3.1.1. Foothills

During winter and summer, foothills moose selected wet, flat terrain, wetland shrub habitat, areas with lower percent conifer, and areas further from streams at the fine-scale, but closer to streams at coarse-scales (Table 3.1). Moose also selected lower elevations during winter and higher elevations during summer. During winter and summer, moose selected areas closer to seismic lines in regions with lower seismic line densities, but moose response to pipelines, harvest blocks, and wellsites varied across seasons (Table 3.1; Figures 3.1, 3.2). During winter, moose selected areas further from pipelines, and during summer, moose selected areas closer to pipelines, irrespective of pipeline densities. Moose selected areas closer to harvest blocks during winter, but during summer, moose were more likely to select areas closer to harvest blocks in regions with lower harvest block densities. During winter, moose selected areas closer to wellsites when in regions with higher wellsite densities, but during summer moose selected areas closer to wellsites in regions with lower wellsite densities (Figures 3.1, 3.2). Finally, although moose generally selected areas farther from roads, during winter moose selected areas closer to roads in regions with higher road densities (Figure 3.2). Model validation indicated good to excellent predictive power of foothills models during winter (mean Obs r_s = 0.89 [range 0.65 – 0.96]; mean Rand r_s = -0.01 [range -0.09 – 0.08]) and summer (mean Obs r_s = 0.84 [range 0.52 – 0.97]; mean Rand r_s = 0.03 [range 0.01 – 0.06]).

Table 3.1. Mean standardized model coefficients (β) and lower and upper 95% confidence intervals (LCL, UCL) describing landscape-scale habitat selection for foothills moose within west-central caribou herd ranges in Alberta, Canada, during winter and summer 2008-2010. Population-level coefficients were calculated using inverse weighting. Variables are described in Table 2.2.

	Winter			Summer		
	β	LCL	HCL	β	LCL	HCL
Intercept	-3.4573	-3.4605	-3.4542	-2.7758	-2.7800	-2.7716
Elev	-0.3449	-0.3464	-0.3435	0.0678	0.0667	0.0689
Flat	0.5063	0.5011	0.5114	0.1169	0.1010	0.1327
eWAM	-0.1799	-0.1802	-0.1795	-0.1349	-0.1353	-0.1345
dWater_20K	0.0354	0.0350	0.0359	0.0254	0.0249	0.0259
dWater_1M	-0.0442	-0.0444	-0.0439	-0.0107	-0.0110	-0.0103
Wet shrub	0.2832	0.2800	0.2864	0.1582	0.1519	0.1646
Conifer.pct	-0.3961	-0.3966	-0.3957	-0.2679	-0.2684	-0.2674
dSeismic[1]	-0.1713	-0.1717	-0.1708	-0.0430	-0.0434	-0.0426
Seismic density	0.3523	0.3510	0.3537	0.2365	0.2358	0.2371
dSeismic[1]*Seismic density	0.2625	0.2616	0.2634	0.1758	0.1754	0.1763
dPipeline[2]	0.0242	0.0238	0.0246	-0.1187	-0.1208	-0.1166
Pipeline density	-	-	-	0.0221	0.0215	0.0226
dCutblock[2]	-0.0111	-0.0119	-0.0103	-0.4221	-0.4241	-0.4202
Cutblock density	-	-	-	0.0881	0.0861	0.0902
dCutblock[2]*Cutblock density	-	-	-	0.3457	0.3448	0.3466
dRoad[2]	0.1400	0.1388	0.1412	0.5141	0.5116	0.5166
Road density	0.1704	0.1696	0.1713	-0.2845	-0.2856	-0.2834
dRoad[2]*Road density	-0.0544	-0.0549	-0.0539	0.0107	0.0094	0.0121
dWellsite[2]	0.1891	0.1866	0.1916	-0.0412	-0.0426	-0.0398
Wellsite density	-0.0023	-0.0029	-0.0018	0.0890	0.0886	0.0894
dWellsite[2]* Wellsite density	-0.0746	-0.0751	-0.0740	-0.0391	-0.0396	-0.0387

[1]exponential decay at 2km, [2]exponential decay at 1km

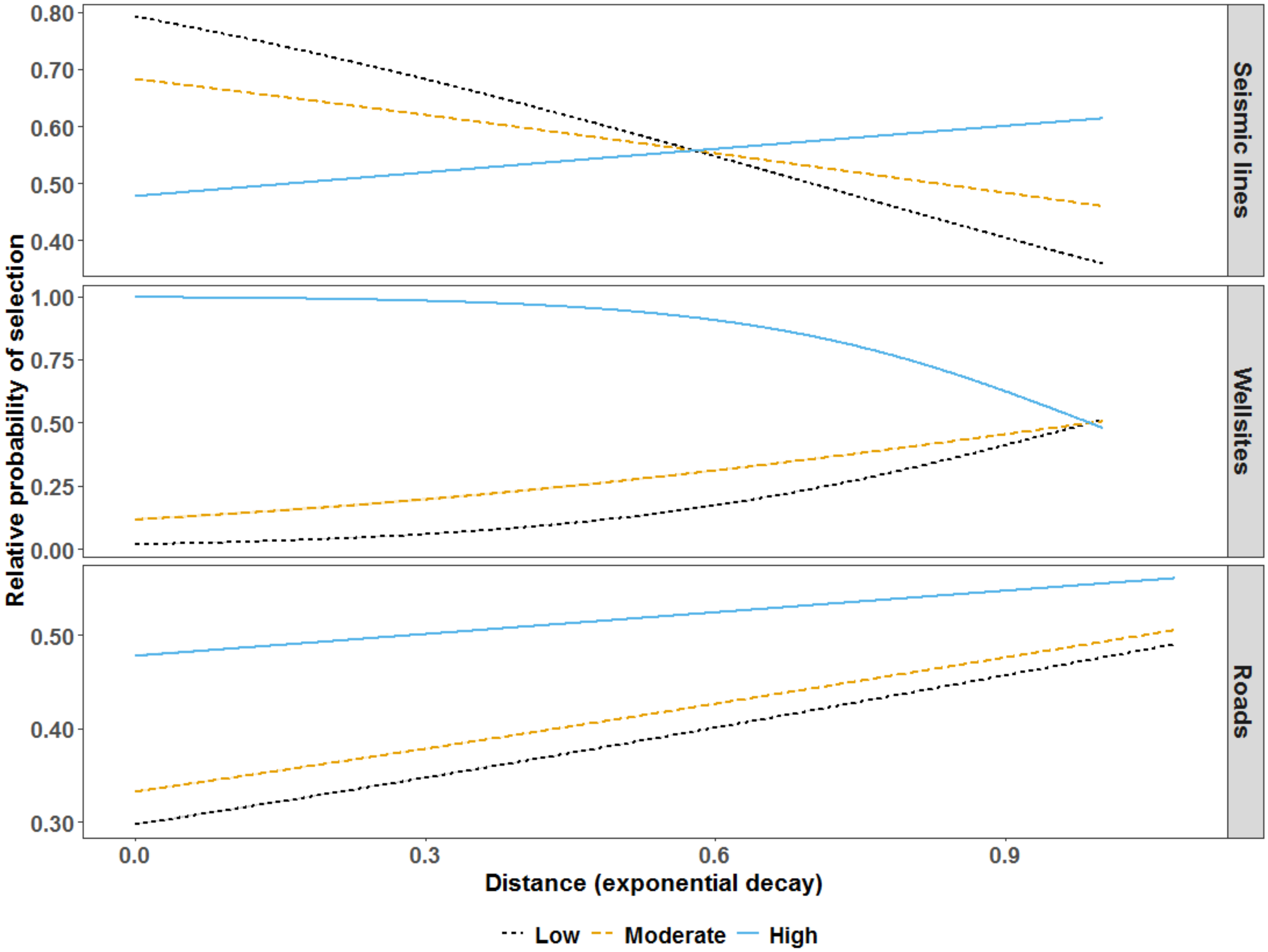

Figure 3.1. Relative probably of habitat selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during winter in relation to the exponential decay distance to seismic lines, wellsites and roads and the density of seismic lines, wellsites, and roads. Densities are represented by the mean of the lower (Low), middle (Moderate), and upper (Higher) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

