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Walking the line: Investigating biophysical characteristics related to wildlife use of linear features

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Abstract

1. Habitat restoration is a necessary component of wildlife conservation in anthropogenic landscapes. To ensure restoration initiatives achieve the desired effects on wildlife communities, it is useful to investigate how animals use landscape features. Understanding the relationships between wildlife use and ecological cues provides specific and measurable targets that can be used to measure restoration success.
2. In western Canada, linear feature networks formed by seismic lines, pipelines and roads have altered the boreal forest landscape and resulted in population declines for woodland caribou. Restoration is aimed at supporting caribou recovery by deterring linear feature use by caribou predators and ungulate competitors. Information on how linear feature characteristics facilitate or deter wildlife use supports restoration initiatives by providing specific targets for restoration.
3. Here, we used wildlife track and sign data to investigate biophysical characteristics related to the use of linear features by canines, bears, deer, elk and moose in caribou ranges of west-central and north-western Alberta and British Columbia. We built generalized linear mixed models consistent with three hypotheses that could explain likely mechanisms for use: (1) ease of movement, (2) risk avoidance and (3) resource availability (prey and forage).
4. Moose, deer, elk and bears were more likely to use linear features with either human or game trails. Bears and canines were less likely to use seismic lines with greater lateral vegetation cover and taller vegetation, respectively. Moose, deer and elk were more likely to use linear features with a greater cover of ungulate forage taxa such as willow, birch, sedges and forbs.
5. These results suggest that restoration focusing on trails, online vegetation structure and online vegetation type should deter predators and ungulate prey species to the overall benefit of caribou. Our study corroborates the findings of other research recommending structural and functional restoration using high-intensity line blocking and vegetative regeneration. We provide specific targets for linear

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feature restoration to assist in prioritization according to restoration objectives, which translates to a broader goal of linking local-level restoration actions to landscape-level conservation goals. This approach to restoration has implications for any major system experiencing anthropogenic landscape change.

KEYWORDS
anthropogenic disturbance, boreal forest, caribou conservation, pipelines, restoration ecology, seismic lines, wildlife forage

1 | INTRODUCTION

In the modern age of anthropogenic landscape change, restoration ecology is gaining traction as a means of conserving biodiversity (McMahen & Klees van Bommel, 2020; Possingham et al., 2015; Wiens & Hobbs, 2015). Over 75% of the Earth's terrestrial surface has been modified by humans and vertebrate populations have shrunk by almost 70% (WWF, 2020), indicating that restoration is needed in addition to habitat protection to conserve remaining vertebrate biodiversity. To this end, the United Nations declared 2021–2030 the Decade on Ecosystem Restoration to encourage member states to support and promote restoration initiatives across degraded ecosystems (United Nations, 2019). Achieving global conservation goals requires that restoration projects have specific, measurable objectives linking actions to desired outcomes (Cooke et al., 2018; Suding, 2011). Furthermore, restoration must be process-based—that is, sensitive to the underlying ecological interactions species have with the landscape (Ford, 2021)—to connect structural restoration techniques to the relationships in need of recovery.

In Canada, a high-profile case of applying habitat restoration to wildlife conservation is linear feature restoration to protect woodland caribou (*Rangifer tarandus caribou*, hereafter caribou). Decades of forestry and energy development have created linear disturbances across the boreal forest that dramatically alter landscape structure; the last published inventory a decade ago measured over 600,000 km of linear disturbances (Pasher et al., 2013; Pickell et al., 2015). Linear feature networks formed by seismic lines, pipelines and industrial access roads contribute to forest fragmentation and a shift towards early-seral vegetation (Dabros et al., 2018; Finnegan et al., 2019; Pattison et al., 2016), both of which affect how wildlife use the boreal forest landscape. The increase in early-seral vegetation on linear features provides browse for moose (*Alces alces*), deer (*Odocoileus* spp.) and elk (*Cervus elaphus*), resulting in enhanced apparent competition between these species and caribou (Finnegan, MacNearney, et al., 2018; Latham et al., 2011; MacDonald et al., 2020). Linear features also form corridors that facilitate predator movement, increasing hunting efficiency for wolves (*Canis lupus*) and bears (*Ursus* spp.) and exacerbating risk for their ungulate prey (Dickie et al., 2019, 2022; McKay et al., 2021; Pigeon et al., 2016). Linear features regenerate slowly in the boreal forest, and in some cases regeneration stalls in an early-seral stage due to legacy construction protocols that damaged or removed topsoil layers. Therefore, active restoration efforts are required to restore community dynamics that are favourable to caribou (MacDonald et al., 2020; Nagy-reis et al., 2021; St-Pierre et al., 2021; van Rensen et al., 2015). To adequately address the impacts of linear features on caribou, restoration must rehabilitate landscape structure and function (Bentham & Coupal, 2015; Ray, 2014).

Multiple linear feature restoration programs have been initiated in recent years with variable success. Treatments focused on high-intensity application of log debris and tree-hinging, which target inhibiting movement along lines, have been successful (Keim et al., 2019; Neufeld, 2006), while treatments aimed at restoring structure and function by both inhibiting movement and reducing early-seral vegetation do not affect landscape use for all target species in the short-term (Beirne et al., 2021; Dickie et al., 2021; Tattersall et al., 2020b). Although vegetation treatments used to date increase tree density on linear features (Filicetti et al., 2019), these treatments do not directly target the biophysical characteristics of linear features to which wildlife respond. Without knowledge of the cues that correspond to wildlife use of linear features, restoration programs lack the specific, measurable objectives linking them to their intended purpose (St-Pierre et al., 2022).

