1 Evaluating the impact of caribou habitat restoration on predator and prey movement

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Keywords: anthropogenic habitat alteration, camera traps, habitat restoration, linear features,

movement, predator-prey, woodland caribou

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the <u>Version of Record</u>. Please cite this article as <u>doi:</u> 10.1111/cobi.14004.

- 23 Article Impact Statement: Restoration treatments slow wolves, bears, and caribou speeds 23-40%,
- addressing a key mechanism hypothesized to lead to caribou declines.

Abstract

Fragmentation of the boreal forest by linear features including seismic lines has destabilized predator-prey dynamics, resulting in the decline of woodland caribou populations. Restoration of human-altered habitat has therefore been identified as a critical management tool for achieving self-sustaining woodland caribou populations. However, only recently has testing of the response of caribou and other wildlife to restoration activities been conducted, with early work centering around assessing changes in wildlife use of restored seismic lines. We evaluated if restoration reduces the movement rates of both predators and their associated prey, which is expected to decrease predator hunting efficiency and ultimately reduce caribou mortality. We developed a new methodological framework using cameras to measure fine-scale movement, and applied this framework to quantify speed of caribou, moose, bears, and wolves on treated and untreated seismic lines. Restoration treatments reduced the travel speeds along seismic lines of wolves by 1.38 km/hr, bears by 0.55 km/hr, and caribou by 1.57 km/hr, but did not reduce moose travel speeds. Reduced predator and caribou speed on treated seismic lines is predicted to decrease encounter rates between predators and caribou, and thus lower caribou kill rates. However, further work is needed

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44 to understand if reduced movement rates results in reduced encounter rates with prey, and

5 ultimately reduced mortality for caribou.

Introduction

Movement is a fundamental process through which individuals acquire resources and mediate interand intra-specific interactions. Changes in movement behaviors therefore have the potential to precipitate change to an individual's survival, as well as mediate inter- and intra-specific interactions (Bélichon et al., 1996; Sawyer et al., 2012). Anthropogenic habitat alteration has resulted in changes to movement behaviors across multiple taxa (Tucker et al., 2018). However, the implications of these modifications are variable and difficult to generalize (Fahrig, 2007). Both declines in, and increases in, vagility of species have been documented (Kot et al., 1996; Russell et al., 2004; Tucker et al., 2018). In the boreal forests of North America, many species have been documented to modify their movement behavior as a result of habitat alteration (Fahrig, 2007; Bayne et al., 2011; Tigner et al., 2014). Changes in movement behaviors can alter the distribution and abundance of species (Tucker et al., 2018), predator-prey dynamics (Fryxell et al., 2007; Vander Vennen et al., 2016), and community structure (Fisher & Burton, 2019).

In western Canada's boreal forest, anthropogenic habitat alteration has led to a high profile example of species declines due to anthropogenic habitat alteration: boreal woodland caribou (*Rangifer tarandus caribou*). Linear features such as roads and seismic lines (i.e. linear forest clearings for oil and gas exploration) have become pervasive, and modify the behavior of large-mammal predator and prey species (Dickie et al., 2020). Moose (*Alces alces*) and caribou perceive these features as risky, avoiding linear features and traveling faster when near them (Dickie et al., 2020). Conversely, black bears (*Ursus americanus*) and gray wolves (*Canis lupus*) use linear features as movement corridors, which has been linked to increased predation rates on caribou via increases in hunting efficiency (McKenzie et al., 2012; Dickie et al., 2017a) and increased incursions into preferred caribou habitat (DeMars & Boutin, 2018).

Restoration of seismic lines has been identified by several studies as a necessary tool to recover caribou populations (Bentham & Coupal 2015; Johnson et al., 2020) and has been mandated as an action in federal legislation (Environment Canada, 2012; Environment and Climate Change Canada, 2020). Vegetation on seismic lines can often take decades to recover passively and can be stagnated by site conditions (van Rensen et al., 2015; Lee & Boutin 2006). Techniques to restore seismic lines

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aim to promote revegetation in the long-term (Dabros et al., 2018) while reducing wildlife use of, and movements along, seismic lines in the short- to medium-term (Dickie et al., 2021; Tattersall et al., 2020). Preliminary research shows that tree regrowth can indeed be facilitated via silvicultural treatments, but long-term monitoring is needed to test the efficacy of these treatments to recover the vegetation community over long time frames (Fillicetti et al., 2019). Deterring use of these features by wildlife species, particularly predators that select them for movements, appears to require intensive treatments such as high intensity tree felling or mounding (Dickie et al., 2021; Keim et al., 2019; Tattersall et al., 2020). However, these studies have examined only the use of seismic lines following treatment, but not the rate of animal movement along seismic lines.