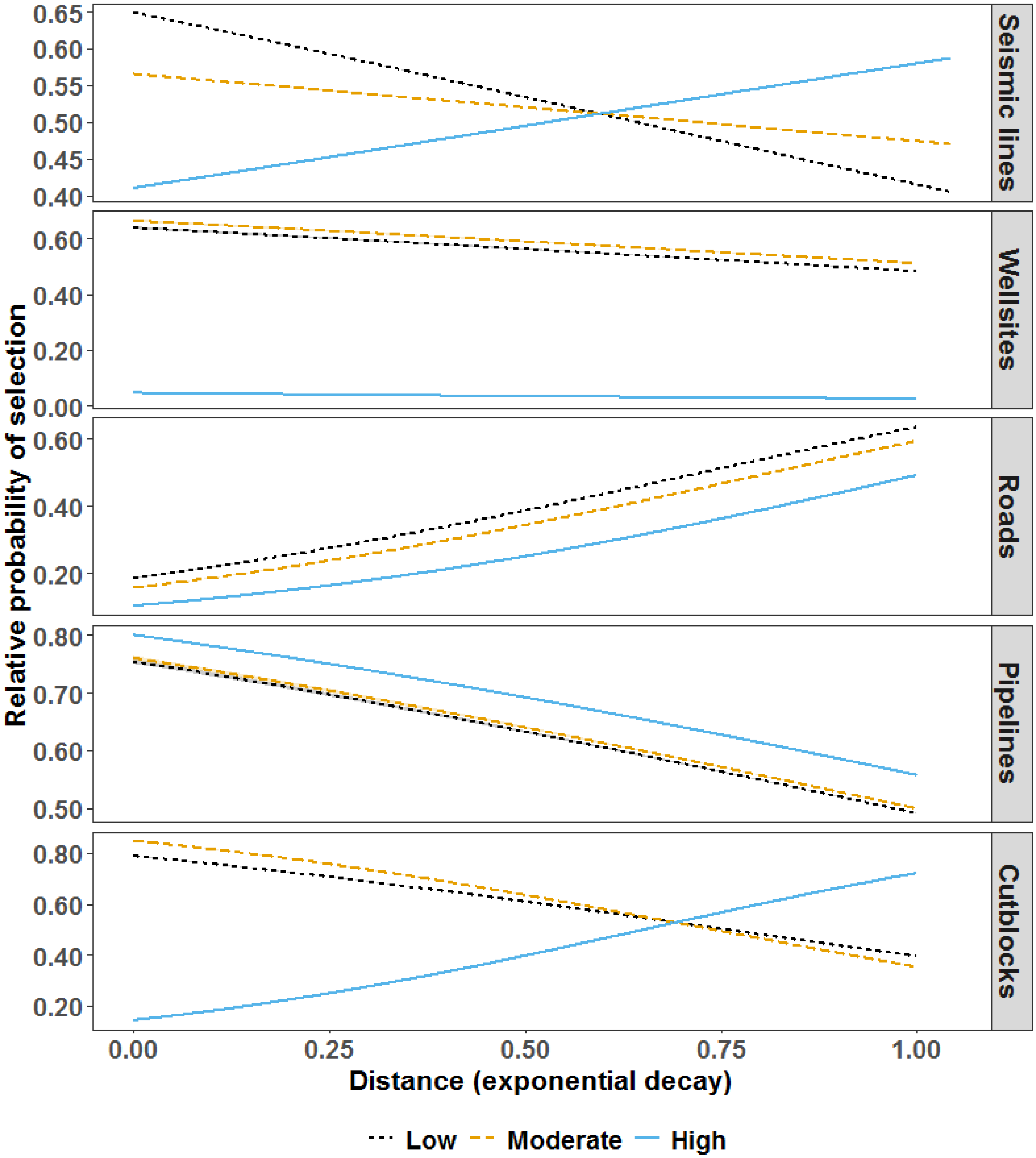

Figure 3.2. Relative probably of habitat selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during summer in relation to the exponential decay distance to seismic lines, wellsites, roads, pipelines, and harvest blocks ('cutblocks') and the density of seismic lines, wellsites, roads, pipelines, and cutblocks. Densities are represented by the mean of the lower (Low), middle (Moderate), and upper (Higher) quantiles. All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

3.1.2. Mountains

We were unable to include disturbance density variables in models fit to mountain moose during winter, and because mountain moose were largely in protected areas during summer we unable to include either distance to or disturbance density variables in models fit to mountain moose that season. During winter, moose selected wetland shrub habitat, and during winter and summer, moose selected wet areas and shrub and herb habitat (Table 3.2). During winter, moose selected areas with lower canopy cover regardless of forest density, and generally selected areas with lower forest densities (Figure 3.3). During winter moose selected areas closer to roads and wellsites and farther from seismic lines and pipelines (Table 3.2). During summer moose selected forest stands with higher canopy cover in regions with lower forest densities, but when moose were in regions with higher forest densities there was no relationship between moose habitat use and canopy cover (Figure 3.3). Model validation indicated fair to excellent predictive power of foothills models during winter (mean Obs r_s = 0.74 [range 0.14 – 0.82]; mean Rand r_s = 0.03 [range -0.13 – 0.01]) and summer (mean Obs r_s = 0.84 [range 0.62 – 0.92]; mean Rand r_s = 0.02 [range -0.06 – 0.09]).

Table 3.2. Mean standardized model coefficients (β) and lower and upper 95% confidence intervals (LCL, UCL) describing landscape-scale habitat selection for mountain moose within caribou herd ranges in west-central Alberta, Canada during winter and summer 2008-2010. Population-level coefficients were calculated using inverse weighting. Variables are described in Table 2.2.

	Winter			Summer		
	β	LCL	UCL	β	LCL	UCL
Intercept	-3.7110	-3.7179	-3.7041	-2.8501	-2.8511	-2.8490
Elev	-1.0308	-1.0335	-1.0282	-	-	-
eWAM	-0.2190	-0.2204	-0.2177	-0.2805	-0.2811	-0.2799
dSeismic[1]	0.0359	0.0357	0.0362	-	-	-
dRoad[1]	-0.1891	-0.1901	-0.1882	-	-	-
Shrub	0.9674	0.9593	0.9755	0.6360	0.6329	0.6390
Herb	1.0262	1.0130	1.0395	0.8259	0.8190	0.8328
Canopy	-0.1167	-0.1177	-0.1157	0.3576	0.3566	0.3586
Forest density	-0.3693	-0.3722	-0.3663	-0.2602	-0.2614	-0.2591
Canopy: Forest density	-0.0575	-0.0595	-0.0556	-0.4928	-0.4940	-0.4916
Wet shrub	0.6027	0.5799	0.6256	-	-	-
dPipelines[1]	0.2241	0.2101	0.2382	-	-	-
dWellsites[2]	-0.4420	-0.4438	-0.4402	-	-	-

