

Evaluating functional recovery of habitat for threatened woodland caribou

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Abstract. Habitat restoration is a core element for the recovery of many declining species. In western Canada, habitat restoration for the recovery of woodland caribou is focused on linear features (LFs) created by oil and gas exploration. At present, the only established criterion for LF restoration is when vegetation structure on LFs is similar to surrounding vegetation. Human-mediated habitat alteration impacts caribou population dynamics by increasing caribou predation rates in two ways: increasing alternate prey populations leading to higher predator numbers and increasing predator hunting efficiency. Linear features increase the movement rates—and may thus increase hunting efficiency—of wolves, a primary predator of caribou and a main hypothesized mechanism for population declines. One approach to determine LF recovery is to identify potential thresholds in the characteristics of regenerating LFs where efficiencies in wolf movement rates are no longer evident. We examined how vegetation affects wolf selection of, and movement on, LFs in northeastern Alberta using five-minute Global Positioning System locations from 20 wolves. Wolves selected LFs with shorter vegetation and traveled faster on LFs with shorter, sparser vegetation and increased vegetation variability. Travel speeds were reduced by 1.5–1.7 km/h when vegetation exceeded heights of 0.50 m, but at least 30% of a LF required vegetation exceeding 4.1 m to slow movement rates to those traveled while in forest. Policy implications: Most of the movement efficiency afforded to wolves by LFs is mediated when vegetation exceeds 0.50 m, and therefore, active restoration could be focused in areas that have not met this value. Rather than treating this value as a clear threshold equating to functional recovery, multiple metrics across trophic levels must also be evaluated to assess population recovery for caribou.

Key words: *Canis lupus*; habitat management; linear features; movement; *Rangifer tarandus*; recovery; restoration; selection.

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INTRODUCTION

Stabilizing or recovering wildlife populations that are undergoing sustained declines requires identifying the probable mechanisms of decline and applying appropriate conservation measures (Caughley 1994). For the majority of threatened and endangered species, habitat loss and alteration are often cited as the primary causes of population declines (Sala et al. 2000, Jantz et al.

2015). Consequently, habitat restoration is a key management tool commonly suggested to stabilize or recover declining populations (Miller and Hobbs 2007). Yet, habitat loss and alteration are pattern-oriented descriptors that frequently mask the underlying ecological processes driving population decline (Fischer and Lindenmayer 2007). Such processes include lowered reproductive performance due to lowered food availability (Zanette et al. 2000), increased predation from

altered species interactions (DeCesare et al. 2010), and lowered survival rates due to changes in microclimate (Stangler et al. 2015). Understanding the relevant ecological process has direct ramifications for habitat restoration. To be most effective, habitat restoration should target the ecological processes affecting the focal species. Moreover, defining when habitat is “restored” should depend on determining when historic ecological processes are restored (Miller and Hobbs 2007, Wortley et al. 2013). The recovery of such ecological processes may occur at rates that differ from the recovery of historic vegetation structure, suggesting that the criteria for defining restored habitat will likely vary by species and geographical context.

In Canada, habitat restoration has been identified as a key management tool for stabilizing and recovering populations of *Rangifer tarandus* (boreal caribou), an ecotype of woodland caribou currently listed as *Threatened* (Environment Canada 2012). This emphasis on restoration stems from substantial evidence linking population declines to human-induced landscape alteration within and adjacent to caribou range (McLoughlin et al. 2003, Wittmer et al. 2007, Courtois et al. 2008, Sorensen et al. 2008). Disturbances such as cutblocks increase early-seral vegetation, leading to higher numbers of ungulate species (e.g., moose and deer) and consequently more predators (Seip 1992, Serrouya et al. 2011). In addition, linear features (LFs) such as seismic lines, pipelines, and roads are a prominent form of landscape alteration in many boreal caribou ranges, particularly those in western Canada. These features are hypothesized to facilitate predator movement into caribou range (James and Stuart-Smith 2000, Latham et al. 2011a; C. DeMars and S. Boutin, *unpublished manuscript*) and increasing predator hunting efficiency (McKenzie et al. 2012). Wolves are believed to be the primary predator causing caribou population declines in western ranges (McLoughlin et al. 2005, Hervieux et al. 2014). Previous research has also demonstrated that wolves highly select LFs when traveling (James and Stuart-Smith 2000, Latham et al. 2011a, Dickie et al. 2017) and that increased wolf movement rates are linked to increased kill rates (Vander Vennen et al. 2016, but see DeCesare 2012). Because of these mechanistic links and the ubiquity of LFs within

