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Multiple lines of evidence for predator and prey responses to caribou habitat restoration

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ABSTRACT

How to mitigate the impacts of anthropogenic habitat alteration and restore ecological processes has become an imperative question facing applied ecology. One high-profile example in Canada is boreal woodland caribou, which are declining across North America largely due to anthropogenic habitat alteration and associated changes to predator-prey dynamics. Habitat restoration is increasingly being implemented to recover habitat, as is mandated by federal law. But given the extent of the disturbance and the cost to conduct restoration, evaluating the effectiveness of restoration treatments is needed for effective recovery of caribou populations. We evaluated the effectiveness of silvicultural treatments to reduce predator (wolf and bear) and prey (moose and caribou) use of linear features using a multiple lines of evidence approach. All four species were less likely to be present at treated sites than untreated sites, and daily photo capture rates of moose and wolves when present at treated sites also declined; though effect sizes were typically small. Complimenting the camera-based results, individual moose, bears, and wolves monitored with GPS collars also showed a decline in the use of treated linear features, particularly those with higher intensity treatments, though the response was non-significant. The reduction in the use of treated lines did not scale-up into a significant decline in overall line-use within the treatment area. While we found more evidence than not supporting that animals reduced use of the restoration sites, our study highlights the complexity of monitoring and evaluating the success of habitat restoration. Understanding long-term responses is imperative to ensure habitat restoration is effective.

1. Introduction

Anthropogenic habitat alteration causes species declines by degrading ecosystem structure and function (Hooper et al., 2005; Suding, 2011). Despite linkages between anthropogenic habitat alteration and species declines worldwide (Foley et al., 2005; Newbold et al., 2015), the effective mitigation of these impacts and the implementation of sustainable working landscapes remain elusive. This uncertainty has sparked an era of restoration, whereby recovering disturbed ecosystems is focussed on aiding habitat recovery to restore ecological processes (Suding, 2011). Beyond converting human-altered habitat back to recovered habitat, restoration targets aim to recover ecological function in a sustainable, community-engaged manner (Perino et al., 2019; Suding et al., 2015). Understanding when restoration can be successful, and what opportunities exist to conduct restoration that maximizes species recovery outcomes, provides critical insights into ecological function while helping to stem the loss of species.

Rapid habitat alteration has occurred in Canada's boreal forest as a result of human expansion and resource development. Species using areas of high resource value, for example timber supply or oil and gas deposits, risk having their critical habitat altered or reduced. Anthropogenic habitat alteration has been linked to declining populations of boreal woodland caribou (*Rangifer tarandus caribou*), hereafter termed caribou, a species listed as threatened in Canada (Bergerud, 1974; Environment Canada, 2012). The primary cause of declines is unsustainable predation as a result of human-mediated changes to predator-prey dynamics (Serrouya et al., 2021; Wittmer et al., 2005). This is hypothesized to occur via two mechanisms; i) increased predator (grey

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wolves *Canis lupus* and black bears *Ursus americanus*) hunting efficiency and access to caribou habitat (DeMars and Boutin, 2018; Dickie et al., 2017b), and ii) increased predator densities via increased moose (*Alces americanus*) and deer (*Odocoileus* spp.) densities resulting from increased early seral vegetation in altered habitat (Latham et al., 2011b; Serrouya et al., 2011). Linear features, such as roads and seismic lines, have been implicated in the declines of caribou within western Canada's boreal forests because predators select these features as movement corridors (Dickie et al., 2019; Whittington et al., 2011). Mitigating the impact of anthropogenic habitat alteration, particularly linear features, on ecological function in these systems is an essential step towards recovery of caribou populations.

A variety of recovery actions are being employed to recover caribou populations, including population-management and habitat-management strategies. Population-management strategies have been proposed as temporary interventions to curb caribou population declines until habitat is restored (Serrouya et al., 2019). Given that natural forest recovery is stagnant on many disturbances in the boreal (Lee and Boutin, 2006), active restoration strategies are necessary to restore forest cover (Bentham and Coupal, 2015) in a timely manner (Filicetti et al., 2019). The goals of population management are clear –increase caribou survival and recruitment via predator reduction, maternal penning, or alternate prey reductions (Serrouya et al., 2019). However, the long-term goals of restoration to address the ultimate cause of caribou declines, habitat alteration, are necessarily complex. The recovery of ecological processes via restoration is expected to occur over a long time-period, and is unlikely to result in measurable increases in caribou population growth rates in the near-term (Johnson et al., 2019). Therefore, the short-term goal of caribou habitat restoration is to reduce animal use of linear features such as seismic lines. This directly targets one of the hypothesized mechanisms linking anthropogenic habitat alteration to caribou declines; hunting efficiency (DeMars and Boutin, 2018; Dickie et al., 2017b).

Simulations suggests that caribou recovery can occur through restoration (Johnson et al., 2019; Serrouya et al., 2020; Spangenberg et al., 2019), but the effectiveness of restoration to ameliorate pathways of decline is less clear. High-intensity, targeted restoration has the potential to reduce predator use of linear features (Keim et al., 2019). However, these targeted treatments are unlikely to be implemented across entire caribou ranges. Less intensive restoration treatments are less effective in reducing predator and prey use of linear features, especially when access to alternate, unrestored linear features remain available (Tattersall et al., 2020). Restoring large areas requires the use of treatments that target short-term reductions in trafficability, while facilitating recovery of pre-disturbance forest cover to meet ecological restoration targets in the long-term.

Here, we evaluated the effectiveness of silvicultural restoration treatments implemented in a large area (378 km^2) intended to reduce predator (wolf and bear) and prey (moose and caribou) use of linear features using a hierarchical study design. Despite the large extent of silvicultural restoration conducted here, the species monitored are wide ranging and typically have home ranges larger than the area treated. We therefore employed a multiple lines of evidence approach to evaluate the response of these four species across spatio-temporal scales and summarized each metric to understand the multi-scale response to restoration treatments. While we were also interested in white-tailed deer response to restoration treatments, our data for deer were limited to camera detections only, and sample sizes were insufficient for analyses (Appendix A).

2. Materials and methods

2.1. Study design

We used a multi-scalar design to evaluate large mammal responses to restoration treatments of varying intensities using multiple analytical approaches (Fig. 1). At the finest (site-level) scale, we used remote wildlife cameras to quantify and compare multi-species use of treated and untreated sites within the treatment area over time. We predicted that caribou, moose, bears and wolves are less likely to use treated sites than untreated sites, that when present at treated sites the frequency of use is lower than untreated sites, and that these responses are stronger when treatment intensity is higher and as treatments progressed throughout the treatment area. We further tested the response of individual animals (individual-level) to restoration treatments using relocation data from Global Positioning System (GPS) collared animals to quantify proportional use of treated and untreated linear features within the treatment area. We predicted that individuals use treated linear features less than untreated linear features, that this response is stronger when treatment intensity is higher, and that use of linear features within the treatment area declines as restoration progressed.