Reduced predator hunting efficiency through slower movement is predicted to be a mechanism through which restoration can reduce caribou mortality (Johnson et al., 2019; Serrouya et al., 2020; Spangenberg et al., 2019). Increased habitat complexity resulting from restoration treatments could hamper the movements of predators and large ungulates, reducing their speeds and maneuverability (Bergman et al., 2006). Reducing the movement of caribou and other ungulates should also decrease encounter rates, as encounters are partly determined by the speed of both predators and prey (Vander Vennen et al., 2016). Evaluating restoration effectiveness to reduce movements of both prey and predators on seismic lines is therefore necessary to understand the efficacy of these treatments to restore predator-prey interactions. While multiple studies have used GPS collars to study wildlife movement along and near seismic lines (Dickie et al., 2017; Finnegan et al., 2018; Latham et al., 2011), movements along restored seismic lines are rare events due to the relatively small proportion of restored seismic lines on the boreal landscape. The effect of

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restoration has been evaluated using cameras (Keim et al., 2019; Tattersall et al., 2020; Dickie et al., 2021), but these studies have not focused on movements along restored seismic features.

We used camera traps in a new methodological framework to examine the fine-scale movement responses of multiple species on seismic lines treated with silvicultural techniques to reduce travel speeds – directly targeting one of the mechanisms in which these features are hypothesized to contribute to caribou declines. We deployed camera traps in arrays along treated and untreated seismic lines, calculating travel times across a known distance between two cameras, to quantify and contrast the travel speeds of caribou, moose, black bears, and wolves. Given the hypothesis that linear features facilitate travel, we predicted that animals would move slower along treated seismic lines and naturally regenerating lines compared to untreated lines, and that the degree of impediment to movement would increase as treatment intensity increased. We hypothesize that the reduction in speed following restoration is dependent on how each species uses the line: wolves are cursorial predators known to use these features as travel corridors (Latham et al., 2011; Dickie et al., 2017a), whereas moose, caribou, and bears are known to use these corridors for forage as well as travel (Dawe et al., 2017; Dickie et al., 2017a; Finnegan et al., 2018). We therefore predict that wolves will show a stronger reduction in speed than bears, moose, and caribou. Moving beyond metrics of habitat use or selection towards an understanding movement behavior will allow a deeper understanding of the effectiveness of restoration treatments to recover predator-prey interactions that have been perturbed by anthropogenic habitat alteration.

Materials and Methods

Our study area was located in the Cold Lake caribou range, within the Central Mixedwood Subregion of the Boreal Plains Ecozone (Fig. 1). The study area consisted of a 378 km² treatment area (TRT) centered at 55.250 °N" and "110.100 °W and paired reference area approximately 70 km west of the treatment area where seismic lines were not treated and industrial activities continued during the duration of the study (business-as-usual area; BAU). Anthropogenic linear features, including ice roads, pipelines, conventional seismic lines, and low-impact seismic lines covered 960 ha, or 1.4% of the study area, with a linear feature density of 1.2 km/km². Oil and gas exploration and development has occurred within the study area since the early 1980s. The area is a mixture of fen and bog peatlands dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*) interspersed with upland forests consisting of jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). See Dickie et al., 2021 for additional details of the study area, including details on anthropogenic habitat alteration and natural habitat within the treatment and business-as-usual areas.

Restoration Treatments

Silvicultural restoration treatments were applied to seismic lines in the TRT beginning in 2013 (Fig. 1). Of the 235.4 km of seismic lines in the TRT, 34.5 km were treated in 2013, 167.4 km were treated in 2014 and 33.5 km were treated in 2015. The restoration program employed mounding and scalping, roll-back of coarse woody debris, and felling of trees across the seismic line. The lines were also planted with a mixture of black spruce, white spruce, jack pine, and tamarack. Planting densities ranged between 1200 and 2000 stems/ha and were site-specific based on moisture regime and line

orientation. Treatment type and intensity varied due to variability in ecological site type and operational and logistical considerations. Areas that were identified as naturally revegetating (8.2 km) were classified as advanced regeneration and are considered as passive treatment of caribou habitat. Areas which were left untreated due to operational constraints were classified as untreated (6.8 km). Additional details on the restoration treatments are provided in Dickie et al. (2021).