caribou range, significant effort has been placed on restoring LFs (Pyper et al. 2014). In addition, many caribou ranges already exceed alteration thresholds associated with population stability (Environment Canada 2012), making habitat protection alone ineffective in the short term (Schneider et al. 2010).

Restoring caribou habitat, however, is not a trivial endeavor given the wide spatial extent of caribou ranges and the significant costs associated with deploying restoration efforts (Schneider et al. 2010). Because of these difficulties, prioritizing areas for restoration will be necessary and will require identifying habitat restoration criteria, either by natural regeneration or by active restoration treatments. Moreover, active restoration is necessary for many LFs due to their slow rates of regeneration (Lee and Boutin 2006, van Rensen et al. 2015). Determining when LFs are restored in the context of caribou conservation remains uncertain yet has important policy implications. The federal recovery strategy for boreal caribou mandates that active management strategies be deployed to reduce the footprint of human disturbances, with a 500-m buffer, within ranges to below 35% (Environment Canada 2012). Currently, the recovery strategy considers any LF visible by remote sensing technology to be a disturbed area (Environment Canada 2012). This criterion, however, is based solely on similarities in vegetation structure on lines compared to surrounding forest and ignores the underlying mechanisms by which LFs affect caribou population dynamics.

Here, we used movement analyses applied to data from Global Positioning System (GPS)-collared wolves to develop alternative criteria for determining when LFs are functionally restored in the context of caribou conservation. Our approach explicitly addressed the underlying mechanism linking LFs to caribou population declines; that is, LFs increase caribou–wolf encounter rates—and hence, caribou predation rates—by increasing wolf movement rates and therefore potentially minimize energy expenditure, a hypothesis consistent with optimal foraging theory (MacArthur and Pianka 1966). We tested for changes in wolf movement behavior as a function of variation in LF structure to evaluate gradients in the restoration status of LFs, placing an emphasis on the state of vegetation recovery.

Increases in movement efficiency are presumably due to differences in vegetation structure between LFs and the surrounding forest. Given this hypothesis, a logical prediction is that wolf selection of LFs should decrease as vegetation structure on LFs becomes similar to the surrounding forest. A similar—and associated—prediction is that wolf speed on LFs will be lower with increasing vegetation height and complexity. We evaluated these two predictions and specifically tested for sharp declines in wolf selection of LFs and movement rates on LFs as a result of small changes in vegetation height and complexity, indicating a natural break in which additional vegetation has diminishing returns in decreased wolf speed. Although our sampling primarily encompasses naturally regenerating vegetation on LFs, how wolves respond to variation in vegetation structure should provide valuable insight for determining when LFs are functionally restored.

MATERIALS AND METHODS

Study site

Our study took place in the boreal forest of northeastern Alberta and northwestern Saskatchewan, near the town of Conklin (55°35' N, 111°00' W). The 18,000-km² area contains homogenous topography with a mosaic of fens, bogs, marshes, deciduous forest, and coniferous forest (Latham et al. 2011a). The mammalian community includes *Odocoileus virginianus* (white-tailed deer), woodland caribou, *Alces alces* (moose), wolves, *Ursus americanus* (black bears), *Lynx canadensis* (Canada lynx), *Vulpes vulpes* (red fox), *Canis latrans* (coyote), *Castor canadensis* (beaver), *Lepus americanus* (snowshoe hare), and other small mammals (Latham et al. 2011c).