In this study, we investigated how wildlife use of linear features related to biophysical characteristics. We used site-level wildlife track and sign data and field measurements of regenerating vegetation and surrounding habitat to investigate the relationships between biophysical characteristics of linear features and use of features by caribou, caribou predators and other ungulate prey species. We analysed each type of linear feature—seismic lines, pipelines and inactive forestry roads—separately to account for the different functions and restoration priority of each line type. We framed our analyses using three hypotheses that relate characteristics of linear features to predicted mechanisms for wildlife use of linear features: (1) ease of movement ('movement'), (2) risk avoidance ('risk') and (3) resource availability, which we subdivided into a prey availability ('prey') hypothesis for predators and a forage availability ('forage') hypothesis for ungulates and bears (Table 1). This approach was not a test of mechanisms for wildlife use of linear features per se; rather, it provided a systematic structure to decide which variables to test by linking habitat structure to function. By outlining specific characteristics to be targeted during restoration, the results from our study can be applied to evidence-based restoration practices that address the over-arching goals of caribou conservation. Our approach is also

TABLE 1 Three hypotheses and associated variables used to relate biophysical characteristics to wildlife linear feature use in west-central and north-western Alberta and British Columbia, Canada in 2014, 2015, and 2017 (variables explained in Table 2). Available literature supporting predictions are included as footnotes.

Hypothesis	Description	Predictions	Variables
1. Ease of movement	Wildlife use of linear features is best explained by trails, soil type and on-line vegetation characteristics that influence movement along lines	1. Line use more likely with the presence of human or game trails[a,b] 2. Line use more likely with dry soil, less likely with moist, spongy or wet soil[a] 3. Line use less likely with greater lateral cover and taller vegetation on-line[a,c]	HumanTrail + GameTrail + Dry + Moist + Spongy + Wet + OnLatCov + OnVegHt
2. Risk avoidance	Wildlife use of linear features is best explained by surrounding forest characteristics that provide cover, and presence of humans or predators that pose a risk	1. Line use more likely with greater lateral cover and taller trees in the surrounding forest[a] 2. Line use less likely with presence of humans and ungulate use less likely with presence of predators	OffTreeHt + OffLatCov + Human + Bear + Canine
3. Resource availability	Prey: Predator use of linear features is best explained by presence of prey species	1. Predator line use more likely with the presence of moose, deer, elk or caribou[d] 2. Predator line use more likely with the presence of any ungulate prey[d]	1. Moose + Deer + Elk + Caribou 2. AllPrey
	Forage: Ungulate and bear use of linear features is best explained by vegetation that provides forage	1. Ungulate and bear line use more likely with greater cover of vegetation used as forage by each species	Alnus + BEGL + Carex + Fother + Graminoids + Rhododendron + Salix + Trifolium + Vaccinium + VAVI

[a]Finnegan, Pigeon, et al. (2018).
[b]Tigner et al. (2014).
[c]Dickie et al. (2017).
[d]St-Pierre et al. (2022).

relevant outside of the boreal linear feature system and has implications for any disturbed landscape in need of restoration.

2 | MATERIALS AND METHODS

2.1 | Study areas

The study areas consisted of caribou ranges in west-central and north-western Alberta and British Columbia, Canada. The west-central area included four caribou ranges—Little Smoky, A la Peche, and the Alberta portions of Redrock-Prairie Creek and Narraway outside of protected areas (−117° W to −120° W, 53° N to 55° N). The north-western area included the Chinchaga range on both sides of the provincial border (−117° W to −122° W, 56° N to 58° N; Figure 1). The areas totalled 47,100 km^2 and contained over 92,943 km of linear features, including seismic lines, pipelines, and inactive forestry roads. Due to GIS data availability, we only sampled roads in Little Smoky and seismic lines in the Alberta portion of Chinchaga. The west-central ranges included portions of the subalpine, upper foothills, and lower foothills natural subregions (Natural Subregions Committee, 2006). Dominant forest cover in west-central ranges is 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. The north-western range included portions of the lower and upper boreal highlands natural subregions (Natural Subregions Committee, 2006) and the boreal white and black spruce biogeoclimatic zone (Meidinger & Pojar, 1991). In the north-western range, upland forests are white spruce, trembling aspen, and balsam poplar (*Populus balsamifera*) and lowland habitats are black spruce, larch and poorly drained muskeg and fen. Dominant soil types in both study areas are loam, organic and clay. Although the Chinchaga study area included north-western Alberta and a portion of north-eastern British Columbia, we hereafter refer to it as the north-western range.

2.2 | Field data collection and variables

The primary goal of field data collection was to collect information on the human use of linear features (Hornseth et al., 2018; Pigeon et al., 2016). No permits were required to carry out this fieldwork. Using a geographic information system (GIS) and a random number generator, we selected linear features that intersected access roads. We created a unique identifier for each linear feature (*LineID*) and established three plots at 0, 100, and 500 m away from the intersecting access road. We visited all west-central and north-western seismic line sampling sites in June–October 2014 and 2015, and north-western pipeline sites in August 2017 to record wildlife and human linear feature use, collect field measurements of linear feature and surrounding forest characteristics, and identify vegetation taxa. On the linear feature ('online'), we identified tracks, scat and