There has yet to be an evaluation of how site-level and individual-level silvicultural changes influence animal behaviours at larger, landscape-level scales. If restoration treatments are effective, site- and animal- level behavioural responses should result in an overall shift in how animals use linear features within the treatment area, regardless of treatment status. Because the progression of restoration within the treatment area occurred over multiple years, it was necessarily confounded with year and thereby with annual variations in animal behaviour unrelated to restoration. Therefore, we evaluated shifts in animal use of linear features within the treatment area relative to reference areas. In the case of site-level responses translating to landscape-level responses, we predicted that camera-trap sites within the treatment area, relative to camera trap-sites in a reference area where no treatment occurred, would be used less by each of the focal species as treatment progressed, and that the frequency of use given presence at these sites would also decline. In the case of individual-level responses translating to landscape-level responses, we predicted that as restoration progressed, individuals monitored with GPS collars would use linear features when they were inside the treatment area less than when they were outside the treatment area. Despite the large area in which restoration treatments occured, these species have large home ranges. Thus, the sample sizes and statistical power of these analyses are necessarily limited. Still, we expected results to be sufficiently informative within our multiple-lines-of-evidence approach.

2.2. Study area

The study area is located in northeastern Alberta and northwestern Saskatchewan, Canada (Fig. 1) within the Boreal Plains ecozone and Central Mixedwood Subregion. Linear features in a 378 km^2 area within the larger study area were restored using silvicultural treatments (Treatment Area; hereafter TRT). A paired 378 km^2 area, where industrial activities continued and linear features were not treated, was used as a reference area (i.e., Business As Usual; BAU). Camera traps were placed within both the TRT and BAU to quantify and compare use at camera trap sites in the treated and reference areas (see Section 2.4.1). Animals were also outfitted with GPS collars within and surrounding the TRT to quantify use of linear features within the TRT, and to compare use of linear features in the TRT to outside the TRT (see Section 2.4.2). See Appendix B for a detailed description of the habitat characteristics of the TRT, BAU, and the composite home range of GPS-collared animals.

The climate is characterized by generally low precipitation (~450 mm per year), short, warm summers and long, cold winters (Environment Canada, 2016). The area supports a mixture of peatland complexes dominated by black spruce (*Picea mariana*), larch (*Larix laricina*), willows (*Salix* spp.), and birch (*Betula glandulosa*) interspersed with upland mixedwood forests dominated by white spruce (*Picea glauca*), jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*). Lakes, rivers, and other aquatic habitats are common. Ungulate species in the area include moose, caribou, and white-tailed deer (*Odocoileus virginianus*). Predators include grey wolves, coyote (*C. latrans*), black bears,

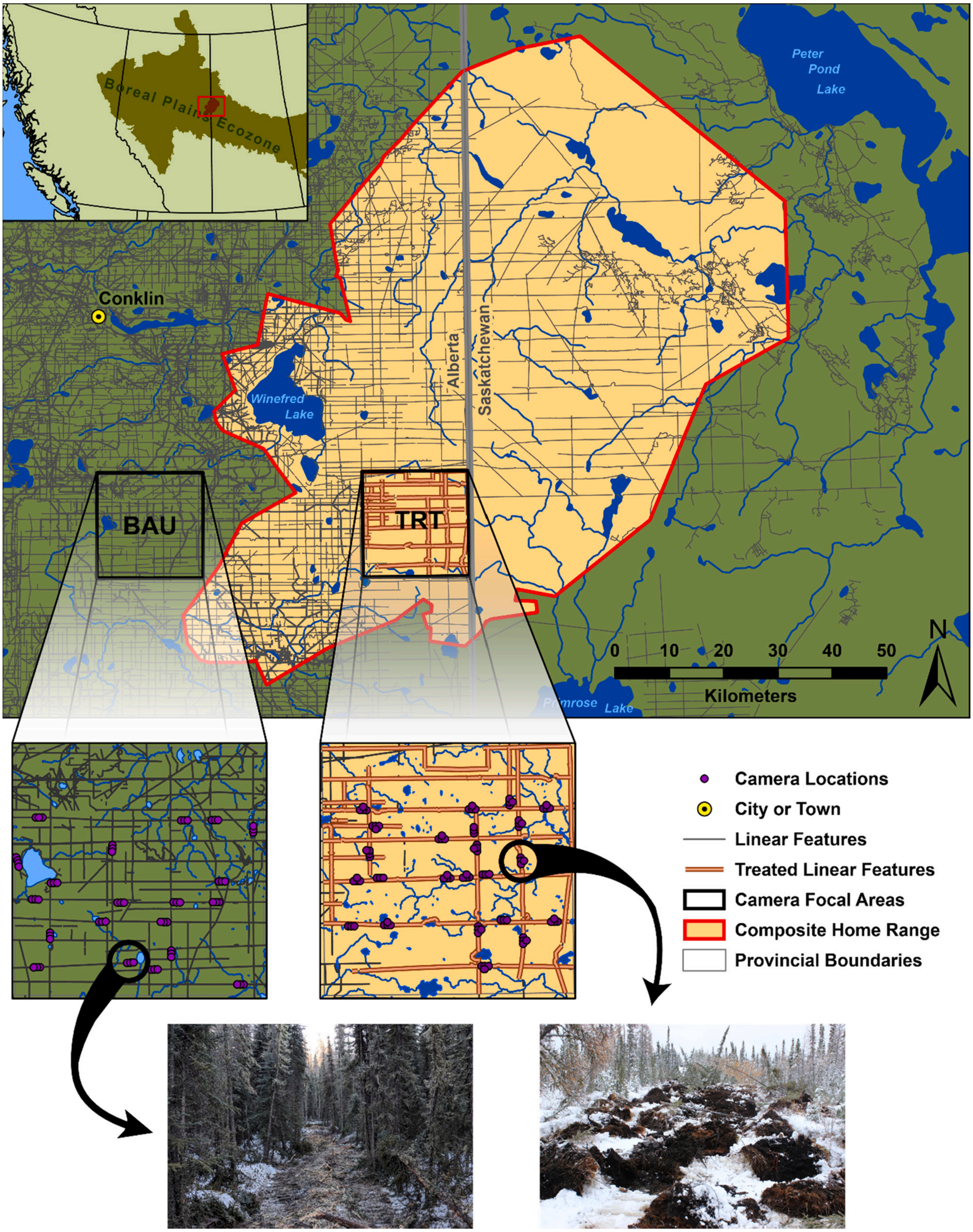

Fig. 1. The location of the restoration treatment area (TRT; 378 km^2), reference "Business As Usual" area (BAU; 378 km^2) used to test the effectiveness of restoration treatments on deterring caribou, moose, bear and wolf use of linear features. The composite 100% Minimum Convex Polygon home ranges of GPS collared animals (7826 km^2) and locations of remote wildlife camera locations used to evaluate site-level (camera), individual-level (GPS collars), and landscape-level (treatment area) responses are shown. Examples of untreated linear features from the BAU and treated linear features from the TRT are shown.

and lynx (*Lynx canadensis*). Other important prey of these predators are beaver (*Castor canadensis*) and snowshoe hare (*Lepus americanus*).