Linear features are abundant within northern Alberta. For example, the two caribou ranges that overlap our study area, Cold Lake and East Side of the Athabasca River caribou ranges, contain ~23,952 and 44,740 km of LFs, respectively (Alberta Biodiversity Monitoring Institute, unpublished data). In the boreal forest, the first step to locating oil and gas reserves involves the creation of seismic lines, which allow access for seismic detection equipment. Historically, seismic line clearings were 8 m wide but were reduced to 5 m wide since the early 1980s. Linear features of this

type are known as conventional seismic lines and are typically between 5 and 8 m wide. Over time, efforts have been made to make seismic lines more narrow and sinuous, and as such, low-impact seismic lines (LIS) as little as 2 m wide are used to obtain more accurate, three-dimensional images of hydrocarbon deposits. Seismic programs deploy LIS in a closely spaced grid pattern, where each line is sinuous but runs parallel or perpendicular to closely spaced lines. Pipelines, roads, and transmission lines are then used to extract oil and gas, and gain access to, and provide power for, processing facilities, and these LFs can range in width from 20 to 40 m. In addition, truck trails and All Terrain Vehicle (ATV) trails are found throughout the study area for recreational use as well as accessing wellpads and facilities.

Wolf capture and collaring

Twenty Iridium GPS collars (Lotek Wireless, Aurora, Ontario, Canada) were deployed on wolves from six packs in 2013 and 2014 in accordance with approved animal care through the University of Alberta (AUP00000480, 2013) and Government of Alberta (Permit 53657 and 54559). Collars provided five-minute locations from 1 January to 30 March in 2014 (defined as winter), as well as on a cycle of 5 min for 2 d and then hourly for 4 d from 15 April to 15 July in 2013 and 2014 (defined as summer).

Environmental attributes

Linear features were visually classified as conventional seismic lines, LIS, trails, roads, pipelines, transmission lines, and railway using 2012 SPOT imagery (2-m resolution) and Valtus Views (0.5-m resolution) at a 1:15,000 scale. Low-impact seismic lines were <5 m wide and sinuous, whereas conventional seismic lines were 5–10 m wide and straight. Trails had no visible road surface and were generally 10 m wide, but varied between 5 and 15 m wide. Seismic lines and trails were truncated at the edge of any clearing with a width ≥20 m. Features were identified as pipelines based on supplementary data from 2012 provided by the Government of Alberta, and ranged from 10 to 100 m wide. Linear features were classified as roads when road surfaces were visible and varied from 10 to 60 m wide, including winter-only roads, all-weather gravel roads, and paved highways. Only roads,

including driveways, exceeding 50 m in length were classified. Features were classified as rail-ways if tracks were visible. Transmission lines were classified using supplementary data from the Government of Alberta. Transmission lines were generally wide, but ranged from 5 to 65 m wide. Transmission lines running along road-sides or to small facilities were not captured. When multiple features followed the same corri-dor, they were classified individually if visibly distinct at a scale between 1:5000 and 1:10,000; otherwise, they were assigned to the widest LF class. We buffered each LF according to its aver-age width by type on the landscape (Dickie et al. 2017) to create polygon representations of LFs.

Vegetation information on LFs was obtained and processed using light detection and ranging (LiDAR). In August 2012, LiDAR was flown using fixed-wing aircrafts at an altitude of 1500 m to obtain a point density of 2.5–4 pulses/ m² and a vertical accuracy of 9.25 cm (see

Charlebois et al. 2015). Light detection and rang-ing in conjunction with color infrared imagery was used to semi-automatically delineate human-created LFs (Charlebois et al. 2015) as well as create terrain (minimum elevation) and top vegetation height (maximum elevation) ras-ter surfaces at 1-m horizontal resolution. Light detection and ranging performed well as an indi-cator of ground vegetation height and cover (Charlebois et al. 2015). Vegetation data on LFs were available for only a sub-set of wolves in a 4315-km² area (Table 1; Appendix S1).