[1] exponential decay at 1km, [2] exponential decay at 2km

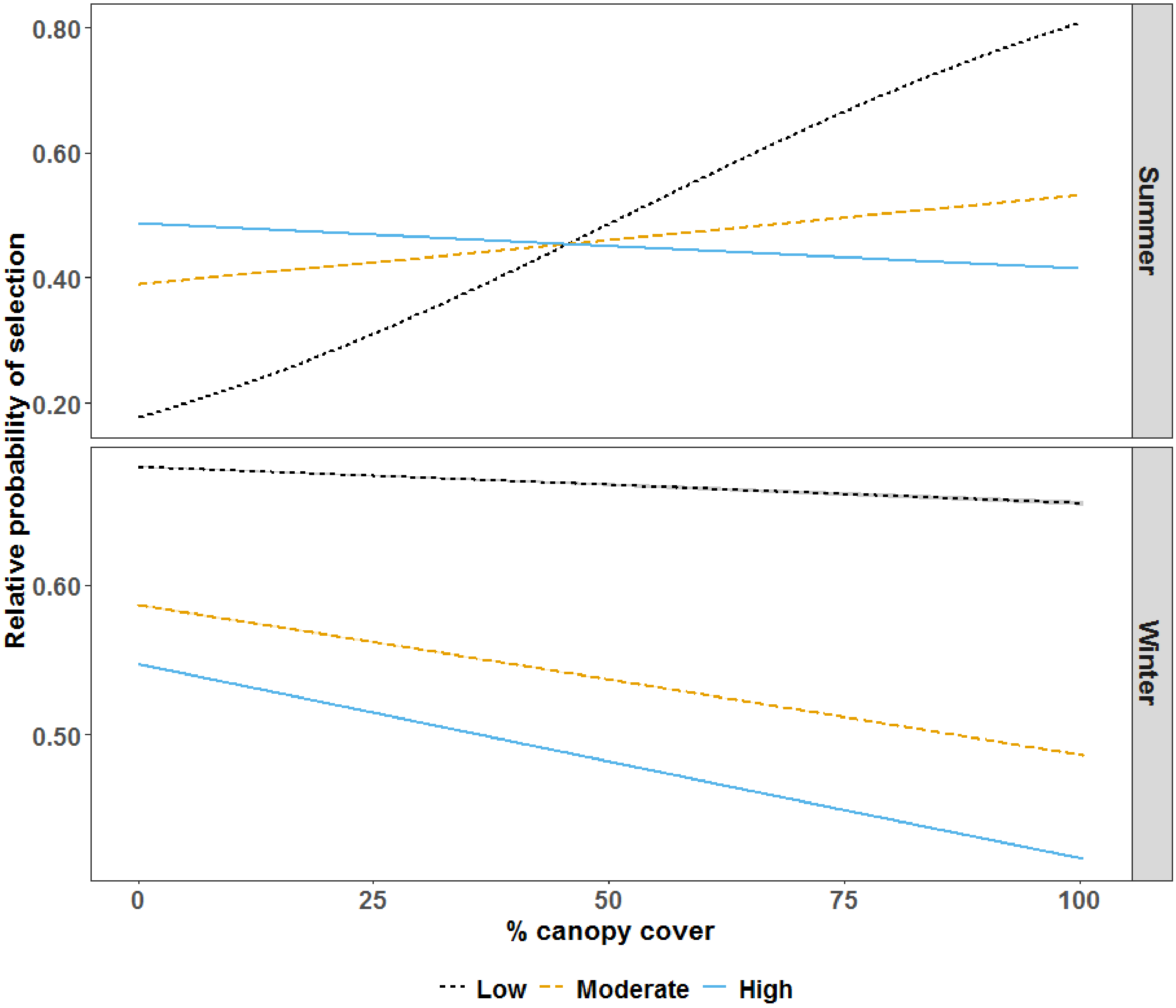

Figure 3.3. Relative probably of habitat selection by mountain moose between 2008 and 2010 in west-central Alberta, Canada, in relation to percent canopy cover and the forest density . Density is represented by the mean of the lower (Low), middle (Moderate), and upper (High) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

3.2. Fine-scale habitat selection

3.2.1. Foothills

At fine-scales, during winter and summer foothills moose selected lower elevations, wet areas, areas closer to water, areas with lower densities of conifer forest, and areas that were wet shrub (Table 3.3).

3.2.1.1. Seismic lines

During winter, foothills moose selected areas closer to seismic lines, specifically they selected areas closer to wetter seismic lines with higher vegetation and drier seismic lines with lower vegetation (Figure 3.4). During summer, foothills moose generally selected areas farther from seismic lines, but when they were close to seismic lines they selected seismic lines with lower vegetation height (Figure 3.5; Table 3.3). K-fold cross validation indicated poor to good model fit during winter (mean Obs r_s = 0.61 [range 0.39 – 0.75], mean Rand r_s = 0.02 [range -0.04-0.07]) and moderate to excellent model fit during summer (mean Obs r_s = 0.69 [range 0.45 – 0.89], mean Rand r_s = 0.03 [range -0.02-0.08]).

3.2.1.2. Harvest blocks

During winter, foothills moose selected areas closer to harvest blocks with higher vegetation, but with lower vegetation heights, moose neither selected areas closer to or farther from harvest blocks (Figure 3.6.). During summer, foothills moose selected areas closer to harvest blocks; specifically, harvest blocks with lower vegetation height (Figure 3.7; Table 3.3). K-fold cross validation indicated poor to good model fit during winter (mean Obs r_s = 0.67 [range 0.34 – 0.87], mean Rand r_s = 0.003 [range -0.05-0.06]) and moderate to good model fit during summer (mean Obs r_s = 0.71 [range 0.53 – 0.80], mean Rand r_s = 0.03 [range 0.01-0.05]).

3.2.1.3. Wellsites

During winter and summer, foothills moose selected areas closer to wellsites. In particular, moose selected areas closer to wetter wellsites during winter (Figure 3.8), and closer to active wellsites during summer (Figure 3.8; Table 3.3). K-fold cross validation indicated moderate to good model fit during winter (mean Obs r_s = 0.65 [range 0.45 – 0.79], mean Rand r_s = 0.02 [range -0.07-0.10]) and moderate to good model fit during summer (mean Obs r_s = 0.71 [range 0.53 – 0.80], mean Rand r_s = 0.03 [range 0.01-0.05]).

3.2.1.4. Roads

During winter, foothills moose selected areas closer to roads that were within other disturbances (i.e., wellsites, harvest blocks) and selected areas farther from roads that were not within disturbances (Table 3.3). During summer, foothills moose selected areas closer to roads that were in forest and areas farther from roads that were not in forest (Table 3.3). K-fold cross validation indicated poor to good model fit during winter (mean Obs r_s = 0.52 [range 0.37 – 0.77], mean Rand r_s = 0.02 [range -0.04-0.07]) and moderate to good model fit during summer (mean Obs $r_s = 0.71$ [range 0.49 – 0.79], mean Rand $r_s = 0.03$ [range 0.01-0.05]).

3.2.1.5. Pipelines

During winter and summer, foothills moose selected areas closer to pipelines and were more likely to select pipelines that were not in forest. K-fold cross validation indicated moderate to good model fit for models during winter (mean Obs $r_s = 0.59$ [range 0.45 – 0.78], mean Rand $r_s = 0.04$ [range -0.03-0.08]) and summer (mean Obs $r_s = 0.71$ [range 0.54 – 0.79], mean Rand $r_s = 0.03$ [range 0.02-0.04]).

Table 3.3 Mean standardized model coefficients (β) and lower and upper 95% confidence intervals (LCL, UCL) describing fine-scale habitat selection for foothills moose within west-central caribou herd ranges in Alberta, Canada during, summer and winter 2008-2010. Population-level coefficients were calculated using inverse weighting. Variables are described in Table 2.2. Non-disturbance coefficients are mean values across all models, disturbance coefficients are values from models fit to each disturbance type.

	Winter			Summer		
	β	LCL	UCL	β	LCL	UCL
Elev	-0.3349	-0.3695	-0.3003	-0.3837	-0.3988	-0.3686
eWAM	-0.0494	-0.0543	-0.0445	-0.1329	-0.1354	-0.1304
dWater_20K[1]	-0.0476	-0.0500	-0.0452	-0.0396	-0.0412	-0.0380
dWater_1M[1]	-0.0135	-0.0159	-0.0112	0.0641	0.0624	0.0657
Wet shrub	0.3115	0.3064	0.3167	-	-	-
Conifer.pct	-0.3162	-0.3193	-0.3131	-0.2065	-0.2078	-0.2052
dPipelines[1]	-0.0081	-0.0108	-0.0054	0.0145	0.0135	0.0155
Pipe_forest	-0.4902	-0.5404	-0.4400	-0.0894	-0.1043	-0.0745
dSeismic[2]	-0.0851	-0.0862	-0.0840	0.0124	0.0115	0.0132
Seismic_veght	-0.0089	-0.0113	-0.0064	-0.0061	-0.0072	-0.0050
Seismic_eWAM	0.0070	0.0056	0.0085	-	-	-
dSeismic[2]*Seismic_veght	-0.0058	-0.0076	-0.0040	0.0030	0.0019	0.0040
dSeismic[2]*Seismic_eWAM	0.0269	0.0259	0.0278	-	-	-
Seismic_veght: Seismic_eWAM	-0.0267	-0.0297	-0.0237	-	-	-
dSeismic[2]: Seismic_veght: Seismic_eWAM	0.0129	0.0108	0.0150	-	-	-
dCut[1]	-0.1025	-0.1065	-0.0986	-0.0620	-0.0654	-0.0587
Cut_veght	-0.1599	-0.1667	-0.1530	-0.0675	-0.0751	-0.0598
dCut[1]: Cut_veght	-0.1674	-0.1728	-0.1619	0.0256	0.0219	0.0294
dRoads[1]	0.0762	0.0747	0.0778	0.0945	0.0925	0.0964
Road_disturbance	-0.2354	-0.2450	-0.2258	-	-	-
Road_forest	-	-	-	0.1894	0.1781	0.2007
dRoads[1]*Road_disturbance	-0.1722	-0.1773	-0.1672	-	-	-
dRoads[1]: Road_forest	-	-	-	-0.1171	-0.1266	-0.1076
dWellsites[1]	-0.0334	-0.0361	-0.0306	-0.0215	-0.0290	-0.0140
Wellsite_eWAM	-0.1296	-0.1341	-0.1250	-	-	-
Wellsite_activity	-	-	-	-0.0965	-0.1091	-0.0840
dWellsites[1]: Wellsite_eWAM	-0.0005	-0.0013	0.0003	-	-	-
dWellsites[1]: Wellsite_activity	-	-	-	-0.0501	-0.0588	-0.0413