2.3. Silviculture treatments

Silviculture treatments were designed to accelerate return to forest cover over the long-term, and to reduce animal use and movements in the interim (Appendix C). Treatments included mounding (digging and heaping of soil), scalping (scraping the surface), bending and/or felling of stems onto the feature from surrounding forest, distribution of coarse woody debris, transplanting, and planting. We considered sites as "treated" on or after the date of the first restoration activity conducted at each site. Locations with advanced tree regeneration (>2 m in height) were left to continue natural regeneration.

Treatment intensity varied based on treatment type and implementation. We classified treatment intensity post hoc as high or low based on a combination of treatment type and the difference in surface relief of the treated site prior to initiation of restoration (2013) and when restoration activities were completed (2015; Appendix C). The greater the difference in post-treatment height the more intensive the treatment was assumed to be (Dickie et al., 2017a). At the end of the restoration program, there was approximately 39 km of linear features classified as natural regeneration, 24 km of which had small amounts of supplemental hand-felling, and 46 km classified as low-intensity treatment, 118 km as medium intensity treatment and 33 km as high-intensity treatment (see Appendix C for details). Medium and high intensity treatments were combined post hoc to empirically contrast the effectiveness treatment intensities.

We quantified the cumulative area treated within the TRT for each season in each year as the proportion of the total area of linear features treated at the end of each season (Appendix C). Silvicultural treatments occurred in bursts, with the majority of treatments occurring in the winter of 2014 and 2015. We therefore categorized the cumulative area treated as low (<60%) and high (>60%), corresponding to years 2012–2013 and 2014–2016, respectively.

2.4. Data collection

2.4.1. Wildlife cameras to monitor treated and untreated sites

We deployed remote wildlife camera traps along linear features in the TRT (1461 camera days between February 2013–December 2016) and the BAU (1054 camera days between February 2014–December 2016) to quantify use of treated and untreated sites. Initially, cameras were placed in linear arrays of three cameras 250 m apart either along linear features (TRT "line" cameras: $n = 54$ in 18 arrays) or in arrays set back 250 m from lines (TRT "interior" cameras: $n = 15$ in 4 arrays). In 2014, these "interior" arrays were removed and their cameras (+3 added cameras) were redeployed as "interior" cameras to the existing "line" arrays. Also, in 2014, 63 cameras in 21 arrays were deployed along linear features in the BAU (see Appendix D). In total, data from 135 cameras (TRT: 54 "line" and 18 "interior" cameras; BAU: 63 "line" cameras) were analyzed (see Appendix D). These cameras operated for 57,018 trap days in the TRT, 30412 of which were under treated conditions, and 41,115 trap days in the BAU. We attributed camera locations as being located on linear features (line) or interior forest (interior) and with four types of treatment intensity (NoTrt: untreated, LFNat: natural regeneration, L_Trt: low intensity, or H_Trt: high intensity; see Appendix B).

We classified each photograph and recorded species, the number of individuals, and time using Timelapse2 (Greenberg, 2018). Counts of capture events (≥1 h between observations were considered independent detections; Harris et al., 2015) were summarized for each species at each camera per day of operation. We assessed the potential influence of treatments on camera field-of-view (Swann et al., 2004; Appendix E). We considered changes to the field-of-view to be minor and uninfluential due to the body-size of our study species relative to the resulting height and density of treated vegetation.

2.4.2. GPS collars to monitor individual animal habitat-use

We deployed GPS collars on 8 moose, 7 bears, and 7 wolves between January 2013 and May 2015. We attempted to capture and collar all individuals observed within and adjacent to the TRT. One caribou was also collared, but was not included in analyses given the limited sample size. All animals were captured and handled in compliance with Alberta Wildlife Animal Care Committee Class Protocols and approved permits. Collars typically collected 12-h relocations, but were sampled more frequently during some periods to meet alternate study objectives: February 1–28 every 3 h; April 15–July 15 every 15 min for two days, then every hour for four days; December 1–31 every hour for two days, then every 12 h for four days. We screened GPS data for potential errors by excluding 3-dimensional locations with a dilution of precision (DOP) >10 and 2-dimensional locations with DOP >5 (Bjørneraas et al., 2010). Accounting for excluded locations, the mean monitoring interval per collared animal was: 46 weeks for moose (range: 17–84), 58 weeks for bears (range: 2–107), and 603 weeks for wolves (range: 36–122).

We attributed GPS relocations as on linear features or non-disturbed areas. We classified relocations as on linear features if they were within 50 m of an anthropogenic linear feature (Dickie et al., 2019). GPS locations on linear features were attributed as untreated (NoTrt), natural regeneration (LFNat), low treatment intensity (L_Trt) or high treatment intensity (H_Trt). Anthropogenic habitat alteration was manually digitized following the methods of Dickie et al. (2019). The study area was predominantly non-disturbed areas (75%) with lesser extents of riparian areas (17%), seismic lines (7%), and other linear features (~1%).

2.5. Statistical analyses

2.5.1. Are treated camera-trap sites used less than untreated sites?

We evaluated the effects of treatment intensity (untreated, natural regeneration, low-intensity and high-intensity) and the cumulative area treated (low, high) on the daily probability of absence from sites along linear features, and the daily intensity of use of sites in the TRT, separated by season (snow: November 1–April 30, snow-free: May 1–October 31). We used a hurdle-model approach based on the truncated-Poisson distribution with a log-link function (Brooks et al., 2017), where the model separately evaluates if there was a capture or not (i.e. the probability of being absent versus present, expressed by the model as the probability of absence) and if there was a capture, the frequency of captures (i.e. the frequency of use when present). We note that while we are modelling whether the species is detected compared to not detected, we interpret this as presence or absence assuming perfect detection. The interpretation of the probability of absence (i.e. the zero-component of the hurdle model) can inversely be considered as the probability of presence.

We were specifically interested in changes to species use of treated linear features compared to untreated linear features. Therefore, here we used only data from cameras on lines and excluded "interior" cameras which would not have informed this objective. We included random intercepts for camera (site) nested within array to account for non-independence of daily captures (Tattersall et al., 2020). For bears we included only detections during the snow-free period, but all other species included both seasons.

We examined model fits and examined all models for quality of fit (see Appendix D for details on the model fitting process). Significance is defined as 95% confidence intervals non-overlapping zero.

2.5.2. Do individual animals monitored with GPS collars use treated lines less than untreated lines?

We evaluated if the proportion of GPS locations within the TRT for each individual animal (termed "proportional use") was lower on linear features with higher treatment intensity than lower intensity (low vs. high), and if use of linear features within the TRT declined as the cumulative area treated increased (low vs. high). Proportional use for each individual animal was calculated as the number of GPS locations on linear features of each treatment intensity class, divided by the number of locations per individual per season. For each species, we used quasi-binomial models with a logit link. Proportional use of riparian areas and non-disturbed habitat were included as fixed effects to account for broader differences in individual-level behaviours. There was insufficient data to test for seasonal effects. We report R^2 values using package '*rsq*' (Zhang, 2020).