Study Design

To test for differences in animal movement, we deployed camera traps in arrays of three cameras along seismic lines to quantify movement speeds as animals moved through the array (Fig. 2). Cameras were deployed in the TRT in February 15, 2013 to February 22, 2017 and in the BAU from February 13, 2014 to February 23, 2017. We randomly selected array locations prior to any restoration activity. Arrays were installed at least 1 km apart to increase the independence between arrays (Tigner et al., 2014). Each array spanned 500-m along the length of a seismic line, with one camera placed at each end and a third camera placed in the middle. Therefore, each array consisted of three cameras spaced 250 m apart, creating two adjacent camera pairs (hereafter termed "segments").

We used Reconyx Hyperfire PC900 infrared cameras (Reconyx, Holman, WI). Cameras were deployed on the south side of east-west lines and on the side facing the taller tree canopy on north-south lines. The cameras were attached to trees approximately 1.2 m above the ground and angled approximately 30⁰ from perpendicular to the line. This setup captured the full width of the line, as well as along the line, to maximize capture area. Cameras were programmed to take three pictures when triggered at a rate of 1 per second with no delay between triggers. In total, 132 cameras were

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distributed in 44 arrays collecting data during the study (TRT: 69 cameras across 23 arrays; BAU: 63
cameras across 21 arrays).

Quantifying Travel Speed

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We used recorded timestamps to quantify travel speeds of moose, caribou, black bears, and wolves as they passed through segments (i.e., adjacent cameras) within the arrays (Fig. 2). There were insufficient sample sizes to quantify and analyse white-tailed deer (Odocoileus virginianus) movements (n=46 total detections across all years in the treatment area). Each photo was examined for the presence of an animal and then sorted by the timestamp found on each picture and stored using Timelapse2 (Greenburg, 2015). If two cameras along a segment captured the same species (assumed to be the same animal or group of animals) less than 60 minutes apart, we considered this a "travel event". Animals were traveling in the same direction (for example moving northward) in both detections. Detections were treated as independent if they occurred more than 60 min apart (Harris et al., 2015). As did Harris et al. (2015), we note that this time-cut off is arbitrary, but serves as a consistent definition of independence that sets the minimum travel speed across the segment. We calculated travel speed, in km/hr, of each travel event as the distance between cameras (250 m) divided by the difference in timestamps $(t_2 - t_1)$. Camera timestamps were standardized to the same time *post-hoc* by taking an image of the time displayed on a handheld Global Positioning System (GPS) during data collection and accounting for the difference for each observation. For animal groups, the travel time was based on the individual that first triggered the camera to start the event.

Model Variables

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We identified if each segment between camera pairs was treated, either via advanced regeneration or by silviculture, and if so, the intensity of treatment. Seismic lines were visually classified into segments of high, moderate, and low intensity treatment based on the amounts of mechanical site preparation and woody debris additions. First, we used video collected by a U8000 FLIR camera flown on a BELL 206 B helicopter to visually assess treatment intensity. We confirmed treatment intensity between camera pairs during site visits for camera servicing. Each treatment class was assigned an index value (high = 4, moderate = 2, low = 1) and multiplied by the length of the treatment class between each pair of cameras. The values for each treatment class were then totaled and divided by 250 m, giving a treatment value between zero (entire length with no active treatment) and four (entire length treated with the highest intensity) for each segment. All sections classified as advanced regeneration were classified as zero intensity treatments.

We also assessed the potential effects of biophysical conditions that we expected to influence the vagility of our study species. To capture habitat-mediated differences in travel speeds among species, we included information on landcover. We summed the lengths of the seismic line segments classified as lowland, grouping ecosites based on moisture regime (Beckingham & Archibald 1996). We also classified the line segments as either containing or lacking micro-topography, which we predicted could slow wildlife movement due to the uneven terrain. The line segments between each camera pair were categorized by field crews as a microtopographic line if more than half of the line segment contained microtopography: the mosaic of hummocks, hollows and uneven ground found in hydric and hydric boreal ecosystems (Sullivan et al., 2008).