Both caribou ecology and vegetation growth are affected by the moisture content of the habitat type. Wetlands are preferred by boreal caribou (Rettie and Messier 2000), but tree growth and regeneration is more rapid on upland, mesic sites (van Rensen et al. 2015). Therefore, we also evalu-ated whether wolf selection of, and movement on, LFs differed between uplands and wetlands. We obtained land-cover information from the Alberta

Table 1. Summary of model structure used for each selection and movement analysis and the sample size (number of individual wolves and number of Global Positioning System [GPS] locations or steps) included in models.

Question	Dependent	Independent	Summer		Winter	
			No. of wolves	No. of locations	No. of wolves	No. of locations
When on LFs, do wolves select areas with shorter vegetation?	Use vs. random	Land-cover + LF class + height (m)	9	4039	4	4398
At what vegetation height is wolf selection of LFs similar to that of non-LF forest?	Use vs. random	Height category on LFs, with non-LF forest as the reference category	8	71,936	4	53,131
Does land-cover influence wolf selection of LFs?	Use vs. random	on/off LFs + upland/wetland + on/off LFs: upland/wetland	20	138,961	11	78,521
How much vegetation is required to decrease wolf travel speed?	Speed (km/h)	Height category	12	1434	4	1264
	Speed (km/h)	Height category stratified by upland/wetland	12	1176	4	1039
	Speed (km/h)	roughness category	12	1434	4	1264
	Speed (km/h)	Proportion LCP* >0.50 m category	12	1434	4	1264
	Speed (km/h)	Proportion LCP* >height equal point category	12	1434	4	1264
How much vegetation is required for wolves to travel the same average speed as non-LF forest?	Speed (km/h)	Vegetation height (m)	12	1434	4	1264
	Speed (km/h)	Vegetation roughness	12	1434	4	1264
	Speed (km/h)	Proportion LCP* >0.50 m	12	1434	4	1264
	Speed (km/h)	Proportion LCP* >height equal point	12	1434	4	1264
Does land-cover influence wolf speed on LFs?	Speed (km/h)	On/off LFs + upland/wetland + on/off LFs: upland/wetland	20	38,197	11	16,537

Notes: We modeled selection for each individual separately using conditional logistic regression to constrain availability and then averaged across individuals for population-level inferences, whereas we analyzed movement using mixed-effects general-ized linear models with individuals and pack as nested random effects. LCP* is the least cost path between successive GPS locations used to evaluate vegetation indices. LF, linear features.

Vegetation Inventory (created 1987–2010, updated 2011) and Saskatchewan Forest Vegetation Inventory (1971–1982). Land-cover was classified as coniferous, deciduous, mixedwood forest, wetland, or other using ecosite characteristics (Beckingham and Archibald 1996).

Wolf selection of linear features

To determine whether wolf selection of LFs was influenced by vegetation height, we compared the environmental attributes associated with the five-minute GPS locations of wolves to those associated with random locations. We defined selection as use greater than the availability on the landscape, and avoidance as use less than availability. We constrained the characterization of availability for each used location by comparing each used location to 10 available locations within a radius of the 90th percentile maximum step length: 0.274 km (i.e., the 90th percentile distance between two consecutive locations; Boyce et al. 2003, Boyce 2006). Each GPS and random location was classified as on a LF if the location was contained within a LF's buffer, or off a LF (hereafter termed "non-LF forest"). If on a LF, the location was also assigned a LF type; if the location fell within overlapping buffers, the location was classified as the feature class with the largest buffer width. We extracted land-cover for each location, categorized as coniferous, deciduous, mixedwood forest, wetland, or other. We extracted the vegetation height value for each location based on the 1-m LiDAR pixel in which the location fell. We excluded data with unknown land-cover. Buffered LFs from imagery did not perfectly overlap with LiDAR-derived LF polygons; therefore, where vegetation height was of interest, we excluded locations that did not fall within both data sets.