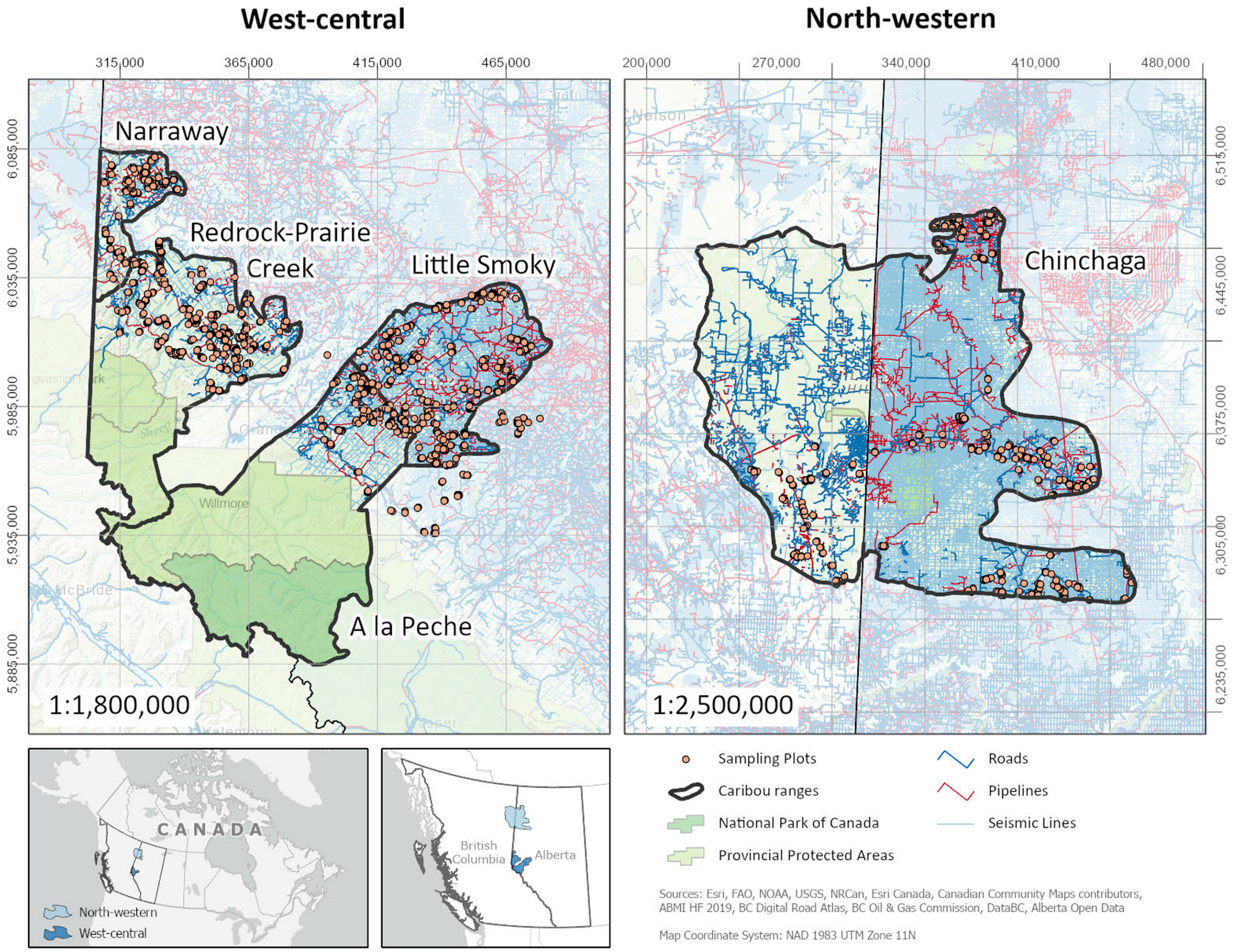

FIGURE 1 Study areas in caribou ranges of west-central and north-western Alberta and British Columbia, Canada, showing sampling locations where field data were collected on and beside linear features in 2014, 2015 and 2017.

any other wildlife and human sign. We classified canines (wolves and coyotes, *C. latrans*), bears (black bears, *U. americanus*, and grizzly bears, *U. arctos*) and deer (white-tailed deer, *O. virginianus*, and mule deer, *O. hemonius*) at the genus level and caribou, moose and elk at the species level. To account for weather impacts on tracks and signs, we assigned a confidence level to each observation and only included observations assigned confidence levels of 'reasonably certain' and 'certain' in statistical modelling. We measured an average online lateral vegetation cover from cover board measurements taken in both directions from the plot (Nudds, 1977), measured average vegetation height, recorded soil moisture and the presence/absence of human and game trails (see Pigeon et al., 2016 for details). In the surrounding forest ('offline', 15 m from the linear feature), we again measured lateral vegetation cover and average tree height. To record vegetation composition data, we established online 10 m^2 and a 1 m^2 subplots at the plot 100 m from the access road; we only recorded vegetation composition data within this plot because of limited time and resources for field data collection. Within these subplots, we identified and recorded percent ground cover of vegetation taxa used as forage by bears and caribou alternate competitors (Finnegan, MacNearney, et al., 2018). We included a full description of field variables used in models in Table 2. We standardized and scaled continuous and percent variables prior to modelling. Although surrounding habitat characteristics such as forest stand type are known to influence wildlife use of linear features (Dickie et al., 2019; Tattersall et al., 2020a, 2020b), we chose not to include these in our models to focus on localized linear feature variables that affect use at a fine scale and can be measured in the field.

2.3 | Model building and validation

We assessed linear feature use from the presence/absence (0 or 1) of sign for each wildlife taxa. We anticipated that our ability to detect wildlife sign would be influenced by site conditions and, therefore, employed a separate model framework to assess imperfect detection (i.e. wildlife linear feature use with an absence of sign). We modelled the number of wildlife detections across taxa as a function of

TABLE 2 Field measurements of wildlife track and sign, linear feature and surrounding forest characteristics and vegetation taxa collected on and beside linear features in west-central and north-western caribou ranges in Alberta and British Columbia, Canada, in 2014, 2015 and 2017. Continuous and percent variables were standardized and scaled prior to modelling.