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To evaluate the effect of restoration treatments on travel speed we modelled travel speed as a function of treatment (treated or untreated) for each species. We also included microtopography, and landcover. To account for repeated measures at each camera segment, potential spatial autocorrelation between segments at each array, and repeated measures across years we included segment, array, or year as random intercepts. For each species we identified the most supported random effects structure and included either segment only, array only, year only, segment or array as well as year, or segment nested within array as random intercepts (Appendix S1). We used Generalized Linear Mixed Models (GLMM) with a log-normal distribution (Appendix S2) and interpreted significant changes in speeds as occurring if 95% CIs did not overlap zero.

We pooled observations from the BAU and TRT, assuming that movement rates were not inherently different between the two areas. If movements were influenced by differences between the BAU and TRT (e.g., linear feature density, density of animals), our interpretation of treatment effects could be confounded. We tested this assumption by comparing the movement rates on untreated lines for each species in each study area using two-sample Mann-Whitney Wilcox tests applied with continuity correction (Appendix S1). Caribou movement speed on untreated seismic lines was significantly different among the BAU or TRT areas, such that caribou moved faster on untreated seismic in the TRT area relative to the BAU area (Table S1.1). While caribou moved faster on untreated lines in the TRT than the BAU, movement speeds still declined on treated lines in both areas, suggesting that area-based effects did not confound the observed differences on treated and untreated lines.

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We further assessed if our inferences were dependent on season and winter snow depth using a sub-analysis for caribou, moose, and wolves (Appendix S1). Bears were denning during the snow season and could not be assessed. Movement differences between winter and summer periods can result from differences in travel speeds on snow-covered terrain (Droghini & Boutin 2018), wolf denning behaviour in spring/summer (Metz et al., 2011) and seasonal changes in diet (Metz et al., 2012). Including season and snow depth did not influence the directionality or significance of the effect of treatment, microtopography, or landcover on travel speeds for any species (Appendix S1). We therefore include models without season and snow depth in the main text for all four species.

To understand if movement speed decreased more strongly on more intensely treated lines, we modelled travel speed as a function of treatment intensity using observations on treated lines only. We again included microtopography and landcover as fixed effects, and segment, array or segment nested within array as random intercepts as described above. See Appendix S3 for additional details.

Models were built using the *Lme4* package (Bates et al., 2015) in R (R Core Team, 2020). We used the DHARMa package (Hartig, 2020) to evaluate the goodness-of-fits of each fitted model.

Results

Over the four-year study period, 23,763 and 33,601 segment-days (days when both cameras within a pair were operating) were recorded in the BAU and TRT area, respectively. In total, 713 movement events were detected for the four target species. Caribou showed the highest number of events

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(total *n*= 369; mean = 52.7 / year), while the number of observed events for the other 3 species (moose, wolves, and bears) were considerably lower (Table 1). There tended to be fewer movement events detected annually in the TRT than the BAU for caribou and black bears, whereas moose and wolves tended to be captured at similar frequencies in the two areas (Table 1). In years where cameras were operating in both the BAU and TRT (2014-2016), on average 14.6% of the annual caribou captures, 36.9% of the annual bear captures, 49.1% of the annual moose captures, and 50.7% of the annual wolf captures were in the TRT. Raw median speeds were lower on treated seismic lines than untreated seismic lines for all species, and except for moose, maximum observed speeds were higher on untreated seismic lines (Fig. 3; Appendix S1).

Caribou, bears, and wolves moved significantly slower on treated seismic lines than on untreated seismic lines (Table 2; Appendix S1). Caribou travelled on average 1.57 km/hr slower on treated seismic lines compared to untreated seismic lines, a 40% reduction in speed. Bears travelled 0.55 km/hr slower on treated seismic lines compared to untreated seismic lines, a 39% reduction in speed. Wolves travelled 1.38 km/hr slower on treated seismic lines compared to untreated seismic lines, a 23% reduction in speed. Moose did not travel significantly differently on treated and untreated seismic lines despite the apparent reduction in median speed (Table 2; Fig. 3). There was no significant effect of microtopography and landcover on caribou, moose, or bear travel speeds on seismic lines (Table 2). Wolves moved significantly slower on seismic lines in lowlands than in upland habitats, although the magnitude of the effect was small (less than 0.01 km/hr; Table 2). Treatment intensity did not significantly influence travel speed while on treated seismic lines for any species (Appendix S3).