[1]exponential decay at 1km, [2]exponential decay at 2km

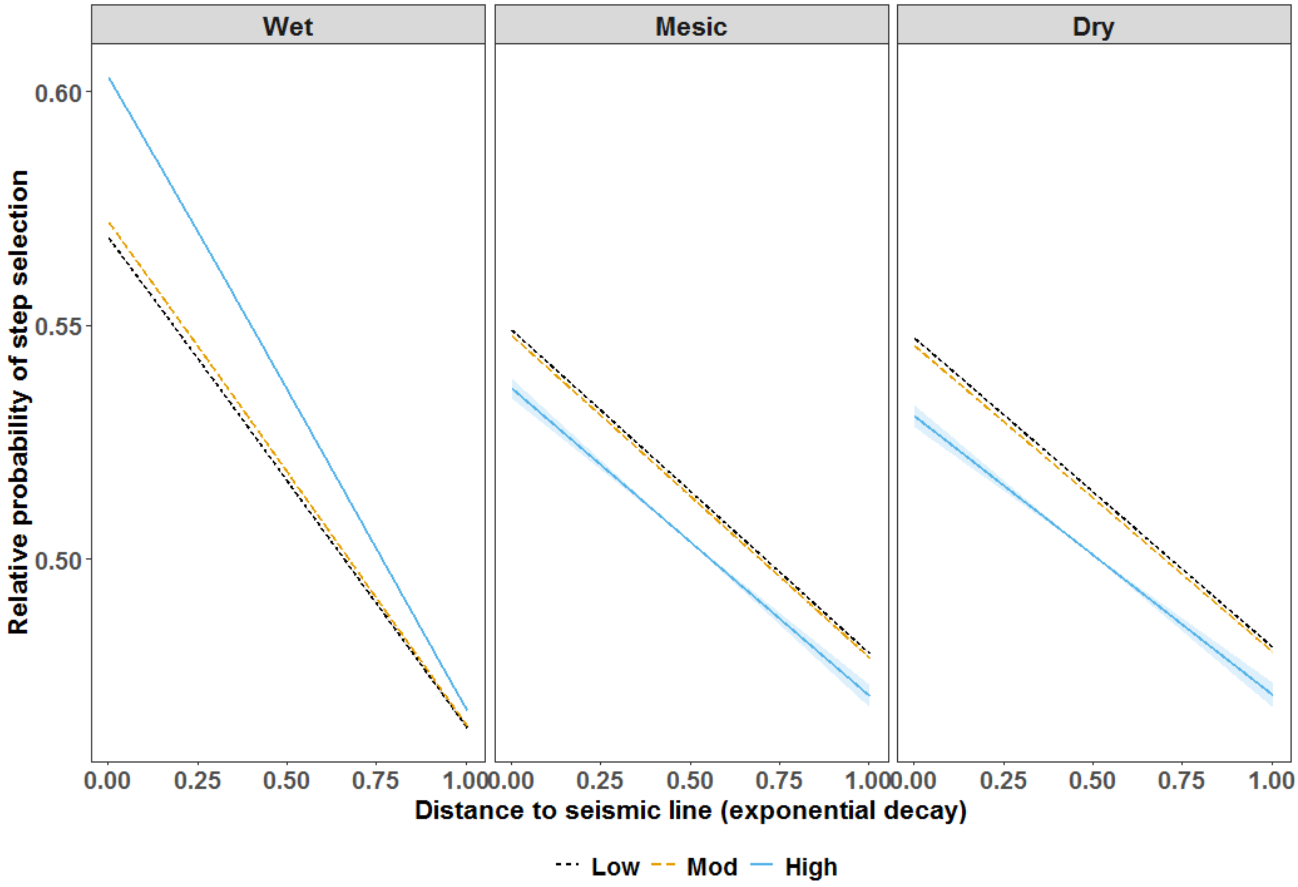

Figure 3.4. Relative probably of step selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during winter in relation to distance to seismic lines vegetation height on seismic lines (visualized using the mean of the lower (Low), middle (Mod), and upper (High) quantiles), and seismic line wetness (visualized using the mean of the lower (Wet), middle (Mesic), and upper (Dry) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

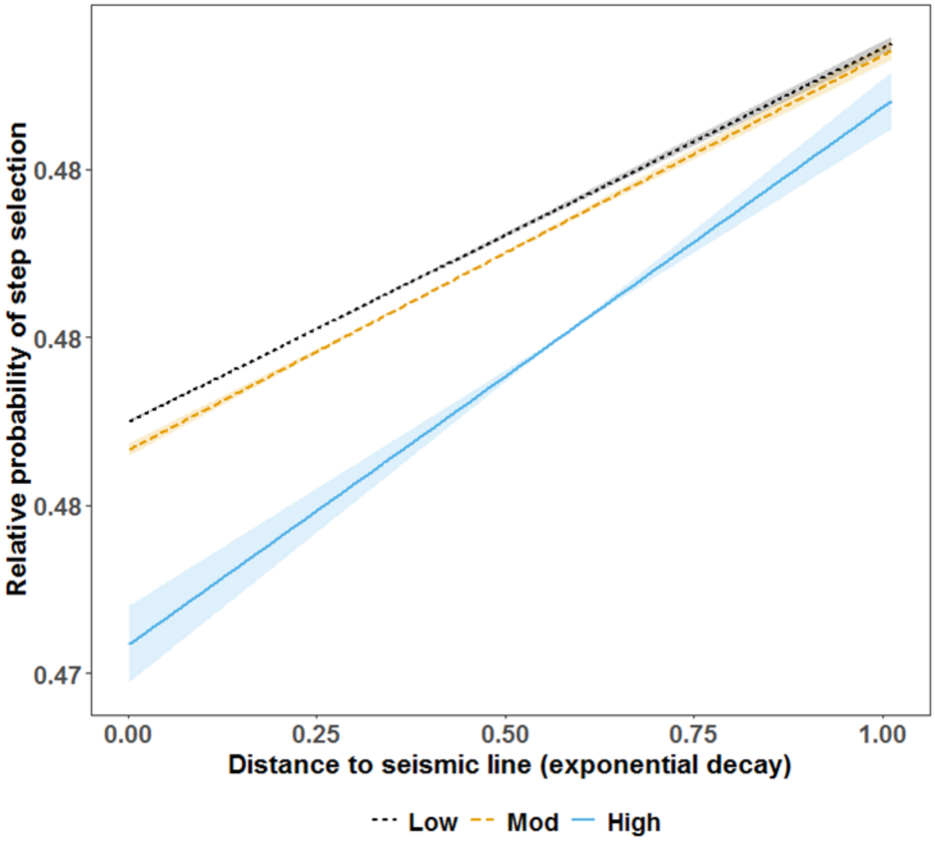

Figure 3.5. Relative probably of step selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during summer in relation to distance to seismic lines and vegetation height on seismic lines (visualized using the mean of the lower (Low), middle (Mod), and upper (High) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