There were insufficient sample sizes to evaluate changes in use relative to availability using a resource selection framework (Boyce et al., 2003). However, we evaluated if our conclusions were sensitive to availability using the Manly-Chesson electivity index, which is robust to small sample sizes (Chesson, 1983; see Appendix F).

2.5.3. *Are camera-trap sites (seismic and interior) within the treatment area used less relative to those in the reference area as restoration progresses?*

At the landscape-scale we examined whether species' use of linear features within the TRT relative to the BAU declined as treatment progressed, regardless of treatment status. We did not explicitly compare the TRT relative to the BAU, but rather used the BAU to provide context to the observed use of sites within the TRT as restoration progressed. We classed captures from all cameras (i.e. both "line" and "interior") as being in either the TRT or the BAU, and further classified captures within the TRT as obtained from time periods of low or high cumulative area treated, separated by season. We used a similar hurdle-model approach as in 2.5.1 above with "line" in low cumulative area treated as the reference condition, and camera (sites) within arrays as random intercepts.

2.5.4. *Do individual animals monitored with GPS collars use seismic inside the treatment area less than outside the treatment area as treatment progresses?*

We calculated the paired differences in proportional use of linear features, regardless of treatment status, inside the TRT relative to outside the TRT for each individual for each season. The proportional use of linear features outside the TRT was subtracted from inside the TRT for each individual, such that a value of zero represents no difference in use inside and outside, a positive value represents higher use inside the TRT, and a negative value represents lower use inside the TRT. We expected the proportional use of linear features inside the TRT relative to outside the TRT to decline as cumulative area treated increased. We used a linear model for each species with cumulative area treated as a fixed effect. We report R^2 values using package '*rsq*' (Zhang, 2020). We again evaluated if our conclusions were sensitive to availability (Appendix F).

2.5.5. *Summarizing multiple lines of evidence*

We summarized whether the response of each species to each of the questions of interest (2.5.1–2.5.4) was consistent with, or counter to, our predictions, as well as if the observed effect was statistically significant. This approach does not explicitly test species' responses to each of the questions of interest, but provides a concise summary in which to interpret patterns. Following the precautionary principle, we provide both the trend and significance given the high risk of Type II error falsely refuting the efficacy of restoration treatments (Kriebel et al., 2001; Lemons et al., 1997), but weight the evidence from significant effects more heavily.

2.5.6. *The influence of landcover on treatment effectiveness*

The effect of anthropogenic habitat alteration depends on landscape context. For example, the abundance of features, or the surrounding habitat, can influence the use or selection of those features (Newton et al., 2017; Pigeon et al., 2020). Indeed, landcover and the distribution of anthropogenic disturbances varied across the study area (Appendix B). To understand if habitat influenced the effect of restoration treatments on animal use of linear features, we tested if the inclusion of landcover was supported in each model using an Information Theoretic framework (Appendix B). If the inclusion of landcover was supported, we further evaluated if including landcover influenced the direction and significance of the coefficients of interest. We found little support for including landcover in models. When the inclusion of landcover was indeed supported, the direction or significance of the effect of restoration treatment was not affected. We therefore present results without landcover in the main text to maintain consistency and parsimony across models, but present models including landcover in Appendix B.

3. Results

For camera data, a total of 3650 detection events were recorded for our four target species (caribou, moose, bears and wolves) in the 2 areas (BAU = 2226; TRT = 1424). Caribou were the most frequently detected species (1746 detections) and wolves the least (445 detections). Below, we present model estimates and standard error for significant effects of restoration treatments only. See Appendix G for full model results.

For individuals monitored with GPS-collars, there was a mean of 1410 GPS locations per individual within the TRT, and 3121 outside the TRT. The mean number of GPS locations per individual inside the TRT was highest for moose ($\text{mean}_{\text{inside}} = 2875$, $\text{mean}_{\text{outside}} = 290$), then bears ($\text{mean}_{\text{inside}} = 592$, $\text{mean}_{\text{outside}} = 1570$) and lowest for wolves ($\text{mean}_{\text{inside}} = 553$, $\text{mean}_{\text{outside}} = 7906$). See Table G2 for sample sizes per individual.

3.1. *Are treated sites monitored with camera traps used less than untreated sites?*

3.1.1. *Treatment intensity*

All four species were more likely to be absent from treated sites than untreated sites (Table 1; Fig. 2). Caribou, moose and wolves were significantly more likely to be absent from sites with natural regeneration and high-intensity treatments (Table 1). Moose and bears were significantly more likely to be absent from sites with low-intensity treatments (Table 1). The probability of each species being absent at untreated sites was typically very high (0.97 to 1.00); the effect of treatment intensity of natural regeneration increased this probability by less than 0.01 in most cases (Appendix G). The frequency of use of sites where found tended to decrease for all treatment intensities for all species except bears, though this effect was significant for moose and wolves only (Fig. 2). Where present, moose were captured 0.19 and 0.29 times less often at sites with natural regeneration and high-intensity treatments, respectively (Table 1). Wolves were captured 0.15 times less often at sites with high-intensity treatments (Table 1).

3.1.2. *Cumulative area treated*

As the cumulative area treated increased, moose and wolves were significantly more likely to be present at treated sites (probability increased from 0.99 to 1.00; Table 1). At sites where found, moose and wolves also tended to increase their frequency of use of sites as area treated increased, though this effect was significant only for moose (Table 1). No other species responded significantly to area treated (Table 1). Caribou tended to be less present as area treated increased, but also tended to be at those sites more frequently. Bears tended to be more present as area treated increased, but also tended to be at those sites less frequently.

3.2. *Do individual animals monitored with GPS collars use treated lines less than untreated lines?*

3.2.1. *Treatment intensity*

Moose, bears, and wolves tended to decrease their use of low and high intensity treated linear features as well as lines with natural regeneration in comparison to untreated linear features (Fig. 3).

Table 1
The effects of treatment intensity and cumulative area treated on the probability of absence at a site, and frequency of use given presence (frequency), at sites located on linear features in the restoration area ($n = 54$ cameras) by species. Seasonal effects are also included. Reference conditions were season (snow), seismic with no treatments, and low area treated (<60% of the treatment area). A random intercept was included for cameras nested within arrays. Sample sizes are total number of captures over the period of the study. Bold signifies significance, defined as 95% confidence intervals non-overlapping zero.