Variable	Description	Variable type	Range
LineID	Unique linear feature identifier	Factor	–
Bear	Presence/absence of bear sign	Binary	0 or 1
Canine	Presence/absence of canine sign	Binary	0 or 1
Moose	Presence/absence of moose sign	Binary	0 or 1
Deer	Presence/absence of deer sign	Binary	0 or 1
Elk	Presence/absence of elk sign	Binary	0 or 1
AllPrey	Presence/absence of ungulate prey sign (moose, deer, elk, and caribou combined)	Binary	0 or 1
Human	Presence/absence of human sign (ex: tracks, garbage, etc.)	Binary	0 or 1
HumanTrail	Presence/absence of trails created by humans or motorized vehicles	Binary	0 or 1
GameTrail	Presence/absence of trails created by animals	Binary	0 or 1
Dry	Presence/absence of dry soil	Binary	0 or 1
Moist	Presence/absence of moist soil	Binary	0 or 1
Spongy	Presence/absence of spongy soil	Binary	0 or 1
Wet	Presence/absence of wet soil	Binary	0 or 1
OnLatCov	Average lateral vegetation cover online, estimated from vegetative interference blocking 0.5 m^2 cover board held 1–2 m off the ground from 10 and 20 m distance	Percent	0–100
OnVegHt	Average height of tallest vegetation measured online (m)	Continuous	0–30
OffTreeHt	Average height of tallest trees in surrounding forest (m)	Continuous	0.4–40
OffLatCov	Average lateral vegetation cover offline, estimated from vegetative interference blocking 0.5 m^2 cover board held 1–2 m off the ground from 5 and 15 m distance	Percent	0–100
Alnus	*Alnus* spp. percent ground cover within 10 m^2 subplot	Percent	0–92
BEGL	*Betula glandulosa* percent ground cover within 10 m^2 subplot	Percent	0–60
Salix	*Salix* spp. percent ground cover within 10 m^2 subplot	Percent	0–80
Carex	*Carex* spp. percent ground cover within 1 m^2 subplot	Percent	0–88
Fother	Forbs spp. percent ground cover within 1 m^2 subplot	Percent	0–90
Graminoids	Graminoid spp. percent ground cover within 1 m^2 subplot	Percent	0–98
Rhododendron	*Rhododendron* spp. percent ground cover within 1 m^2 subplot	Percent	0–60
Trifolium	*Trifolium* spp. percent ground cover within 1 m^2 subplot	Percent	0–53
Vaccinium	*Vaccinium* spp. percent ground cover within 1 m^2 subplot	Percent	0–71
VAVI	*Vaccinium vitis-idaea* spp. percent ground cover within 1 m^2 subplot	Percent	0–34

linear feature characteristics we predicted would influence the detection of sign: soil type, soil moisture and online vegetation height (Table S1). We conducted statistical analyses with R (R Core Team, 2019), using the package *lme4* for model building (Bates et al., 2015). Prior to analyses, we used data exploration techniques to assess for outliers and correlations between predictor variables as well as to test link functions to account for asymmetry in the distribution of the response variable (Prasetyo et al., 2019; Zuur et al., 2010).

We applied 'movement' and 'risk' hypotheses to predators (canines and bears) and ungulates (moose, deer and elk) and the 'prey' hypothesis to predators only (Table 1). We divided the data by linear feature type and built binomial generalized linear mixed models to relate wildlife linear feature use to field variables predicted to influence movement, riskiness and prey availability on pipelines, seismic lines, and roads (Table 1). As we collected data at three plots per linear feature, we included a random effect of *LineID* to account for non-independence and spatial autocorrelation of sampling units (although this does not account for spatial autocorrelation between linear features). We first built full models for each hypothesis individually (Table 1), performing manual backward selection using the 'drop1' function and Akaike's information criterion (AIC) to determine which variables from that hypothesis most influenced linear feature use. This approach provided a systematic structure for testing a wide range of predictive variables against limited sample sizes of wildlife sign and allowed us to assess the effects of correlated variables independently of one another. Hypotheses were not meant to be mutually exclusive, and some variables may relate to more than one hypothesis. We assessed the 'prey' hypothesis using two separate models: one modelling each prey species individually, and one modelling all prey species combined as one variable (Table 1). We compared the two prey models using AIC and kept the model with the lowest AIC score (Burnham & Anderson, 2002). We then combined variables from all three hypotheses into a global model to obtain effect sizes for the main characteristics influencing wildlife linear feature use (Bolker, 2018). Where correlated variables were to be included in the global model, we chose the variable that was originally included in the model with the lowest AIC (i.e. the variable that best explained use between the two) based on its performance in the backward selection stage of analysis.

We modelled forage variables in a separate binomial generalized linear model because we only collected vegetation data at one plot on each linear feature. To relate wildlife linear feature use to online vegetation, we modelled wildlife use against vegetation taxa that were more likely to occur online than offline (Finnegan, MacNearney, et al., 2018). As with the other hypotheses, we performed manual backward selection using 'drop1' to determine whether percent online vegetation cover influenced wildlife linear feature use. We present all results as odds ratios (OR) with 95% confidence intervals (CI), where the OR describes the likelihood of wildlife line use given a unit increase in the predictor variable.

We validated models with k-fold cross-validation using the *cvms* package (Olsen & Zachariae, 2019). For the combined hypotheses model, we used blocked cross-validation methods to account for the dependence structure introduced by the random effect (Roberts et al., 2017). The *cvms* package includes the 'cross_validate' function, which creates a receiver operating characteristic curve and calculates area under the curve (AUC) and 95% CIs for binomial models. The AUC statistic determines the model's discriminatory capabilities, where values greater than 0.5 indicate a better-than-chance ability to predict the response outcome (Jiménez-Valverde, 2012).

Model building for each study area, linear feature type, and hypothesis was limited to taxa with sufficient sample sizes (Tables S3 and S4). We were able to model use of linear features for most taxa except caribou and elk in the north-western range, although these were still included as predictor variables in prey models. The predictor variables human trails ('move') and human occurrences ('risk') were highly correlated in all datasets (Pearson correlation coefficient range = 0.49–0.94); we, therefore, removed human trails where human trails and occurrences occurred in the global models (deer on west-central pipelines and bears and canines on north-western pipelines).

3 | RESULTS

3.1 | Track and sign detections, model performance

Moose sign occurred most frequently on all linear feature types in both study areas, while the caribou sign occurred least frequently in west-central ranges and elk sign occurred least frequently in north-western range (Tables S3 and S4). West-central pipelines had more sign detected in organic soil (OR = 1.35, CI = 1.09–1.66), west-central seismic lines had more sign detected in clay (OR = 1.34, CI = 1.15–1.56), while north-western pipelines had more sign detected in sandy soil (OR = 2.17, CI = 1.52–3.02; Table S2). West-central pipelines and north-western seismic lines had fewer detections with taller vegetation (OR = 0.88, CI = 0.80–0.97 and OR = 0.77, CI = 0.68–0.87, respectively; Table S2).

3.2 | Move, risk and prey hypotheses

Table 3 presents variables in final models for each taxon and linear feature type, and Figure 2 compares ORs across variables. In west-central ranges, pipeline models indicated that moose were more likely to use pipelines with human trails (OR = 16.94,

TABLE 3 Global models for each taxon combining predictor variables from the movement, risk and prey hypotheses to estimate the effect each characteristic had on wildlife linear feature use in west-central and north-western caribou ranges in Alberta and British Columbia, Canada during 2014, 2015 and 2017.