When on LFs, do wolves select areas with shorter vegetation?—To determine whether wolves selected areas with shorter vegetation when on LFs, we used a data sub-set to isolate used and available locations on linear features and modeled wolf selection as a function of vegetation height, linear feature class, and land-cover type. Note that because LFs have a small footprint, and the number of LFs varied within each used location's bounding area of availability, the number of available points per used location in this sub-set was <10 and varied by location. We included

environmental attributes as model covariates because the effect of vegetation height on wolf selection of LFs could differ among LF classes and land-cover types.

At what vegetation height is wolf selection of LFs similar to that of non-LF forest?—Further, we modeled wolf selection as a function of categorical vegetation height (<0.5 m, 0.5–1.0 m, 1.0–5.0 m in 1-m increments, >5.0 m) on LFs with non-LF forest as a reference category to evaluate at what vegetation height selection for LFs became similar to that for non-LF forest.

Does land-cover influence wolf selection of LFs?—We evaluated wolf selection as a function of whether the location was on or off LFs, in uplands (coniferous, deciduous, mixedwood forest, or other) or wetlands (bogs, fens, and marshes), as well as the interaction to determine whether land-cover influenced wolf selection of LFs. While the interaction among each LF class and land-cover type was initially of interest, models with multiple LF classes failed to converge.

We modeled each wolf separately using conditional logistic regression ("survival" package in R); see Table 1 for a description of each model (Therneau 2014). However, sub-setting to only used and available locations on lines to evaluate how wolves select vegetation heights when on LFs only resulted in a low sample of available locations per used location for conditional logistic regression. Therefore, for this one case, we present results from a general linear model with a binomial logit link (i.e., regular logistic regression), and note that these results did not change in direction (negative/neutral/positive) or significance (confidence intervals overlapping/not overlapping 0) for vegetation height from conditional logistic regression (analysis not shown).

To obtain population-level inferences, we averaged coefficients across individuals and weighted by the inverse square root of the variance to give individuals with more precise estimates more weight (Fieberg et al. 2010). We used bootstrap analyses with 2000 permutations to calculate 95% confidence intervals for population-level coefficients within each model set (Canty and Ripley 2015). We analyzed summer and winter seasons separately and removed individuals with insufficient sample sizes for convergence from analyses. We modeled individuals separately and average for population-level

inferences because constraining availability using conditional logistic regression was important to account for the patchy availability of some LF classes. Mixed-effects conditional logistical regression could theoretically compare matched used and available locations while accounting for non-independence among individuals in the same pack; however, these approaches are still in the infancy of development for most statistical software and are seldom used in ecological literature (but see Duchesne et al. 2010).

Wolf movement on linear features

We evaluated how wolf traveling speed was influenced by vegetation height, cover, and roughness (see below) to determine whether wolf movement on LFs is influenced by vegetation. We quantified wolf movement behavior by estimating traveling speed (km/h) between successive five-minute GPS locations. The natural logarithm of traveling speed revealed a bimodal distribution with a breakpoint of 0.21 km/h, calculated using the segmented package in R (Muggeo 2014). We assumed that step lengths <0.21 km/h corresponded to resting and feeding, while step lengths \geq 0.21 km/h corresponded to traveling movements, and because we were interested in the latter, we included only steps with traveling speeds greater than, or equal to, 0.21 km/h (Dickie et al. 2017). We classified steps as on LFs if the entire straight line-interpolated path between GPS locations fell completely within any LF's buffer. We calculated the proportion of each step that fell within uplands or wetlands (see description in *Does land-cover influence wolf selection of LFs?*).