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275 Discussion

Seismic lines have been implicated in caribou declines by facilitating predator movements and incursions into caribou habitat, thereby increasing predation (Dickie et al., 2017a; DeMars & Boutin, 2018). As such, restoration of seismic lines has been identified as a conservation priority (Dabros et al., 2018; Johnson et al., 2020). However, the effectiveness of restoration treatments to recover predator-prey dynamics by reducing predator and prey movement rates on linear features is unknown. We found evidence that restoration treatments reduced the movement rates of caribou, bears, and wolves, suggesting that habitat restoration treatments are reducing predator and prey vagility on these features. All else being equal, these results suggest that restoration treatments may help mitigate the effect of seismic lines on caribou populations through a reduction in encounters between caribou and their predators (Mumma et al., 2017; Spagenberg et al., 2019).

Previous studies have shown that wolves travel twice as fast on seismic lines than surrounding forest (Dickie et al., 2017a), which is hypothesized to increase wolf hunting efficiency (McKenzie et al., 2012; Latham et al., 2011). We therefore suggest that the 1.38 km/hr reduction in wolf speeds on treated seismic lines relative to untreated seismic lines observed here likely reduces the benefits ascribed to these features on movements of wolves. While a decrease of 1.38 km/hr is only a 23% reduction relative to untreated seismic lines, it is similar to the difference in wolf travel speed on vegetated seismic lines relative to unvegetated seismic lines (1.3 - 1.7 km/hr) observed by Dickie et al. (2017b). Reduced movement rates on treated features, particularly when considered in concert with reduced use of these features (Dickie et al., 2021), suggests that restoration treatments may

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contribute to reductions in predation on caribou populations in the short- to medium- term (Spagenberg et al., 2019; Serrouya et al., 2020), as well as the longer-term goal of accelerating return to forest cover (Filicetti et al., 2019). The degree in which kill rates of ungulates would decline as a result of a decrease in wolf travel speeds is unknown, and kill rates should be monitored as restoration treatments continue to expand over both space and time. There is widespread recognition of the importance of evaluating the effectiveness of management interventions, particularly using experimental manipulations designed to test hypotheses (Caughley, 1994; Walters & Holling, 1990). Yet, experimental manipulations are often difficult to conduct, particularly for wide-ranging species like large mammals, and are thus rare (Westgate et al., 2013). Our study represents a key first step in an experimental adaptive management framework to test caribou habitat restoration effectiveness.

Caribou also reduced travel speeds by an average of 40% along treated seismic lines compared to untreated seismic lines. While studies have often shown avoidance of seismic lines by caribou (Dyer et al., 2002; DeMars & Boutin 2018), other studies have documented use of linear features by caribou for high-speed movements (Dickie et al., 2020, Serrouya et al., 2017). We found that caribou movements along seismic line segments were the most common among these four species. Our finding of relatively high use of seismic lines by caribou could be a result of the fine spatial resolution of this study as compared to telemetry-based studies. While increased movement efficiency along seismic lines has been primarily studied in terms of predator movement, any use of seismic lines by caribou as a movement corridor has the potential to create an ecological trap for caribou (Serrouya et al., 2017) by increasing chance of encountering wolves which are known to select for seismic lines

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(Latham et al., 2011; Pigeon et al., 2020). By slowing both caribou and wolves we expect encounter
rates on treated lines to decrease further than if we solely focussed on the speed reduction for
wolves (Vander Vennen et al., 2016).

We did not detect a significant effect of restoration treatments on the travel speeds of moose. Moose are hypothesized to forage along seismic lines which have increased availability of preferred forage, including forbs and graminoids (Finnegan et al., 2018). While restoration treatments are designed to alleviate successional stagnation (Lee & Boutin 2006) by stimulating tree regeneration (Filicetti et al., 2019), restoration treatments do not necessarily remove early successional vegetation and may result in increased forb and grass growth in the short-term (Peltzer et al., 2000). Because this study did not measure forage availability, we can only speculate about its influence on movement speed by moose. Incorporating this component into future studies may aid in determining the influence of active restoration on moose movements.