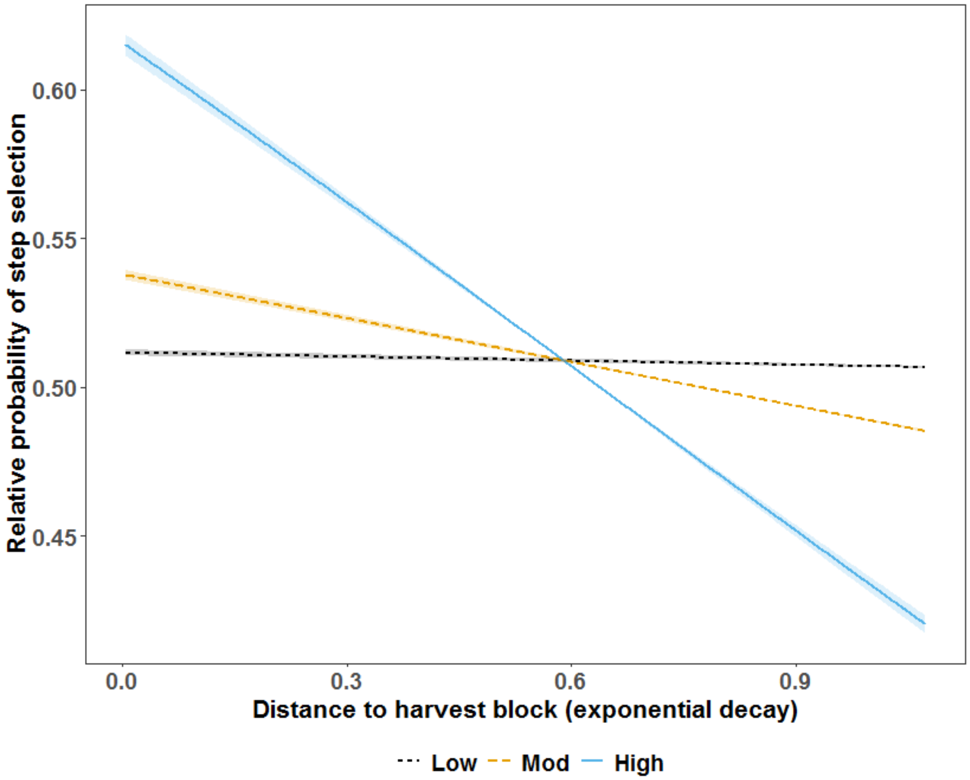

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Figure 3.6. Relative probably of step selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during winter in relation to distance to harvest blocks and vegetation height within harvest blocks (visualized using the mean of the lower (Low), middle (Mod), and upper (High) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

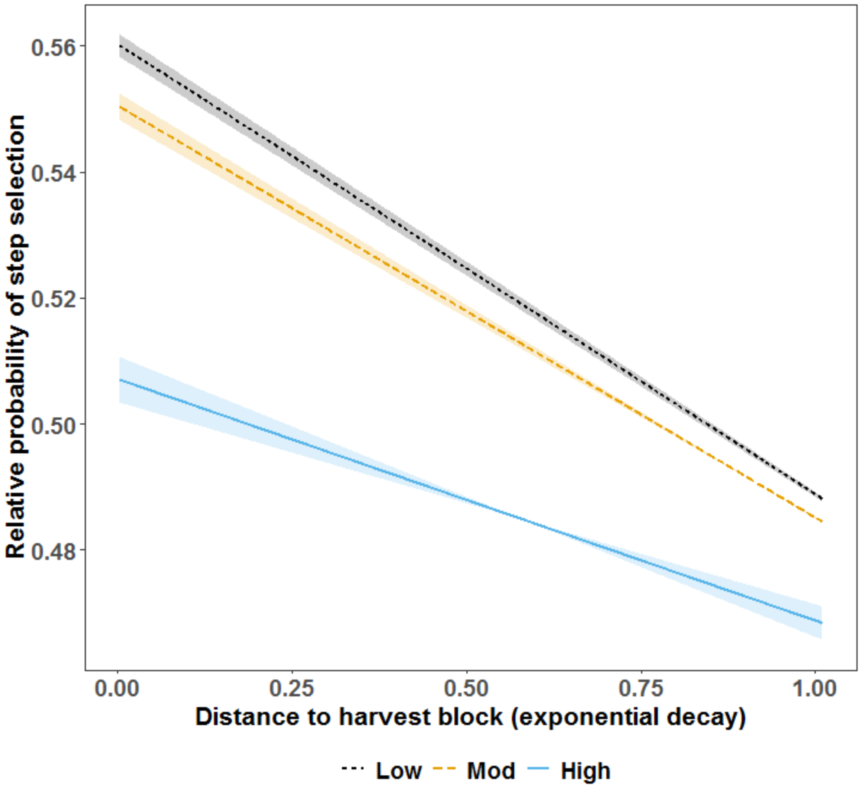

Figure 3.7. Relative probably of step selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during summer in relation to distance to harvest blocks and vegetation height within harvest blocks (visualized using the mean of the lower (Low), middle (Mod), and upper (Higher) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

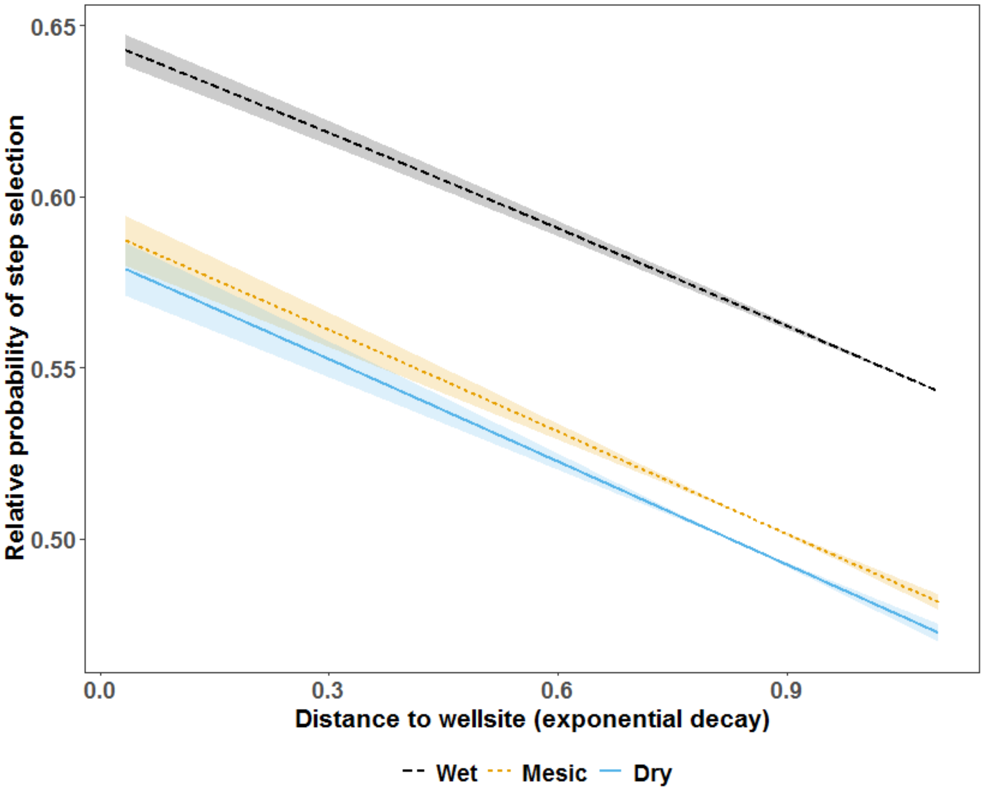

Figure 3.8. Relative probably of step selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during winter in relation to distance to wellsites and wellsite wetness (visualized using the mean of the lower (Wet), middle (Mesic), and upper (Dry) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