Vegetation height and cover are typically used to measure vegetation structure (Tigner et al. 2014); however, feature edges become more indistinct as lines regenerate, which is problematic for measuring vegetation cover. Alternatively, roughness can be used as an index to evaluate vegetation structure remotely. Therefore, we characterized vegetation on LFs using least cost paths (LCPs) between successive five-minute GPS locations, which acted to delineate the lowest and sparsest route on LFs along wolf steps. Least cost paths were generated using a LiDAR-derived normalized canopy height model as a cost surface, thereby delineating a "path of least resistance." Average vegetation height along LCPs was significantly correlated with average vegetation height along

straight line-interpolated paths (Appendix S2), but we chose to characterize the minimum vegetation using LCPs. We extracted the average vegetation height along each LCP, the roughness of each LCP (the ratio of surface height over the top of vegetation to horizontal length between GPS locations), and cover (here defined as either the proportion of the path above 0.50 m or the proportion of the path above the calculated height equal point, see below). Mean vegetation height, roughness, and cover were highly correlated ($r = 0.99$ for height and roughness; $r = 0.90$ for height and cover; $r = 0.91$ for roughness and cover; $P < 0.001$ for all pairs). As such, each variable was modeled separately to provide different but equal lines of evidence that can be used as indices of vegetation on LFs.

How much vegetation is required to decrease wolf travel speed?—We evaluated the relationship between wolf traveling speed and mean vegetation height, roughness, and cover using incremental bins to determine whether small changes in average vegetation indices significantly changed average wolf traveling speed. We used the same bin categorization for average height as described above. We categorized roughness as <1.5, 1.5–2.0, 2.0–2.5, and >2.5. For both cover >0.50 m and cover above the height equal point (see *How much vegetation is required for wolves to travel the same average speed as non-LF forest?*), we used bins of <0.25, 0.25–0.5, 0.5–0.75, and >0.75. In addition, we stratified steps into upland or wetland to visually assess differences between land-cover types. Steps were classified as upland if at least 75% of the step intersected uplands, and the same for wetlands. While it would be ideal to sample only steps that were completely within each land-cover category, there were few steps in each category once further stratified by vegetation height.

How much vegetation is required for wolves to travel the same average speed as non-LF forest?—Next, we modeled traveling speed as a function of the mean vegetation height and roughness for each step, and then used the resulting model outputs to calculate the average vegetation height or roughness in which wolf speed was equal to that of steps in non-LF forest (Dickie et al. 2017), hereby termed "equal points." We modeled the relationship between wolf traveling speed and vegetation cover above 0.50 m as well as above the calculated height equal point and used the

resulting model parameters to calculate the cover equal points.

Does land-cover influence wolf speed on LFs?—We evaluated the effect of land-cover (e.g., uplands or wetlands) on wolf speed on LFs by evaluating the interaction between LFs and if the step was within uplands or wetlands. We modeled wolf traveling speed as a function of whether the step was on or off a LF, if the step was through uplands or wetlands and their interaction. We restricted analyses to steps that were completely in either uplands or wetlands. While the interaction among each LF class and land-cover type was of interest, models with multiple LF classes failed to converge.

For each movement model, we estimated mixed-effects generalized linear models with individuals and pack as nested random effects (see Table 1 for a description of each model). We approximated *P*-values using the package lmerTest with a Satterthwaite approximation in R (Kuznetsova et al. 2014). When we analyzed the effect of linear features on traveling speed, conditional models were not appropriate. Therefore, we obtained population-level inferences by using mixed-effects models with individuals nested within their packs (Hebblewhite and Merrill 2008). To normalize distributions, we used the natural logarithm to transform traveling speed, vegetation height, and roughness. We conducted pairwise comparisons for each categorical vegetation index using Tukey tests with the package multcomp in R (Hothorn et al. 2016). Summer and winter seasons were analyzed separately. Analyses evaluating the influence of vegetation indices on movement were restricted to five-minute traveling steps that were completely within the buffer of LFs where LiDAR and hand-digitized LF boundaries overlapped. We matched a random sample of traveling steps in non-LF forest by individual and season to increase sample size. The impact of vegetation height on wolf traveling speed did not differ between LFs and non-LF forest; however, the effect of roughness and cover differed between LFs and non-LF forest depending on season (Appendix S2).