Species		Covariate	Absence[a]			Frequency[b]		
			Estimate	−CI	+CI	Estimate	−CI	+CI
Caribou		Intercept	**6.448**	**5.981**	**6.916**	−0.833	−1.722	0.055
352		Season (snow-free)	**−2.055**	**−2.407**	**−1.703**	**−0.901**	**−1.746**	**−0.056**
captures		Area treated (H)	0.216	−0.286	0.718	0.444	−0.798	1.686
	Treatment intensity	LFNat	**1.149**	**0.417**	**1.880**	−17.123	−5768.5	5734.2
		L_Trt	0.465	−0.180	1.111	−0.881	−2.451	0.689
		H_Trt	**0.578**	**0.042**	**1.114**	−0.694	−1.951	0.563
Moose		Intercept	**5.834**	**5.516**	**6.151**	**−5.335**	**−7.388**	**−3.282**
484 captures		Season (snow-free)	**−1.492**	**−1.734**	**−1.251**	**2.037**	**0.514**	**3.560**
		Area treated (H)	**−0.814**	**−1.168**	**−0.460**	**2.744**	**1.139**	**4.349**
	Treatment Intensity	LFNat	**1.384**	**0.885**	**1.883**	**−1.677**	**−3.311**	**−0.042**
		L_Trt	**1.260**	**0.755**	**1.766**	−1.460	−2.921	0.001
		H_Trt	**1.010**	**0.658**	**1.361**	**−1.236**	**−2.201**	**−0.271**
Bears[c]		Intercept	**4.778**	**4.442**	**5.114**	**−2.648**	**−3.810**	**−1.485**
297 captures		Area treated (H)	−0.016	−0.487	0.455	−0.361	−2.883	2.162
	Treatment Intensity	LFNat	0.013	−0.615	0.640	0.476	−2.046	2.998
		L_Trt	**0.879**	**0.048**	**1.710**	−14.48	−5023.7	4994.7
		H_Trt	0.222	−0.282	0.726	0.012	−2.728	2.753
Wolves		Intercept	**5.639**	**5.253**	**6.025**	**−2.603**	**−4.050**	**−1.155**
291 captures		Season (snow-free)	0.009	−0.232	0.250	0.206	−1.008	1.420
		Area treated (H)	**−0.717**	**−1.148**	**−0.286**	1.064	−0.591	2.719
	Treatment Intensity	LFNat	**0.983**	**0.402**	**1.563**	−1.576	−3.739	0.586
		L_Trt	0.446	−0.140	1.032	−0.954	−2.625	0.717
		H_Trt	**0.710**	**0.290**	**1.130**	−1.899	−3.617	−0.182

[a] Estimates are logit values. Positive values indicate increasing probability of absence from sites per day (i.e. decreasing use of sites).
[b] Estimates are log values. Positive values indicate increasing # predicted captures per day (i.e. increasing intensity of site use).
[c] Effects for bears are modelled for summer only (i.e. with no seasonal covariate).

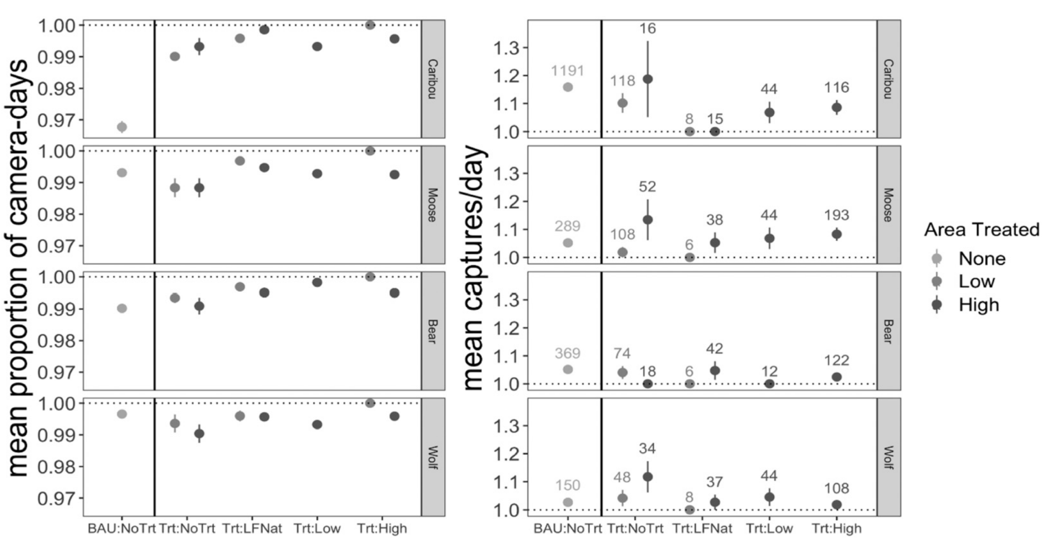

Fig. 2. Observed patterns in daily capture rates of caribou, moose, bears and wolves monitored using wildlife cameras in the Business as Usual (BAU) and Treatment (TRT) areas. Data from sites on linear features with no restoration treatments (NoTrt), natural regeneration (LFNat), low intensity treatments (L_Trt), and high intensity treatments (H_Trt) are shown in relation to cumulative area treated (Low, High, and None which represents the BAU). Data are pooled across seasons. Shown are the mean proportions of cameras per day per stratum at which no captures for each species were recorded (N camera-days/stratum are BAU:NoTrt = 1054; Trt:NoTrt/Low = 365; Trt:NoTrt/High = 396, Trt:LFNat/Low = 301; Trt:LFNat/High = 1096; Trt:Low/Low = 0; Trt:Low/High = 1076; Trt:High/Low = 19; Trt:High/High = 1060), and the mean number of captures per camera per day when animals were recorded (N = number of capture events, annotated on right panel). Standard errors of the means are also presented. Dotted lines indicate maximum (left panel) and minimum (right panel) values, respectively.

However, there was no significant effect of treatment intensity ($R^2_{\text{Moose}} = 0.95$; $R^2_{\text{Bears}} = 0.40$; $R^2_{\text{Wolves}} = 0.64$; Appendix G). Individual moose, bears, and wolves used non-disturbed habitat and riparian features significantly more than untreated linear features (moose $\beta_{Non\text{-}disturbed} = 4.595$ [3.743, 5.466]; bears $\beta_{Non\text{-}disturbed} = 3.811$ [1.485, 6.137]; wolves $\beta_{Non\text{-}disturbed} = 2.933$ [1.727, 4.140]; moose $\beta_{Riparian} = 2.073$ [1.219 = 0, 2.937]; bears $\beta_{Riparian} = 2.796$ [0.438, 5.154]; wolves $\beta_{Riparian} = 2.191$ [0.960, 3.423]; Appendix G).

3.2.2. *Cumulative area treated*

Moose tended to decrease their use of untreated linear features as restoration progressed, whereas wolves tended to increase their use as restoration progressed (Fig. 3). However, there was no significant effect of cumulative area treated (Appendix G).