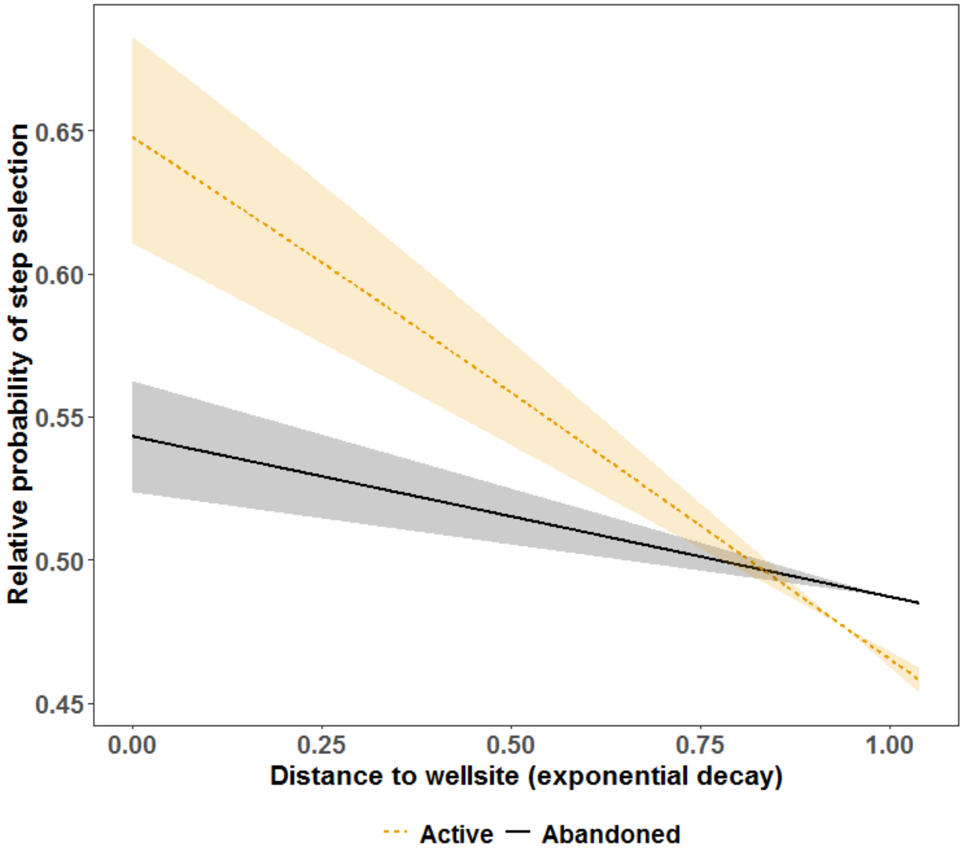

Figure 3.9. Relative probably of step selection by foothills moose between 2008 and 2010 in west-central Alberta, Canada, during summer in relation to distance to wellsites and wellsite activity (Active or Abandoned). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

3.2.2. Mountains

During winter and summer, mountain moose selected lower elevation areas (Table 3.4). During winter, moose selected areas with lower canopy cover regardless of forest density, but moose generally selected forests with less canopy cover when they were in areas with lower forest densities (Figure 3.10, Table 3.4). During winter, mountain moose generally selected areas farther from seismic lines, but when they were in areas close to seismic lines they selected seismic lines with lower vegetation (Figure 3.11, Table 3.4). During summer, moose selected forest stands with greater canopy cover when they were in areas with lower forest densities, but when moose were in areas with higher forest densities there was generally no relationship between moose habitat use and canopy cover (Figure 3.10, Table 3.4).

Table 3.4 Standardized model coefficients (β) and lower and upper 95% confidence intervals (LCL, UCL) describing fine-scale habitat selection for mountain moose within west-central caribou herd ranges in Alberta, Canada, during summer and winter 2008-2010. Population-level coefficients were calculated using inverse weighting. Variables are described in Table 2.2.

	Winter			Summer		
	β	LCL	UCL	β	LCL	UCL
Elev	-1.6135	-1.6490	-1.5780	-0.0995	-0.1061	-0.0929
Canopy	-0.0745	-0.0762	-0.0727	0.1042	0.1029	0.1054
Forest1km	0.1111	0.0863	0.1360	-0.1087	-0.1171	-0.1004
dSeismic[1]	0.0066	0.0058	0.0074	-	-	-
Seismic_veght	-0.0086	-0.0112	-0.0061	-	-	-
Seismic_eWam	0.1112	0.1089	0.1136	-	-	-
Canopy*Forest1km	-0.0082	-0.0119	-0.0046	-0.2686	-0.2706	-0.2665
dSeismic[1]*Seismic_veght	0.0143	0.0135	0.0152	-	-	-
dSeismic[1]*Seismic_eWam	0.0440	0.0436	0.0444	-	-	-
Seismic_veght*Seismic_eWam	0.0100	0.0084	0.0116	-	-	-
dSeismic[1]*Seismic_veght*Seismic_eWam	0.0146	0.0140	0.0151	-	-	-

[1] exponential decay at 1km

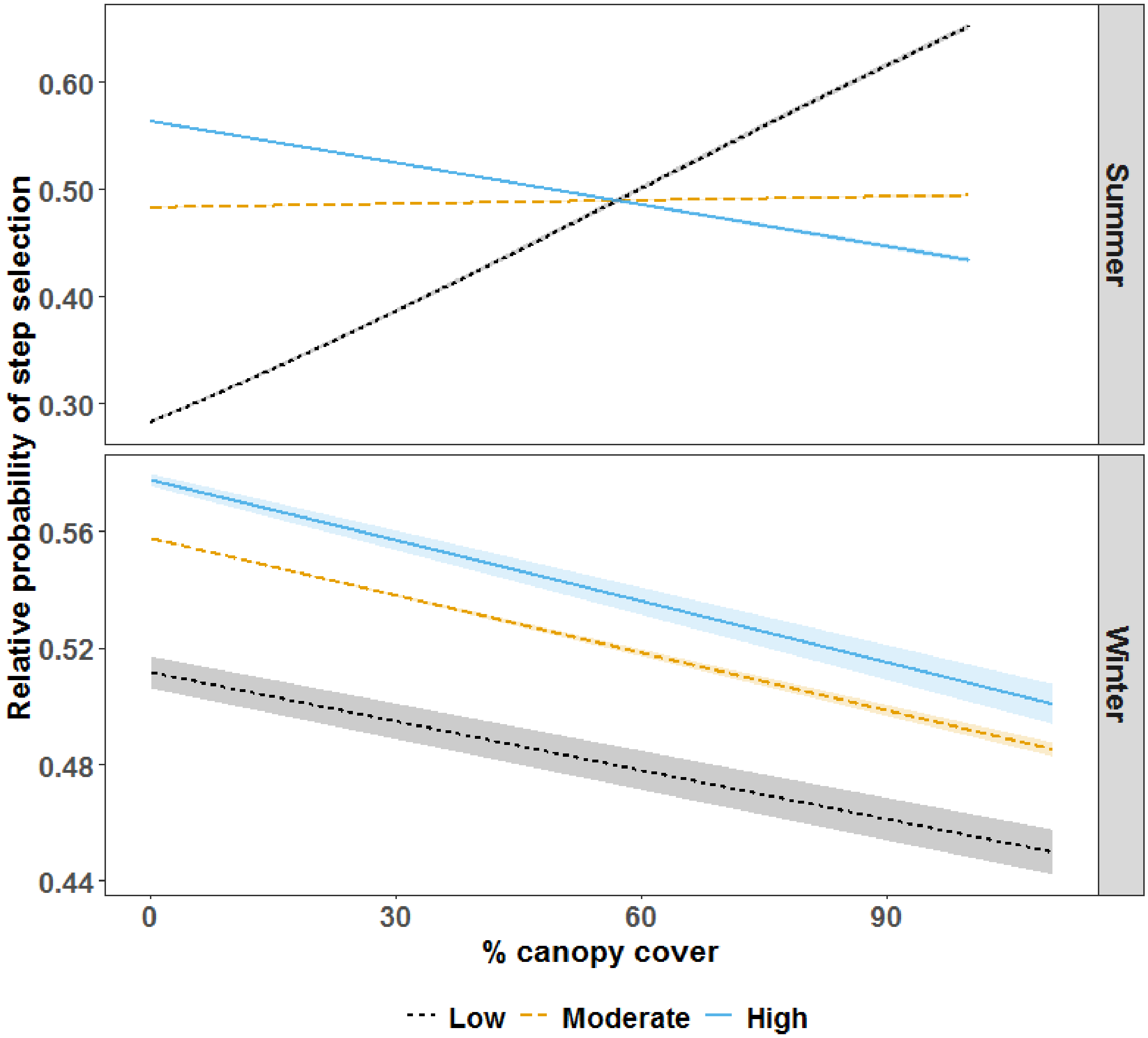

Figure 3.10. Relative probably of step selection by mountain moose between 2008 and 2010 in west-central Alberta, Canada, during winter in relation to the percent canopy cover and the density of forest (visualized using the mean of the lower (Low), middle (Moderate), and upper (High) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