RESULTS

We obtained 138,961 GPS locations in summer and 78,251 in winter, 12% and 16% of which

were on LFs. Of those, 8190 locations from nine wolves in three packs (summer) and 9155 locations from four wolves in three packs (winter) were on LFs with data for both vegetation height and LF class. Vegetation height on LFs used by wolves ranged from 0 to 28 m (higher values often corresponding to the edges of LFs where surrounding tree crowns extended onto the LFs; these were rare but should be interpreted with caution). We identified 8197 traveling steps completely within uplands ($n = 27,109$) or wetlands ($n = 11,088$), 5% of which were on LFs. Of the five-minute traveling steps on LFs, 717 (summer) and 632 (winter) were on lines with vegetation information.

Wolf selection of linear features

When on LFs, do wolves select areas with shorter vegetation?—When on LFs, two of nine individuals in summer ($\beta = -0.059$, standard error [SE] = 0.015 and $\beta = -0.056$, SE = 0.018) and two of four individuals in winter ($\beta = -0.022$, SE = 0.008 and $\beta = -0.054$, SE = 0.021) significantly selected areas with shorter vegetation. The remaining wolves did not significantly respond to vegetation height while on LFs. While six of the wolves in summer selected shorter vegetation, their confidence intervals overlapped zero (Appendix S3). On average, with every one-minute increase to vegetation height, the odds of wolves selecting that area decreased by 5% on average in summer (Table 2). However, on average, wolves did not significantly select areas on LFs with shorter vegetation in winter.

At what vegetation height is wolf selection of LFs similar to that of non-LF forest?—Compared to non-LF forest, wolves on average selected LFs regardless of vegetation height until vegetation exceeded 5 m in summer, but only selected LFs with vegetation height <0.5 m in winter (Table 3). However, selection varied among individual wolves (Appendix S3), with some individuals avoiding LFs once vegetation exceeded a height of 3 m in summer.

Wolves showed selection for LFs in both wetlands and uplands, though the response was stronger in uplands (Table 4). The odds of wolves selecting LFs in wetlands were 1.46 \times and 1.15 \times lower than those in uplands in summer and winter, respectively.

Table 2. Average wolf selection coefficients of land-cover, linear feature (LF) class, and vegetation height (m) for summer and winter derived from logistic regression.

Variables	Summer estimate	Summer <i>n</i>	Winter estimate	Winter <i>n</i>
Intercept	0.866 (0.668 to 1.051)	8	0.516 (0.229 to 0.891)	4
Land-cover				
Wetland	-0.190 (-0.370 to 0.071)	8	0.23 (-0.028 to 0.384)	4
Other	-0.504 (-0.659 to -0.215)	8	-0.156 (-0.589 to 0.093)	4
Deciduous	0.180 (-0.302 to 0.557)	8	0.408 (0.203 to 0.575)	4
Mixedwood	0.479 (-0.124 to 0.873)	8	0.177 (0.012 to 0.294)	4
Vegetation height	-0.044 (-0.055 to -0.028)	8	-0.007 (-0.026 to 0.007)	4
LF class				
Low-impact seismic	-1.091 (-1.279 to -0.960)	5	-0.689 (-0.898 to -0.509)	4
Trail	-0.777 (-1.444 to -0.023)	8	-0.68 (-1.243 to -0.129)	4
Pipeline	-0.592 (-0.836 to -0.314)	8	-0.609 (-0.913 to -0.29)	4
Railway	-0.603 (-0.823 to 0.033)	3	-	0
Road	-0.754 (-0.813 to -0.677)	8	-0.377 (-0.68 to -0.156)	4
Transmission line	-0.940 (-1.588 to -0.650)	3	-	0

Notes: Model estimates were weighted according to the inverse standard error and averaged across individual wolves. Sample size (*n*) and 95% confidence intervals derived from bootstrapping are shown. Coniferous forest and conventional seismic lines were set as the land-cover and LF reference categories, respectively. Significant estimates are bolded.