	West-central		North-western	
Wildlife	Pipelines	Seismic lines	Pipelines	Seismic lines
Moose	GameTrail + HumanTrail + OnLatCov + Bear + (1|LineID)	GameTrail + HumanTrail + OnVegHt + (1|LineID)	GameTrail + (1|LineID)	GameTrail + OnVegHt + OffTreeHt + Canine + (1|LineID)
Deer	GameTrail + OnVegHt + Human + (1|LineID)	GameTrail + OnVegHt + OnLatCov + Canine + (1|LineID)		OffLatCov + Canine + (1|LineID)
Elk	GameTrail + (1|LineID)	GameTrail + OnVegHt + Bear + (1|LineID)		
Bear	GameTrail + AllPrey + (1|LineID)	OnLatCov + OffTreeHt + Human + Elk + (1|LineID)	GameTrail + OnLatCov + OffTreeHt + Human + (1|LineID)	GameTrail + AllPrey + (1|LineID)
Canine		Caribou + Deer + (1|LineID)	GameTrail + Human + Deer	OnVegHt + OffLatCov + (1|LineID)

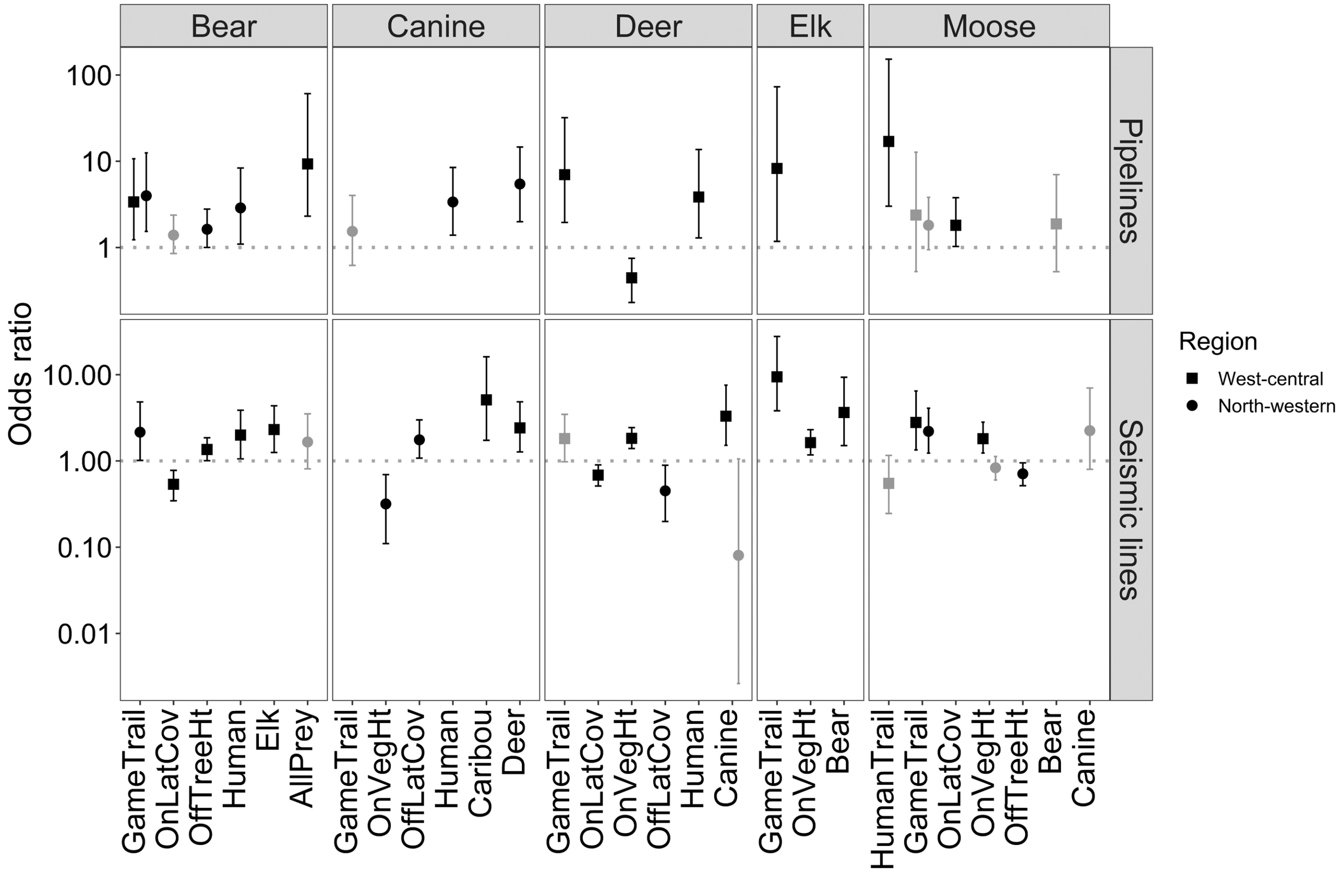

FIGURE 2 Odds ratios (±95% confidence intervals) describing the likelihood of wildlife presence for a unit increase of each predictor variable relating linear feature use to movement, risk, and prey in west-central and north-western caribou ranges in Alberta and British Columbia, Canada, during 2014, 2015 and 2017. An odds ratio value of one is indicated by the horizontal dotted line. Black points denote variables with a significant effect on linear feature use (confidence intervals not overlapping 1), and grey points denote variables with a non-significant effect.