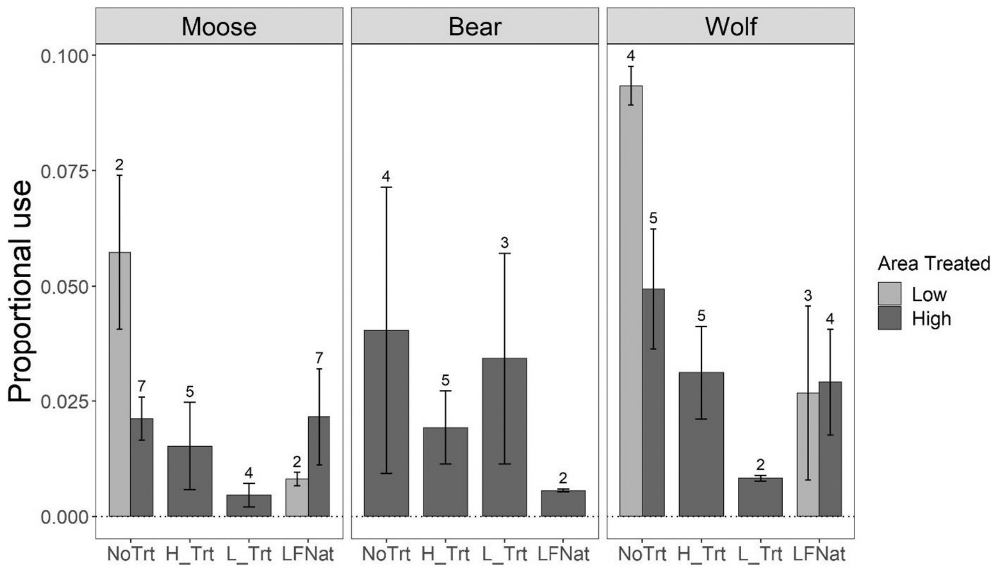

Fig. 3. The proportional use of linear features with no restoration treatments (NoTrt), high intensity treatments (H_Trt), low intensity treatments (L_Trt), lines naturally regenerating (LFNat) by moose, bears and wolves monitored with GPS collars. Proportional use is summarized by cumulative area treated (light grey = low, dark grey = high). The proportional use was calculated as the number of locations in each category divided by the total number of locations for each individual. The mean, standard error of the mean, and number of individual-season combinations used to calculate proportional use are presented.

3.3. Are sites (on seismic lines & in forest interior) monitored with camera traps within the treatment area used less relative to those in the reference area as restoration progresses?

The likelihood of caribou and bears being present at sites within the TRT was significantly lower than in the BAU (Table 2; Appendix G). Furthermore, caribou and bears tended to be even less likely to be present at sites when area treated was high, but the Confidence Intervals overlapped between low and high area treated for both on-line sites and interior sites (Table 2). Where these species were found, the frequency of use of sites tended to be higher as area treated increased, but the Confidence Intervals overlapped between low and high area treated for both on-line sites and interior sites (Table 2). Moose more likely to be present at sites on lines in the TRT relative to the BAU, though this effect was non-significant (Table 2). Moose were significantly less likely to be present at interior sites than sites in the BAU, and tended to be even less likely to be present as area treated increased, but Confidence Intervals overlapped between low and high area treated (Table 2; Appendix G). At sites where found, moose tended to use lines more as area treated increased, and interior sites less, though Confidence Intervals overlapped. Wolves were significantly more likely to be present at sites in the TRT relative to the BAU, though Confidence Intervals between low and high area treated overlapped (Table 2). Where found, wolves tended to more frequently use sites as area treated increased, although again Confidence Intervals overlapped. There were insufficient captures of wolves at interior sites to evaluate responses.

Table 2
The effects of cumulative area treated on the probability of absence (presence/absence), and frequency of use given presence (frequency), at sites located near linear features among monitored areas (BAU and TRT; $n = 135$ cameras) by caribou, moose, bears and wolves. Seasonal effects are also included. Reference conditions were area (BAU), season (snow), and low area treated (<60% of the treatment area). A random intercept was included for each camera and array. Bold signifies significance, defined as 95% confidence intervals (1.96 * standard error) non-overlapping zero.

Species	Covariate	Absence[a]			Frequency[b]		
		Estimate	−CI	+CI	Estimate	−CI	+CI
Caribou 1732 captures	Intercept	**4.806**	**4.471**	**5.141**	**−1.107**	**−1.347**	**−0.866**
	Season	**−0.932**	**−1.047**	**−0.816**	−0.143	−0.426	0.140
	Line: Area treated (L)	**0.934**	**0.435**	**1.432**	−0.451	−1.036	0.134
	Line: Area treated (H)	**1.661**	**1.176**	**2.145**	**−0.588**	**−1.097**	**−0.079**
	Interior: Area treated (L)	**2.979**	**1.880**	**4.078**	−13.698	−1857.116	1829.720
	Interior: Area treated (H)	**3.625**	**2.721**	**4.530**	−0.662	−2.606	1.283
Moose 788 captures	Intercept	**6.089**	**5.840**	**6.340**	**−3.185**	**−4.295**	**−2.075**
	Season	**−1.504**	**−1.690**	**−1.318**	0.754	−0.192	1.700
	Line: Area treated (L)	−0.076	−0.396	0.244	−1.114	−2.625	0.396
	Line: Area treated (H)	−0.023	−0.303	0.258	0.450	−0.273	1.172
	Interior: Area treated (L)	**1.286**	**0.563**	**2.009**	1.214	−0.509	2.937
	Interior: Area treated (H)	**1.608**	**1.074**	**2.143**	−0.193	−2.281	1.894
Bears[c] 685 captures	Intercept	**4.514**	**4.242**	**4.786**	**−2.577**	**−3.383**	**−1.771**
	Line: Area treated (L)	0.355	−0.070	0.780	−0.181	−1.477	1.115
	Line: Area treated (H)	**0.553**	**0.163**	**0.941**	−0.569	−1.625	0.488
	Interior: Area treated (L)	**0.961**	**0.212**	**1.711**	−14.151	−2855.551	2827.249
	Interior: Area treated (H)	**2.367**	**1.580**	**3.154**	0.697	−1.367	2.761
Wolves 445 captures	Intercept	**6.756**	**6.341**	**7.170**	**−2.980**	**−4.013**	**−1.948**
	Season	**0.334**	**0.141**	**0.528**	0.107	−0.922	1.136
	Line: Area treated (L)	**−1.036**	**−1.606**	**−0.467**	0.290	−1.399	1.979
	Line: Area treated (H)	**−1.236**	**−1.758**	**−0.715**	0.393	−0.800	1.587

[a] Estimates are logit values. Positive values indicate increasing probability of absence from sites per day (i.e. decreasing use of sites).
[b] Estimates are log values. Positive values indicate increasing # predicted captures per day (i.e. increasing intensity of site use).
[c] Effects for bears are modelled for summer only (i.e. with no seasonal covariate).

3.4. Do individual animals monitored with GPS collars use linear features inside the treatment area less than outside the treatment area as treatment progresses?

The proportional use of linear features inside the TRT relative to outside by moose and wolves tended to decrease as cumulative area treated increased (Fig. 4), but this effect was non-significant (Appendix G). Bears showed variable proportional use of seismic inside the TRT compared to outside ($R^2_{\text{Moose}} = 0.05$; $R^2_{\text{Wolves}} = 0.18$; Fig. 4), however there were no GPS data from bears inside the TRT in 2013, and as such the effect of area treated on proportional use inside compared to outside the TRT could not be evaluated.