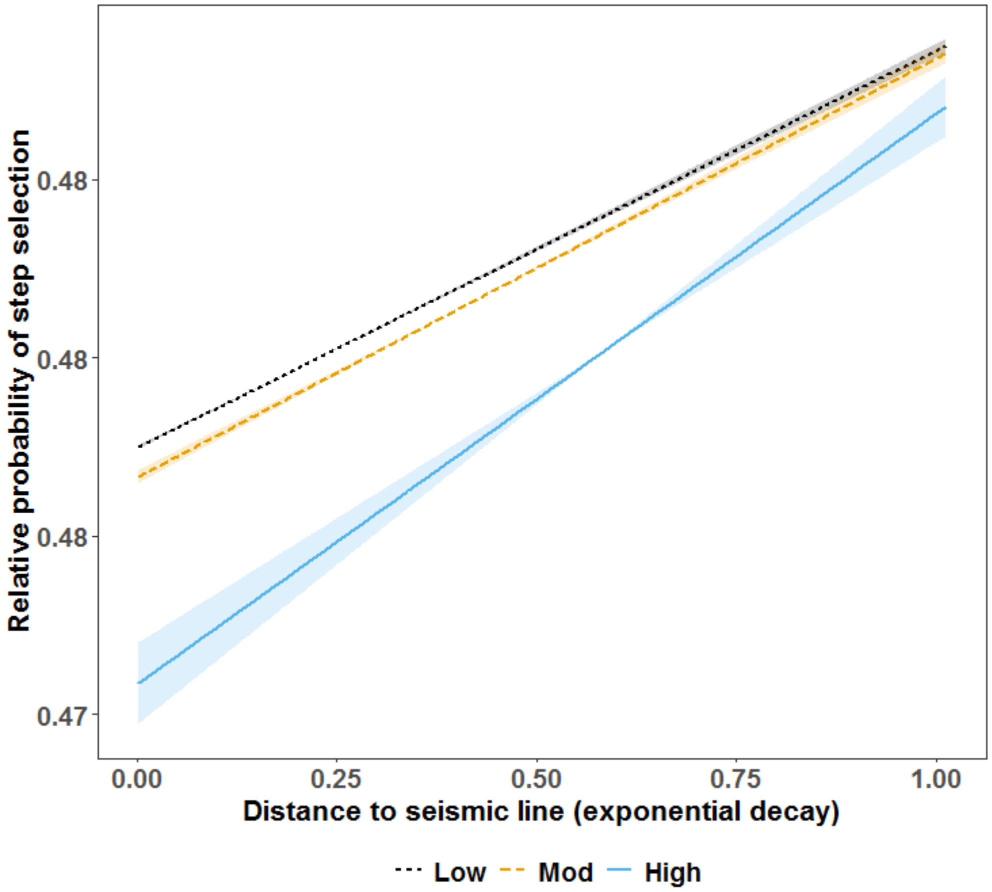

Figure 3.11. Relative probably of step selection by mountain moose between 2008 and 2010 in west-central Alberta, Canada, during winter in relation to distance to seismic lines and vegetation height on seismic lines (visualized using the mean of the lower (Low), middle (Mod), and upper (High) quantiles). All other variables were held at their mean or reference categories for prediction. Shaded areas are 95% confidence intervals around the mean.

4. DISCUSSION

In accordance with previous research (Cassing et al., 2006; Gagné et al., 2016; van Beest et al., 2010), we found moose selected areas associated with forage availability at both the landscape- and fine-scales. However, we also found that moose response to disturbance varied with the density of those disturbances on the landscape and with differing attributes of disturbances (e.g., vegetation height and soil moisture) at fine-scales (Melin et al., 2016). Our study is one of the first to directly assess moose functional response to habitat disturbance at the landscape-scale and moose response to attributes of disturbances at a fine-scale; providing valuable information that could be used for conservation and restoration planning to benefit caribou.

4.1. Response to habitat and terrain

At landscape- and fine-scales, moose habitat selection was related to topography, habitat, and soil wetness. Specifically, moose in the foothills and mountains selected wetter areas, and foothills moose also selected areas with lower percent conifer cover. These results are in accordance with previous research describing moose selection of wet areas and areas with abundant deciduous shrub forage (Courtois et al., 1998; Dickie et al., 2019; Mumma et al., 2018; Peters et al., 2013; Street et al., 2015b). Moose response to elevation varied across seasons and scales; moose selected lower elevations during winter and higher elevations during summer at the landscape-scale, but selected lower elevations during both winter and summer at the fine-scale. During winter, landscape-scale selection for lower elevations is likely driven by avoidance of the deeper snow pack at higher elevations (Peters et al., 2013; Telfer and Kelsall, 1984), while the year-round fine-scale selection for lower elevations might be indicative of moose selecting valley bottoms and low-lying wetter areas with abundant forage.

Moose response to canopy cover varied with the density of forest at landscape and fine-scales. During summer, at both scales, mountain moose selected greater canopy cover when they were in areas with lower forest densities, but during winter, mountain moose selected decreased canopy cover regardless of forest densities. Moose are susceptible to heat stress (Dussault et al., 2004). Therefore moose habitat selection during summer is a trade-off between access to thermal cover and access to forage, and moose tend to seek the shade provided by mature conifer stands (Beest et al., 2012), and generally select cooler areas (Pigeon et al., 2019; Schwab and Pitt, 1991). Therefore, when mountain moose are in areas with low forest densities, it is probable that access to thermal cover drives the selection of stands with greater canopy cover. In areas with higher forest densities, thermal cover is more available to moose, and canopy cover is likely less important. Although winter habitat selection by moose can also be limited by thermal cover (Schwab and Pitt, 1991), moose tend to select thermal cover over forage availability more during summer when compared to winter (Beest et al., 2012), and moose in our study selected stands with less canopy cover during winter, regardless of forest densities. Moose selection for more open canopy forest in winter may be driven by better access to forage in open canopy and deciduous stands (Courtois et al., 2007; Gagné et al., 2016).

4.2. Seismic lines

During winter and summer, we found that moose selected areas closer to seismic lines in regions with lower seismic line densities, while moose selected areas farther from seismic lines in regions with higher seismic line densities. Mumma et al. (2018) reported that moose in north-western British Columbia selected areas with lower densities of seismic lines during summer, and Dickie et al. (2019) reported that moose in north-eastern Alberta avoided seismic lines during summer. However, neither study assessed both distance to seismic lines and densities of seismic lines. Furthermore, Dickie et al. (2019) found that when moose were on seismic lines they moved faster, and the authors suggested that moose may perceive seismic lines as areas with high predation risk. As numerous studies have described selection of seismic lines by predators (James and Stuart-Smith, 2000; Tigner et al., 2014), and because seismic lines are also used for travel by predators (Dickie et al., 2017; Finnegan et al., 2018b), it is likely that moose associate seismic lines with predation risk. However, seismic lines also contain abundant moose forage (Finnegan et al., 2018a), and seismic lines may also be efficient movement routes during winter (Collins and Helm, 1997; Telfer and Kelsall, 1984). In areas with high densities of seismic lines, moose selection of seismic lines may be masked by the high availability of seismic lines on the landscape, or moose may simply avoid these features because they are used by predators. In areas with low seismic line densities, moose may be more likely to select for these less available features as they contain forage or serve as attractive movement routes in otherwise undisturbed forest stands. Assessing functional responses of moose selection of seismic lines relative to large disturbances associated with abundant forage (e.g., harvest blocks) and natural and anthropogenic linear features associated with movement (e.g., rivers, roads, pipelines) will help to further understand this relationship, and to determine whether the functional response we observed is driven by access to forage or by movement efficiency. In contrast to foothills moose, mountain moose avoided seismic lines during winter. In high elevation areas, wolves use linear features like trails and seismic lines for travel, and to increase hunting efficacy (Whittington et al., 2011), and mountain moose may be avoiding seismic lines to avoid encounters with predators.