We did find a small but statistically significant reduction in bear speeds along seismic lines that had undergone active treatment. Bears are known to select for seismic lines (Tigner et al., 2014; DeMars & Boutin, 2018) and may be using the lines to facilitate movement (Dickie et al., 2020) in addition to opportunistically or actively hunting for vulnerable caribou (Bastille-Rouseau et al., 2011). While use of lines in peatlands has been found to vary between individual black bears, selection for peatlands by certain bears might be contributing to caribou calf mortality in Alberta (Latham et al., 2011). For this reason, decreased movement efficiency should lead to decreased encounters between bears and caribou. Bears are also hypothesized to forage along seismic lines in the boreal forest as they

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often have abundant fast-growing graminoids (Dabros et al., 2018) and berry-producing plants preferred by black bears (Dawe et al., 2017). Similar to moose, bears may be altering their speeds as they encounter areas of rich vegetation growth. Active treatments, especially mounding, may create site conditions which environmentally favour shrub growth (Smith et al., 2012) and act as an attractant to bears. We do caution interpretation of the bear models as they had the smallest sample size of 14 movement events in treated areas, potentially causing the low precision in our models. The small sample size may be reflective of how bears use seismic lines. For example, Tigner et al. (2014) only recorded two movements between adjacent cameras on seismic lines spaced at 900 m and suggested movements by bears along seismic lines are short distance ones.

Aside from the overall reduction in speed observed across caribou, bears, and wolves, we also found that there was reduced variability in movement rates on treated seismic lines. This suggests that the faster travelling movements occurred less often, but these species still used these lines. Because linear features are hypothesized to provide forage subsidies to omnivores and herbivores (Finnegan et al., 2018), we suggest a direction for future research would be to examine camera trap images to classify behavior of these species to understand if they are foraging or traveling while using treated and untreated seismic lines.

Effects of other biophysical variables on travel speeds

We did not find significant movement speed responses to other biophysical variables, such as snow depth, microtopography or surrounding habitat on travel speeds. The exception was that wolves travelled slower on lowland seismic lines than upland seismic lines, as well as in deeper snow, as

expected (Dickie et al., 2017a). Moose and caribou tended to travel slower despite lack of statistical significance. The number of observed movements between cameras over the four-year period may have not had the statistical power to detect subtler movement responses. It is also possible that our measures of habitat condition were insufficient to measure fine-scale variation that would affect movement between cameras in a segment. Additionally, our index of snow depth combines information on both snow depth and density, which may not fully represent the energetic costs of locomotion through snow (Bunnell et al., 1990; Droghini & Boutin, 2017; Parker et al., 1984).

Utility of cameras to monitor movement rates

Camera traps have been used extensively for estimating space-use metrics such as occupancy and relative abundance (O'Connell et al., 2011), but their use for movement behaviours has been limited. A single-camera method was developed by Rowcliffe et al. (2016) tracing of movement paths within photo sequences of animals crossing the camera's detection zones, but this method can fail to record faster speeds as multiple photos of the same animal are required to estimate travel paths and animals may alter their movement when directly in front of the camera. The two-camera methodology employed in this study requires only one photo at each camera, and can capture a much longer portion of the linear movement. However, animals must travel on a predictable and repeatable path for the two-camera method to work. Even in this study where animals travelled along a highly predictable pathway, low sample sizes were a limitation especially in actively restored areas. Importantly, the two-camera approach assumes that an individual passing through camera pairs is the same individual. In our study area where animal densities are low, (travel events for the most frequently detected species, caribou, occurred on average only once per 155 segment-days)

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this assumption is plausible. However, to use this method for more abundant species, individual identification or partial identification would be necessary. Additionally, because rate of movement is estimated using pairs of cameras, the loss or malfunction of one of the cameras could limit realized samples obtainable with the methodology. These methods could be useful for studying riparian corridors, linkages, wildlife trails and known migration routes, similar to the methods used by Tape and Gustine (2014) to record the arrival time and herd movement speeds for caribou.