3.5. Summarizing multiple lines of evidence

Caribou and bear data were available for six and seven of the questions of interest, respectively, whereas moose and wolf data were available for all nine of the questions of interest. In five of six cases caribou followed expected patterns, but responded significantly to restoration treatments in only one of the analyses (Table 3). Bears tended to follow expectations for both the site and individual-level analyses (questions 3.2–3.4), but responses were more variable at the landscape scale. Bears responded significantly in accordance with expectations as treatment intensity increased at the site-level. Moose and wolves tended to follow expectations with treatment intensity, but responses were variable to the cumulative area treated. Moose and wolves responded significantly in accordance with expectations in two cases (Table 3). Moose responded significantly counter to expectations in two cases, and wolves in one case (Table 3).

4. Discussion

Using a hierarchical, multiple-lines-of-evidence approach, we found variable responses by predator and prey species to a large-extent trial of silvicultural restoration of linear features. The direction of each species' responses to silvicultural restoration treatments was most often consistent with our expectations of reduced use, though mostly non-significantly so. In cases where significant, the effect sizes tend to be small due to already low use of sites by species. Responses were significant most often when evaluated at the site-scale (i.e. use of sites via camera data or individual use of lines via GPS collars). Responses tended to be less consistent with expectations and also were less frequently significant when evaluated at larger spatial scales as restoration progressed. Both camera-based and GPS-collar based data showed that the species we monitored decreased their use of lines following restoration treatments. The response to cumulative area treated was more variable. In particular, all four species were significantly more likely to be absent from treated sites monitored with camera traps, and the frequency of use of those sites was significantly lower for moose and wolves, as expected. However, moose and wolves were significantly more likely to be observed at sites in the TRT as cumulative area treated increased, counter to expectations. Finally, caribou, moose, and wolves were significantly less likely to be present at sites classified as natural regeneration, suggesting that these features may be on a trajectory to ecological recovery (Tattersall et al., 2020). While no single test showed clear responses to restoration, we argue that the accumulation of evidence within this study provides valuable information to support confidence in observed patterns that are currently apparent only as trends in individual tests, and moreover the variation in responses observed are nonetheless informative. The value of accumulating evidence continues to be echoed in the academic and management communities alike (Nichols et al., 2019).

Restoration treatments were designed to impede animal use in the short-term, while promoting return to forest cover in the long-term. In the short-term, treatments were therefore specifically targeted to reduce use by predators that use these features as movement corridors (Dickie et al., 2019). As such, wolves were most expected to show a decrease in use of treated linear features in the short-term. We found evidence that wolves did decrease their use of these features, similar to the findings of Keim et al. (2019) where treatments were intensive, but counter to the findings of Tattersall et al. (2020) and Neufeld (2006) where treatments were more intermittent or of lower intensity. This suggests that intensive seismic line restoration can be successful in deterring wolves from using linear features. However, our effect was estimated to be small, and

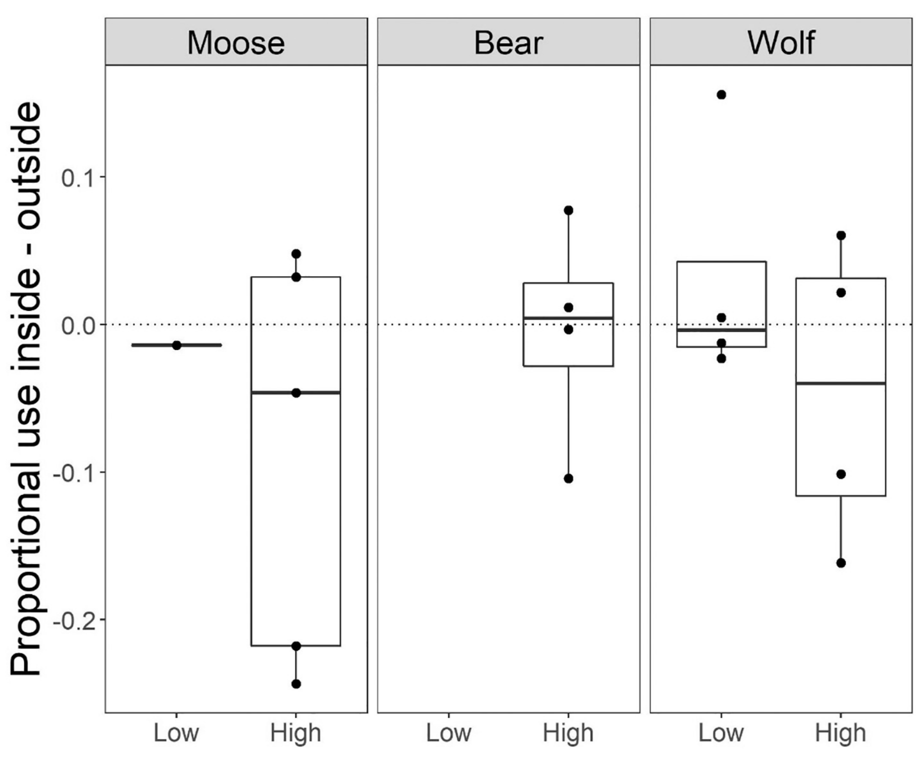

Fig. 4. The effect of cumulative area treated (low ≤ 60% and high ≥ 60%) on the proportional use of linear features inside the treatment area relative to outside the treatment area by moose, bears and wolves monitored with GPS collars. The proportional use (total number of locations on linear features, divided by the total number of locations) outside the treatment area was subtracted from inside the treatment area for each individual, such that a value of zero represents no difference in use inside and outside, a positive value represents higher use inside the treatment area, and a negative value represents lower use inside the treatment area. The bold horizontal line represents the median value, box hinges represent the 25th and 75th percentiles, and each individual-season data point is displayed.

Table 3
Summarizing the multiple lines of evidence evaluating species response to restoration treatments in northeastern Alberta. For each question, and sub-question asked, the metric (and data type; CT = Camera Trap, GPS = Global Positioning System) and results are summarized. Section headings are provided for cross-referencing. Y and N signify that the trend followed, or did not follow, the expectation respectively. An asterisk signifies the trend was significant.

Question	Sub-question	Metric	Species			
			Caribou	Moose	Bear	Wolf
3.1 Are treated sites used less than untreated sites?	*3.1.1 Treatment intensity*	Absence (CT)	Y*	Y*	Y*	Y*
		Frequency (CT)	Y	Y*	Y	Y*
	3.1.2 Area treated	Absence(CT)	Y	N*	N	N*
		Frequency (CT)	N	N*	Y	N
3.2 Do animals use treated lines less than untreated lines?	*3.2.1 Treatment intensity*	Proportional use (GPS)	Untested	Y	Y	Y
	3.2.2 Area treated	Proportional use (GPS)	Untested	Y	Untested	N
3.3 Are sites in the restoration area used less as restoration progresses?	*3.3 Area treated*	Absence (CT)	Y	Y	Y	N
		Frequency (CT)	Y	N	Y	N
3.4 Do animals use lines inside the treatment area less than outside the treatment area?	*3.4 Area treated*	Proportion use inside TRT - outside TRT (GPS)	Untested	Y	Untested	Y

whether this would translate into decreased hunting efficiencies is uncertain. Despite the omnipresence of linear features within the boreal forests of western Canada, the direct footprint of linear features is quite low (less than 2%; Alberta Biodiversity Monitoring Institute, 2018). Therefore, even though linear features significantly modify the space-use and movement behaviour of these species (Dickie et al., 2019), the proportional use of linear features is low (DeMars and Boutin, 2018; Mumma et al., 2018). Even small changes to use of linear features may influence predator-prey interactions, and should be evaluated as restoration continues to expand in time and space. Furthermore, while we provide evidence of how restoration treatments influence use, future work should evaluate if restoration treatments are able to reduce the use of these features for travel movements specifically, as well as to reduce travel speed, which is the presumed mechanism in which encounter rates between caribou and predators are increased (Latham et al., 2011a).