CI = 3.01–152.64) and greater online lateral cover (OR = 1.81, CI = 1.03–3.78). Moose were also more likely to use seismic lines with game trails (OR = 2.79, CI = 1.34–6.48) and taller online vegetation (OR = 1.81, CI = 1.24–2.82). Deer were more likely to use pipelines with game trails (OR = 6.99, CI = 1.95–32.08), shorter online vegetation (OR = 0.45, CI = 0.23–0.75) and human occurrences (OR = 3.85, CI = 1.29–13.70). Deer were more likely to use seismic lines with taller online vegetation (OR = 1.83, CI = 1.39–2.44), less online lateral cover (OR = 0.69, CI = 0.51–0.91) and canine occurrences (OR = 3.30, CI = 1.52–7.56). Elk were more likely to use pipelines with game trails (OR = 8.25, CI = 1.18–73.14), and more likely to use seismic lines with game trails (OR = 9.44, CI = 3.82–27.75), taller online vegetation (OR = 1.63, CI = 1.18–2.30) and bear occurrences (OR = 3.65, CI = 1.51–9.34). Bears were more likely to use pipelines with game trails (OR = 3.38, CI = 1.23–10.70) and any ungulate prey occurrences (OR = 9.30, CI = 2.31–60.82). Bears were more likely to use seismic lines with less online lateral cover (OR = 0.54, CI = 0.35–0.78), taller offline trees (OR = 1.36, CI = 1.01–1.86), human occurrences (OR = 2.00, CI = 1.06–3.88) and elk occurrences (OR = 2.31, CI = 1.26–4.37). Canines were more likely to use seismic lines with occurrences of caribou (OR = 5.11, CI = 1.74–16.15) and deer (OR = 2.42, CI = 1.27–4.85).

In north-western ranges, moose were more likely to use seismic lines with game trails (OR = 2.21, CI = 1.23–4.09) and shorter offline trees (OR = 0.71, CI = 0.52–0.95). Deer were more likely to use seismic lines with less offline lateral vegetation cover (OR = 0.45, CI = 0.20–0.89). Bears were more likely to use both pipelines and seismic lines with game trails (OR = 3.98, CI = 1.54–12.52 and OR = 2.15, CI = 1.02–4.84, respectively), and more likely to use pipelines with taller offline trees (OR = 1.63, CI = 1.00–2.78), and human occurrences (OR = 2.88, CI = 1.10–8.35). Canines were more likely to use pipelines with occurrences of humans (OR = 3.38, CI = 1.39–8.49) and deer (OR = 5.44, CI = 1.99–14.64). Canines were more likely to use seismic lines with greater offline lateral cover (OR = 1.76, CI = 1.08–3.00). Mean AUC values for all models were between 0.51 and 0.69, indicating slightly greater-than-chance predictive capabilities (Table S5).

3.3 | Forage hypothesis

In west-central ranges, moose were more likely to use pipelines and roads with greater cover of *Salix* (OR = 2.62, CI = 1.49–5.35 and OR = 4.12, CI = 1.14–24.22, respectively; Figure 3a) but were

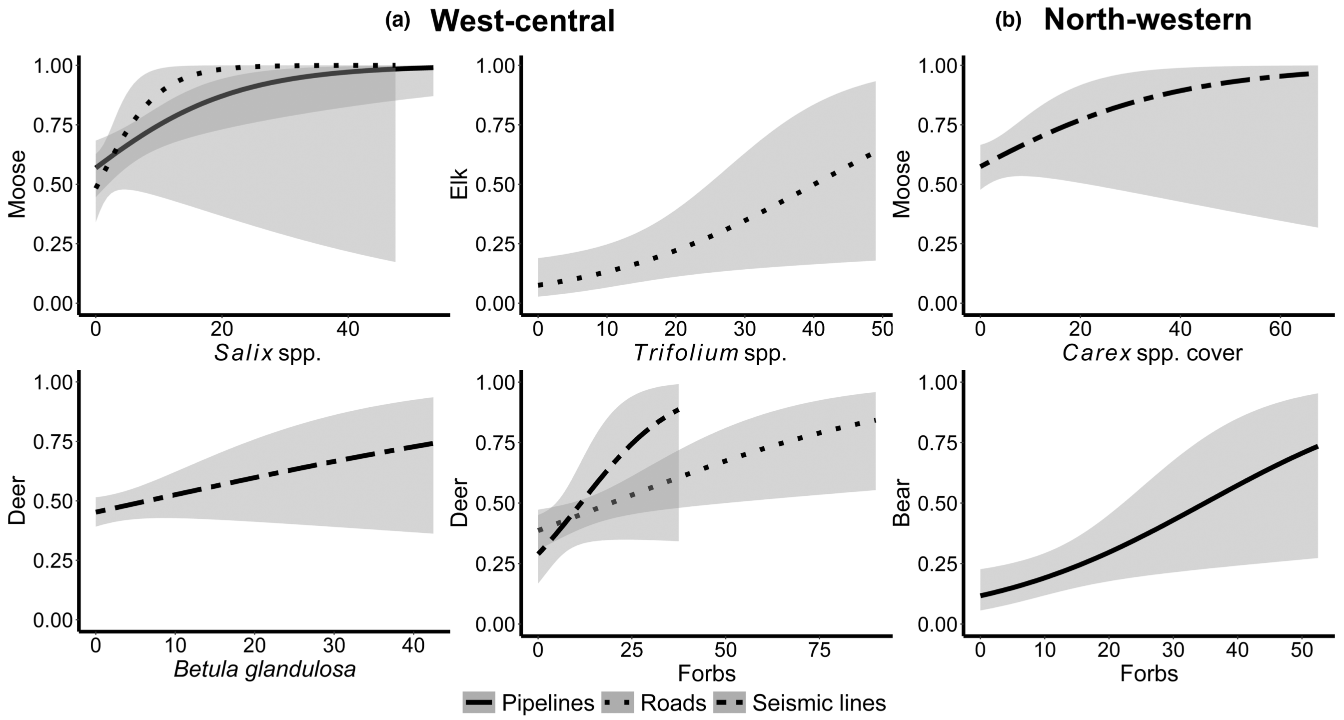

FIGURE 3 Predicted wildlife use of linear features in relation to percent cover of vegetative forage species in west-central (a) and north-western (b) Alberta and British Columbia, Canada, between 2014 and 2017.