While GPS collars are more commonly used to evaluate movement behaviours as these units allow for remote collection of animal positions at pre-determined times over large geographic areas, they have limitations for calculating animal movement speed, especially short-term movements in response to small-scale habitat variability. Short-term rapid changes in movement might be underrepresented in many GPS datasets depending on fix rates, as minimum and maximum speeds are averaged between fixes (Prichard et al., 2014). We argue that the potential to miss short-term changes in speed is important when evaluating the effectiveness of seismic line restoration because both natural and treatment variability along seismic lines can be high. While travel speeds measured from GPS collars and camera traps may therefore not be directly comparable, travel speeds measured in our study are within biological plausibility based on speeds reported in other studies. For example, Finnegan et al. (2018) reported a maximum travel speed for wolves of approximately 6.5 km/hr, and 3.5 km/hr for grizzly bears using 1-hour GPS locations, whereas Dickie et al., (2019) reported a maximum speed of 27.5 km/hr for wolves, 19.9 km/hr for black bears, 8.5 km/hr for caribou and 9.6 km/hr for moose using 15-minute locations. Although wildlife collar studies are well suited to study the large-scale patterns of space-use of individual animals, wildlife cameras have the

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advantage of being able to target restored features directly and information captured can be directlyrelated to the conditions at the features of interest.

Limitations and Next Steps

Our results document short-term responses following implementation of restoration treatments. Active treatments change over time as mounds shrink, woody debris decomposes, and trees grow. While we suggest that active restoration techniques as applied in this operational trial are effective at reducing movement of wolves and caribou, we acknowledge that this effect may change with time. Trees will grow over time, creating obstacles, whereas mounds constructed of unconsolidated peat and woody debris will diminish. These areas are also the preferred habitat of caribou (James & Stuart-Smith, 2000). However, the diminishment of some aspects of the applied restoration technique will be co-occurring with vegetation regeneration on the lines, with treated lines showing a trend towards higher tree regeneration in many cases (Filicetti et al., 2019). We recommend that future studies should monitor movement rates as restoration treatments age over decades and proceed through succession to monitor this process. Perhaps more important is testing both the spatial extent and temporal period in which changes in use and movement on treated linear features translates into changes in kill rates.

It is also unknown what intensity of restoration treatments on seismic lines is required to result in the desired behavioural and demographic responses. Given that there are millions of km of seismic lines on the Alberta landscape (Komers & Stanjevic, 2013), and the estimated cost for restoration treatments is approximately \$12,500/km (Filicetti et al., 2018), understanding if current restoration

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practices are effective is essential. In Dickie et al. (2017b), wolves increased their movement speed by a factor of two on seismic lines as compared to forests. This suggests that the levels of treatment used in this study is not reducing wolf travel speeds to the ranges of speeds occurring in the adjacent forests. Determining at what intensity treatments replicate movement in the adjacent forest is important in determining the feasibility of large-scale linear restoration. While we tested the effect of treatment intensity on movement speed, low sample sizes across intensity levels hampered our statistical power. Larger restoration areas and increased monitoring is needed to fully understand the influence of treatment intensity.

Slowing wolves, bears, caribou, and moose is expected to result in decreased predator-prey encounters (Johnson et al., 2019; Serrouya et al., 2020; Spangenberg et al., 2019). However, the long-term demographic effects of such fine-scale movement rate reductions on caribou survival remains unknown and is outside the spatio-temporal scope of this study. Restoration treatments were designed to simultaneously facilitate vegetation regrowth, thereby addressing the ultimate mechanism in which boreal habitat is affected by anthropogenic habitat alteration, as well as reduce movement in the near-term, addressing increased hunting efficiency and encounter rates between predators and prey. The effects of habitat restoration on caribou demographics – the ultimate goal of habitat restoration - will require long time periods (i.e. decades) to become evident. **Acknowledgments:** We would like to thank Bruce Nielsen and Javad Iqbal, who prescribed silviculture treatments and collected and interpreted intensity data and Terri Perron, Spencer Thome, Jordan Hayes for assistance in the field (Woodlands North Inc.). Silvicultural treatments were implemented by Global Restoration Corp. Devon Energy and the Regional Industry Caribou

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450 Collaboration also provided funding. Thank you to three anonymous reviewers and Dr. James
451 Schaefer, who's comments on previous versions of this work has improved it substantially.