At fine-scales, foothills moose selected wetter seismic lines with higher vegetation and drier seismic lines with lower vegetation during winter, but consistent with Dickie et al. (2019), moose generally avoided seismic lines during summer. Wetter seismic lines have more moose forage, and seismic lines with higher vegetation have more larger browse species like willow (*Salix* spp.) and alder (*Alnus* spp.) (Finnegan et al., 2018a) which are accessible as forage during winter as they are taller than the snow pack. In contrast, drier seismic lines with lower vegetation may be preferred for movement. We found that moose avoided seismic lines during summer, and as wolves use seismic lines for travel primarily during the snow free months (Finnegan et al., 2018b), it is probable that moose respond to seismic lines as areas with elevated predation risk during summer. Combined, our results at the landscape and fine-scales reveal that moose response to seismic lines varies across regions, seasons, and spatial scales, and is linked to characteristics of seismic lines such as vegetation height and seismic line wetness. Moose response to seismic lines in caribou ranges is likely driven by a number of non-exclusive factors relative to food availability, predation risk and movement efficacy.

4.3. Roads and Pipelines

At landscape-scales we found that moose avoided roads, and were more likely to be closer to roads only when they were in areas with higher road densities. High-traffic linear features like roads are generally avoided by moose (Bartzke et al., 2015; Bowman et al., 2010), which can create barriers to movement and gene flow (Finnegan et al., 2012). However, our results indicate that in areas with higher road densities, moose were more likely to be closer to roads, which could increase mortality risk for moose due to the vehicles, hunters, and predators associated with roads (Bangs et al., 1989; Seiler, 2005). At fine-scales, when moose were close to roads, moose response to roads was driven by the surrounding habitat matrix, with foothills moose selecting roads in disturbances like harvest blocks and wellsites during winter, and roads in forest during summer. During winter it is probable that moose are selecting areas closers to roads in disturbances to access the abundant forage associated with large disturbances (Bergqvist et al., 2018; Bjørneraas et al., 2012; Telfer, 1970), while during summer, when moose are close to roads may be selecting roads to balance thermal cover in forests (Schwab and Pitt, 1991; Street et al., 2015a) against access to vegetative food at road edges (Roever et al., 2008).

Both foothills and mountain moose avoided pipelines at the landscape scale during winter. However, during summer, foothills moose selected pipelines irrespective of the densities of pipelines in the surrounding landscape. At fine-scales, foothills moose selected pipelines during winter and summer, especially pipelines in forest. Unlike seismic lines, pipelines are actively maintained (Alberta Energy Regulator, 2016), so although they contain abundant moose forage, this forage is primarily low growing species such as graminoids and sedges (MacDonald et al., 2020) which are unavailable during winter. Our results suggest that moose avoid pipelines at broad-scales in winter, but at fine-scales when moose are close to pipelines they may use them as movement routes (Collins and Schwartz, 1998), and may be using pipelines as a source of forage or as movement routes during summer (MacDonald et al., 2020). Linking moose selection of roads and pipelines to abundance of forage species could help to further interpret moose use of roads and pipelines across seasons.

4.4. Harvest blocks

During summer and winter, foothills moose selected areas closer to harvest blocks. We also found a functional response of foothills moose to the density of harvest blocks during summer, with moose selecting areas closer to harvest blocks when they were in areas with lower densities of harvest blocks. Moose preference for harvested areas has been described previously (Fisher and Burton, 2018; Peters et al., 2013; Street et al., 2015b; Telfer, 1970). However, the functional response that we observed during summer is most likely driven by access to forage in areas where the densities of early seral habitat area are lower. This could be confirmed by assessing functional responses of moose to harvest blocks relative to other disturbances (e.g. linear features, wellsites).

At fine-scales, foothills moose selected areas closer to harvest blocks with higher vegetation, while during summer they selected areas closer to harvest blocks with lower vegetation. As with patterns observed for seismic lines and pipelines, harvest blocks with higher vegetation may have taller woody shrubs available to moose during winter, while harvest blocks with lower vegetation may have the graminoids and forbs preferred by moose during summer (Street et al., 2015b; van Beest et al., 2010). In a previous analysis we found that moose selected harvest blocks with higher canopy cover (Pigeon et al., 2019), and we hypothesized that this was due to higher snow interception and sheltering properties (Bjørneraas et al., 2011; Telfer, 1978); therefore, it is also possible that moose are selecting harvest blocks with higher vegetation during winter due to the higher snow interception by the vegetation, providing lower snow pack on the ground and greater ease of movement.

4.5. Wellsites

We also found a functional response of moose to wellsites, with foothills moose selecting areas closer to wellsites during summer regardless of wellsite densities, but selecting areas closer to wellsites during winter when they were in areas with higher wellsite densities. These results suggest that wellsites are preferred by moose during summer, but are used similar to their availability on the landscape during winter. Inactive wellsites contain forbs and graminoids (McKay et al., 2014), which are important moose summer forage (Street et al., 2015b; van Beest et al., 2010), and may explain moose preference for wellsites during that season. However, at fine-scales we found that moose selected active wellsites rather than inactive wellsites. Active wellsites are avoided by wolves, so active wellsites may be refugia for moose during summer, however wolves primarily avoid wellsites with high activity during winter rather than during summer (MacNearney et al., 2017) so why moose prefer active wellsites during that season is unclear. Further analysis including additional levels of wellsite activity (e.g. drilling, active, abandoned) rather than simply active and abandoned status.

4.6. Conclusions

By assessing how moose respond to disturbance at multiple scales and how response varies as function of the surrounding habitat matrix, regeneration, and activity levels of the disturbance, this study has provided valuable information that may be used to prioritize habitat restoration and mitigations to benefit caribou. Specifically, for seismic lines, by demonstrating functional responses of moose to seismic lines, this study has illustrated the importance of considering the density of seismic lines across landscapes when directing restoration efforts. Both moose and wolves (Pigeon et al., 2020) are more likely to select seismic lines in areas with lower densities of seismic lines; therefore, if all but a few seismic lines are restored within an area, predation risk for caribou could actually increase near the remaining unrestored seismic lines. We also found that other linear features like roads and pipelines were selected in some seasons and regions, and assessing functional responses of seismic lines relative to those disturbances could help understand how restoration activities may change the distribution of moose. Like wolves (Finnegan et al., 2018b), we found that moose select seismic lines with higher vegetation during winter, which we hypothesize is linked to the availability of browse on those features (Finnegan et al., 2018a) which likely attracts moose and their predators. This study provides further evidence that restoration aimed at reducing predator movement on seismic lines (‘functional restoration’) and focused on the specific composition of vegetation on seismic lines (‘structural restoration’) is likely to be the most beneficial for caribou (Ray, 2014).

At fine-scales, we also demonstrated that moose response to disturbance varied with characteristics of disturbances. Focusing on forest harvesting, moose selected harvest blocks with more deciduous trees, more deciduous shrubs, fewer pine or spruce trees planted (Pigeon et al., 2019), and selected harvest blocks with lower vegetation heights during summer, and higher vegetation height during winter. Forest land managers could consider these habitat preferences into future harvest planning in caribou ranges. Finer-scale analysis of additional attributes of harvest blocks and the collection of data regarding ungulate use of harvest blocks is underway. When combined with the results from this project, these finer-scale analyses will provide valuable information that could be used to inform which silviculture practices could best contribute towards caribou conservation. Overall this study has illustrated the importance of considering functional responses to disturbance for generalist herbivores like moose and highlights that research focusing only on densities of disturbances (Fisher and Burton, 2018; Mumma et al., 2018) or distance to disturbances (Dickie et al., 2019) may provide incomplete information.

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