more likely to use pipelines with less graminoid cover (OR = 0.56, CI = 0.35–0.85), and more likely to use seismic lines with less cover of *Trifolium* (OR = 0.73, CI = 0.55–0.94) and *Vaccinium* (OR = 0.73, CI = 0.56–0.96). Deer were more likely to use pipelines with less *Vaccinium vitis-ideaa* cover (OR = 0.61, CI = 0.36–0.0.92). Deer were more likely to use seismic lines with greater *Betula glandulosa* cover (OR = 13.9, CI = 1.06–1.92, Figure 3a), less *Carex* cover (OR = 0.67, CI = 0.46–0.90), and greater forbs cover (OR = 1.40, CI = 1.09–1.83; Figure 3a). Deer were more likely to use roads with less *Alnus* cover (OR = 0.35, CI = 0.05–0.87) and more forbs cover (OR = 2.94, CI = 1.38–7.62; Figure 3a). Elk were more likely to use pipelines with less *Salix* cover (OR = 0.54, CI = 0.25–0.97), more likely to use seismic lines with less *Carex* cover (OR = 0.71, CI = 0.48–0.98) and more likely to use roads with greater *Trifolium* cover (OR = 2.03, CI = 1.10–3.95; Figure 3a). Bears were more likely to use pipelines with less *Vaccinium* cover (OR = 0.25, CI = 0.05–0.65). In the north-western range, moose were more likely to use seismic lines with greater *Carex* cover (OR = 1.96, CI = 1.07–5.03; Figure 3b). Bears were more likely to use pipelines with a greater cover of forbs (OR = 1.75, CI = 1.07–3.04; Figure 3b). Mean AUC values for forage models ranged between 0.44 and 0.72 (Table S6).

4 | DISCUSSION

The results of this study emphasize that there is no 'one size fits all' approach to linear feature restoration. We found that biophysical characteristics associated with wildlife use of linear features varied considerably across taxa, linear feature type, and region, suggesting that no single restoration target will address line use for all taxa. Nevertheless, consistent with previous research (Dickie et al., 2019; Finnegan, MacNearney, et al., 2018), our results show that 'movement' and 'forage' characteristics do influence use of linear features across wildlife taxa. Therefore, targeting trails, vegetation structure and vegetation type in restoration could, therefore, reduce predator and alternate prey line use to disrupt the current dynamics that harm caribou.

We found that game trails were a significant predictor of pipeline use for deer, seismic line use for moose and pipeline and seismic line use for elk and bears. Additionally, human trails were a significant predictor of pipeline use for moose in west-central ranges (Figure 2; Table S5). This is an intuitive result given that linear features facilitate wildlife movement (Dickie et al., 2019; Finnegan, Pigeon, et al., 2018) and that frequent use would create game trails. Although we did not find a significant effect of trails on canine use, we did find that canine use was more likely on north-western pipelines with human occurrences, which was highly correlated with human trails. Therefore, canine use of linear features with human trails should not be ruled out (St-Pierre et al., 2022; Tattersall et al., 2020b). Similar to other studies (Dickie et al., 2017; Finnegan, Pigeon, et al., 2018; St-Pierre et al., 2022), we also found that bear and canine use of seismic lines was less likely with greater lateral vegetation cover and taller vegetation, respectively. Previous research has suggested that trails may contribute to the continued use of lines even after vegetative regeneration makes the rest of the line impassable (Finnegan, Pigeon, et al., 2018;

Tigner et al., 2014). We could not test interactions between variables for vegetation structure and trails due to limited occurrence data, but this is a possible area for further research. We also note that taller vegetation negatively affected sign detection on northwestern seismic lines, which may confound the observed canine and bear response to vegetation height. Sign detections were also less likely with taller vegetation on west-central pipelines, which may support the apparent decreased use of those lines by deer.

We found that canines were more likely to use pipelines with shared deer occurrence and that bears were more likely to use pipelines with shared ungulate prey occurrence. Additionally, we found that canines were more likely to use seismic lines with shared deer and caribou occurrence and that bears were more likely to use seismic lines with shared elk occurrence. We are cautious to interpret these results directly as predators selecting linear features for prey availability because these data do not describe a causal relationship and the resolution of this study does not address dynamics occurring at fine temporal scales. Indeed, the seismic line model for deer showed a greater likelihood of use with canine occurrence, and the seismic line model for elk showed a greater likelihood of use with bear occurrence. Although it is likely that predators, particularly wolves, select habitats with high prey use (e.g. Latham et al., 2013), it is also likely that multiple species share use of linear features as they prioritize differing ecological needs (movement efficiency, food resources, shelter, etc.; Tattersall et al., 2020a). Regardless, these results indicate patterns in linear feature use between predators and prey species, suggesting restoration targeting one taxon is likely to affect use by other taxa as well.

Wildlife responses to 'risk' variables followed predicted patterns for predators, but not for prey. Canines were more likely to use seismic lines with greater offline lateral cover, while bears were more likely to use pipelines with taller offline trees. In contrast, moose and deer were less likely to use seismic lines with taller offline tree height or greater offline lateral cover, respectively. These results suggest that the offline vegetation variables used here contributed less to risk avoidance and more to movement than we hypothesized. We expected variables describing offline vegetation structure—such as tree height and lateral cover—to represent shelter and provide refuge to wildlife using linear features. In recent years, the Government of Alberta has implemented predator removal programs in response to caribou declines (Hervieux et al., 2014), which could affect predator perceptions of risk (Baillie-David, 2022). However, it is also possible that offline vegetation structure represents access to forage, particularly for moose and deer where regenerating stands with shorter vegetation provide understory forage (Courtois et al., 1998). Although predator results suggest that they use linear features to reduce their risk of exposure, another explanation is that taller offline vegetation and greater offline lateral cover make movement in the surrounding forest more difficult relative to linear features in these areas. Dickie et al. (2019) interpreted moose behaviour on linear features to be risk avoidance, as GPS-collared moose avoided linear features and moved faster on them. Combining use data with movement data (i.e. comparing speed) and offline vegetation structure could help differentiate the influences of risk avoidance and ease of movement driving wildlife use of linear features.