Supporting Information

Supporting information provides additional details on the statistical analyses of movement speeds (Appendix S1), exploratory analysis of movement speed distributions (Appendix S2), and Evaluation of effects of treatment intensity on movement speeds (Appendix S3). The additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these

materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Figure 1: Study area map depicting the location of the restoration treatment area (TRT) and reference "business-as-usual" area (BAU) in which the effects of restoration treatments on

movements of caribou, moose, bear, and wolves using seismic lines were studied. Cameras trap
locations and examples of treated and untreated linear features are shown.

Figure 2: Example camera array used to quantify travel speed of caribou, moose, wolves and bears on treated and untreated seismic lines. In the schematic, green represents the seismic line, the black dashed line represents and animal path (direction signified using arrows), and grey shaded triangle represents the field of view of each camera. Cameras are placed along seismic lines in an array of 3 cameras. Two cameras are placed 500 m apart with one camera in the middle, creating two "segments" in each array. As animals move through the array and trigger both cameras in an array, speed can be calculated as the distance (250 m) divided by the difference in timestamps from the photos (t_2 - t_1).

Figure 3: Travel speeds (km/hr) of caribou, moose, wolves and bears on untreated (N; light gray points) and treated (Y; dark gray points) seismic line segments. Travel speeds were estimated using camera traps placed 250 m along seismic lines. Overlaid boxplots outline the 25th and 75th quartiles (rectangles), black vertical lines indicate 1.5 times the interquartile distance, and the bold horizontal line indicates the median movement speed for each distribution.

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Treatment type

Figure 3: Travel speeds (km/hr) of caribou, moose, wolves and bears on untreated (light gray points) and treated (dark gray points) seismic line segments. Overlaid boxplots outline the 25th and 75th quartiles (rectangles), black vertical lines indicate 1.5 times the interquartile distance, and the bold horizontal line indicates the median movement speed for each distribution.

Table 1. Numbers of movement events of caribou, moose, wolves, and bears captured between paired cameras on seismic lines in the business-as-usual area (BAU), Treatment area (TRT), per year monitored. Also presented is the mean number of events per year for each area, and combined.

	Annual										
Species	2013		2014		2015		2016		Mean (Events/Year)		
	BAU	TRT	BAU	TRT	BAU	TRT	BAU	TRT	BAU	TRT	Combined
Caribou	-	30	81	16	137	16	74	15	97.3	19.3	52.7
Moose	-	33	24	20	17	21	8	7	16.3	20.3	18.6
Wolf	-	21	12	31	31	15	10	9	17.7	19.0	18.4
Bear	-	15	30	7	17	3	3	10	16.7	8.8	12.1

Table 2. The effects of treatment, microtopography, and landcover on travel speeds (km/hr) of caribou, moose, wolves and bears on seismic lines. Model estimates and 95 % confidence intervals (CI) are provided.

 Species	Covariate ^a	Estimate ^b	Lower 95% Cl	Upper 95% Cl
 Caribou	Intercept ^d	1.370	1.168	0.1.57
(<i>n</i> = 369) ^c	Treated	-0.508	-0.752	-0.266
	Microtopography	-0.048	-0.296	0.200
	Landcover	-0.001	-0.003	< 0.001
Moose	Intercept	0.796	0.481	1.108
(<i>n</i> = 130)	Treated	-0.111	-0.400	0.170
	Microtopography	-0.004	-0.312	0.301
	Landcover	< 0.001	-0.001	0.002
 Wolf	Intercept	1.792	1.644	1.940
(<i>n</i> = 129)	Treated	-0.290	-0.491	-0.090
	Microtopography	0.023	-0.206	0.253
	Landcover	-0.001	-0.002	< -0.001

Bear	Intercept	0.342	0.046	0.638
(<i>n</i> = 85)	Treated	-0.497	-0.913	-0.073
	Microtopography	0.164	-0.309	0.635
	Landcover	0.002	< -0.001	0.005

^aThe fitted global model is ln(Travel speed) ~ Treated + Microtopography + Landcover + RE using the most supported RE (random effects structure) for each species (see Appendix S1). Reference conditions were seismic with no treatments (untreated), low microtopography = low, and landcover = upland.

^bEstimates and CIs are untransformed (i.e. units are presented in the log_e scale).

^cSample sizes are total numbers of captures over the period of the study. Data were collected in two areas and the two areas were pooled.

^dBold signifies significance, defined as 95% confidence intervals not overlapping zero.