Species that use linear features for foraging may still use treated linear features in the short-term given the expected temporal lags in establishing later-successional vegetation communities less preferred as browse (Finnegan et al., 2018a). The apparent increase in use of sites within the TRT as restoration progressed by moose and bears is perhaps because their use of linear features is associated with feeding behaviour and is therefore influenced by browse and berry availability upon lines (Dawe et al., 2017; Finnegan et al., 2018a). Indeed, moose were often photographed browsing as they passed by camera traps. Conversely, caribou have repeatedly been documented to avoid linear features such as seismic lines and are hypothesized to perceive these features as risky (DeMars and Boutin, 2018; Dyer et al., 2002; Mumma et al., 2017). Supporting this, caribou were rarely photographed feeding along the linear features. This observation could either reflect perceived risk (Dickie et al., 2019), or decreased lichen availability on these features, which is consumed by caribou but is not an important food source for moose. The understanding of how linear features, and their restoration, influences prey species behaviours would benefit from evaluating the use of these lines for foraging. While amplified declines in caribou use of these features following treatments may result in further habitat loss, restoration treatments such as those used here may reduce encounter rates between caribou and wolves via spatial partitioning. The initial avoidance of these features by caribou (Dickie et al., 2019), and decreased permeability following treatments, perhaps explains why treatments had a more consistent effect on caribou than other species.

Our work extends the reported findings of natural regeneration (i.e., vegetation regrowth), and its effect on wolf behaviour (Dickie et al., 2017a; Finnegan et al., 2018b) to cases of active restoration (i.e., silvicultural). Evaluating the effects of active habitat restoration on large mammal communities is still in its infancy. Clearer evidence of behavioural effects from active restoration on linear features is unlikely to occur until the treatment application is extended to broader areas and longer time periods, highlighted by previous findings that less intensive restoration treatments are less effective at reducing use of linear features (Tattersall et al., 2020). This reality stems from the unavoidable linkage between animal behaviour and time lags in response to conservation management (Berger-Tal et al., 2011). While active restoration may achieve a desired change in habitat use, it may still require further predator behavioural responses via larger areas treated to manifest in reduced encounters with prey, kill rates, and/or predator abundance. In fact, multiple generations may be required to disrupt learned behaviours, and the time frame of our study was considerably shorter than the generation time of any of our species.

This study has a number of limitations that should be addressed in future work to more fulsomely understand species responses to linear feature restoration treatments. Despite being one of the most comprehensive restoration programs implemented to date in boreal Western Canada, the TRT was small relative to the overall landscape used by these wide-ranging species, particularly wolves. Therefore, the sample sizes and statistical power of each of the analyses is necessarily limited. The lack of power is primarily a result of the scales in which habitat restoration is occurring relative to the life-history of the species studied. Despite this limitation, the GPS-based analyses largely corroborate the responses seen at the site-level, supporting that restoration treatments are altering animal behaviour across the restoration area. Furthermore, we were unable to explicitly test for differential behaviours across seasons by each of the species of interest. Our camera-trap based analyses did include season to account for this variation, but future work should specifically evaluate responses across seasons. Likewise, future work should clarify if the response to restoration treatments depends on surrounding habitat to best support habitat restoration efforts. Restoration treatments could prioritize areas expected to see the largest response. Further, both the camera-based and GPS-based results may be confounded by seasonal-range shifts by animals moving in and out of the TRT. While difficult to implement at scales necessary to see these behavioural responses, a Before-After-Control-Impact study design can help to mitigate some of the limitations of work to date on restoration effectiveness.

Our work suggests that habitat restoration can be effective at modifying the behaviour of large mammals. However, current empirical and theoretical research indicates that large areas and time scales are needed to observe population-level response by caribou (Johnson et al., 2020, 2019; Spangenberg et al., 2019). Further longitudinal studies and more extensive treatment application will be required to understand how changes in habitat use following habitat restoration treatments will translate into increased caribou survival. Defining the spatial extent of treatments needed to reduce predator hunting behaviours and reduce encounter rates, as well as the time-span required to achieve a significant impact on predator-prey relationships involving woodland caribou is imperative for effective species conservation.

4.1. Conclusions

Our results suggest that silviculture can be successful in mitigating some components of the effect of anthropogenic linear features on large mammal predators and prey in the short-term. While we found more evidence of a reduction of animal use of sites in the restoration area than not, the effect sizes were typically small. This observation reflects that, despite the extent of habitat restoration, treatments occurred at a small-scale relative to the life-history of the intended species of interest. Therefore, our study highlights the complexities and spatiotemporal scale-dependencies of monitoring and evaluating the success of habitat restoration. Furthermore, understanding medium- and long- term effects is imperative. Habitat restoration is predicated on an untested assumption that habitat recovery will result in restoration of predator-prey assemblages and dynamics, which will provide conditions that then allow for caribou persistence. It is unclear if the observed changes in predator or prey behaviour as a result of restoration treatments will translate into meaningful changes in predator-prey interactions; both because of the challenge of implementing habitat restoration at large scales, as well as the intricacies of the animal behaviours involved. Nonetheless, this study represents the next step in the necessary accumulation of evidence that will inform recovery efforts of woodland caribou. If the system has reached a new steady state in which alternate prey and predator populations are higher than historical levels, reductions in predation may only occur once primary prey, and thus predator, populations have returned to lower levels (Carpenter, 2002). Despite these uncertainties, continued restoration, and reducing new habitat alteration, is essential. To understand the potential for restoration to provide meaningful changes in predation on caribou, deployment of restoration at larger scales combined with monitoring is needed. To effectively recover, and prevent the extirpation of, woodland caribou while restoration occurs across the landscape, habitat restoration should likely be combined with additional management actions to reduce predation such as predator reductions, primary prey reductions, or maternal penning.

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Data availability

Data will be made available via Dryad upon acceptance of the manuscript.

CRediT authorship contribution statement

Melanie Dickie; Formal analysis, Writing Original Draft and Review & Editing, Visualization, Supervision.

Scott McNay; Conceptualization, Methodology, Formal analysis, Data Curation, Writing - Original Draft, Writing - Review & Editing

Glenn Sutherland; Conceptualization, Methodology, Formal analysis, Data Curation, Writing - Original Draft, Writing - Review & Editing

Geoff Shermann; Methodology, Validation, Data Curation, Writing - Review & Editing

Michael Cody; Conceptualization, Methodology, Supervision, Project administration, Funding acquisition

Declaration of competing interest

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Appendix A. Supplementary data

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