Contrary to the predictions for the movement hypothesis, we found that online vegetation variables were significant predictors of moose use of pipelines, and deer and elk use of seismic lines (Figure 2; Table S5). These results align with those from our forage models and support the hypothesis that ungulates use of linear features for forage availability. Specifically, we found tall shrubs predicted ungulate linear feature use: moose were more likely to use pipelines with a greater cover of *Salix* spp., while deer were more likely to use seismic lines with greater *B. glandulosa* cover (Figure 3). Although not significant, elk use of seismic lines was also associated with greater cover of *Salix* (Table S6). Other forage taxa such as *Carex* and *Trifolium* and forbs also predicted linear feature use for moose, elk, deer and bears, respectively (deer and bear use were associated with forbs, Figure 3). Vegetation structure has been found to be a predictor of ungulate linear feature use in other studies (Tattersall et al., 2020b), and earlier investigations of this dataset demonstrated that these forage taxa were more likely to occur on seismic lines and pipelines than in offline reference sites (Finnegan, MacNearney, et al., 2018; MacDonald et al., 2020). These findings offer strong support to the idea that ungulates, particularly moose and deer, use linear features for the greater forage subsidy that they provide relative to the surrounding forest. Future studies could explicitly test this hypothesis by quantifying ungulate browsing on linear features and in surrounding forests.

The field data presented in this study provide a site-level depiction of specific biophysical characteristics that influence linear feature use by wildlife. Nevertheless, the temporal resolution of these data is limited to the summer period when data were collected. Responses to vegetation structure and composition may vary seasonally, and snow can have a significant effect on linear feature use (Droghini & Boutin, 2017; Tattersall et al., 2020b). Additionally, we found that detections of wildlife sign were influenced by the substrate (soil type) on linear features. Future work using monitoring techniques that standardize detectability and extend the detection period (e.g. camera traps) or winter tracking could corroborate the associations found here.

4.1 | Restoration implications

Overall, our study highlights that trails, online vegetation structure, and online vegetation type should be the focus of linear feature restoration activities. Restoration practitioners could use these results to design restoration programs that fit their specific objectives (e.g. targeting particular regions, linear feature types or wildlife species). These findings support past recommendations to implement functional and structural restoration: impeding movement along trails prevents linear features from functioning as movement corridors, while reducing early-seral vegetation online contributes to the structural restoration of habitat (Bentham & Coupal, 2015; Ray, 2014). To date, successful restoration initiatives have focused on high-intensity line blocking using techniques like tree felling and tree hinging (Keim et al., 2019; Neufeld, 2006). In contrast, restoration programs with low-intensity line blocking and a greater focus on vegetative restoration have had fewer desired effects on wildlife (Dickie et al., 2021; Tattersall et al., 2020b). Given that line blocking and vegetative regeneration techniques are likely effective at different time scales, we recommend implementing a combination of techniques and methods that achieve both objectives. For example, tree felling and tree hinging can provide movement barriers while also creating microsites to protect seedlings (Dabros et al., 2018; Neufeld, 2006). Mounding creates elevated microsites and impedes human access to linear features (Bentham & Coupal, 2015) but may not have the same effect on wildlife (Tattersall et al., 2020b). Therefore, a combination of tree felling, tree hinging, and mounding could inhibit the use of linear features by humans and wildlife, particularly in west-central caribou ranges. Additionally, vegetative restoration focused on reducing forage taxa like *Salix*, *B. glandulosa*, *Trifolium*, *Carex* and forbs may reduce use of linear features by moose, elk, deer, and bears in both ranges. Appropriate techniques will vary according to site conditions, restoration costs and priorities, and we recommend adaptive monitoring of restoration projects to achieve desired outcomes.

5 | CONCLUSIONS

Linear feature restoration is a vital aspect of caribou recovery in the boreal forest (Environment Canada, 2012). However, it is costly and caribou population modelling suggests that it will only be effective at reversing caribou declines if restoration is aggressive and widespread (Johnson et al., 2019; Spangenberg et al., 2019). In this study, we used site-level data to understand wildlife associations to biophysical characteristics of linear features, which can help prioritize restoration work by providing specific targets for restoration objectives. Focusing restoration on trails, vegetation structure, and targeting forage species will improve the efficiency of restoration projects by directly addressing the ecological cues related to wildlife use. Site-level investigations link restoration actions to conservation goals and allow local restoration initiatives to scale up to landscape-level effects to achieve global biodiversity targets (United Nations, 2019; WWF, 2020).

AUTHOR CONTRIBUTIONS

Erin Tattersall: methodology, formal analysis, writing – original draft, writing – review and editing, visualization. Karine Pigeon: conceptualization, methodology, investigation, data curation, writing – review and editing. Doug MacNearney: conceptualization, methodology, writing – review and editing. Laura Finnegan: conceptualization, methodology, investigation, data curation, writing – review and editing, supervision, project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial or personal interests that would influence the work reported in this study.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data for this study are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.gxd2547qz (Tattersall et al., 2023).

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SUPPORTING INFORMATION

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

Table S1. We predicted that certain linear feature characteristics could obscure wildlife signs occurring on linear features in caribou ranges in west-central and north-western Alberta and British Columbia, Canada.

Table S2. Odds ratios for models of wildlife detections on linear features as a function of soil type and soil moisture in west-central and north-western Alberta and British Columbia, Canada, between 2014 and 2017.

Table S3. Sample size used for movement, risk and prey models of wildlife track and sign occurrence on linear features in west-central and north-western Alberta and British Columbia, Canada, between 2014 and 2017.

Table S4. Sample size used for forage models of wildlife track and sign occurrence on linear features in west-central and north-western Alberta and British Columbia, Canada.

Table S5. Odds ratios (±95% confidence intervals) for variables in the global models relating linear feature use to ease of movement, risk avoidance, and prey availability for five wildlife taxa in west-central and north-west caribou ranges of Alberta and British Columbia, Canada, between 2014 and 2017.

Table S6. Odds ratios (±95% confidence intervals) for variables in models relating linear feature use to forage availability for four wildlife taxa in west-central and north-west caribou ranges of Alberta and British Columbia, Canada, between 2014 and 2017.

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