Wolf movement on linear features

How much vegetation is required to decrease wolf travel speed?—Compared to where there was virtually no vegetation (i.e., <0.50 m), wolves traveled 1.3–1.7 km/h slower when vegetation was at least 0.50 m high. Similar results were evident for cover and roughness, when wolves traveled slower on all categories compared to the respective lowest vegetation categories in summer and winter (Figs. 1, 2; Appendix S4). For example, wolves traveled 1.5 km/h (summer) to

1.7 km/h (winter) slower when average vegetation height was 0.50–1.0 m compared to <0.50 m (Appendix S4). Wolves traveled slower in wetlands than in uplands in summer regardless of vegetation on LFs, reaching the average traveling speed in non-LF forest at an earlier state of vegetation recovery (Fig. 1). Wolf traveling speed continued to decrease with each increasing cover category (Fig. 2; Appendix S4), but no height, cover, or roughness categories greater than the minimum categories were significantly different from each other ($P > 0.05$; Appendix S4).

Table 3. Mean wolf selection coefficients and bootstrapped 95% confidence intervals of vegetation height on linear features (LFs) compared to non-LF forest in summer ($n = 8$ individuals) and winter ($n = 4$ individuals).

Height (m)	Summer mean	Winter mean
<0.5	0.615 (0.419 to 0.985)	0.459 (0.291 to 0.695)
0.5–1.0	0.357 (0.167 to 0.558)	-0.087 (-0.317 to 0.043)
1.0–1.5	0.463 (0.341 to 0.729)	-0.002 (-0.115 to 0.057)
1.5–2.0	0.454 (0.287 to 0.552)	0.129 (-0.028 to 0.190)
2.0–3.0	0.669 (0.254 to 0.802)	0.068 (-0.001 to 0.116)
3.0–4.0	0.574 (0.358 to 0.795)	0.130 (-0.006 to 0.260)
4.0–5.0	0.465 (0.146 to 0.596)	0.333 (0.110 to 0.401)
>5.0	0.299 (-0.004 to 0.477)	0.304 (0.033 to 0.443)

Notes: Individuals were modeled separately using conditional logistic regression and then averaged for each category for population-level inferences. Individual coefficients were weighted by the inverse of the square root of the variance. Significant estimates are bolded.

How much vegetation is required for wolves to travel the same average speed as non-LF forest?—Wolf traveling speed was equal to the average forest traveling speed when average vegetation height was 4.1 m (3.6–4.9 m) in summer and 2.4 m (2.1–2.7 m) in winter, or when 92% (82–100%) and 80% (70–94%) of the vegetation exceeded 0.50 m in summer and winter, respectively (Appendix S5). For average roughness, wolf traveling speed equated to that within forest at values of 1.90 (1.76–2.11) in summer and 1.82 (1.69–2.00) in winter. Further, wolf traveling speed was equal to the average forest traveling speed once vegetation cover above the height equal point exceeded 28% (24–33%) and 30% (26–34%) in summer and winter, respectively (Appendix S5).

Does land-cover influence wolf speed on LFs?—Regardless of land-cover type, wolves traveled

Table 4. Average wolf selection of linear features (LFs), compared between uplands and wetlands in summer and winter.

Variables	Summer estimate	Summer <i>n</i>	Winter estimate	Winter <i>n</i>
On LFs	0.574 (0.461 to 0.705)	20	0.486 (0.366 to 0.811)	11
Wetland	0.074 (−0.08 to 0.213)	20	0.205 (−0.024 to 0.453)	11
On LFs Wetland	−0.381 (−0.510 to −0.256)	20	−0.144 (−0.446 to −0.002)	11

Notes: Off LFs and in upland were set as the reference category. Model estimates were weighted according to the inverse standard error and averaged across individual wolves. Sample size (*n*) and 95% confidence intervals were derived from 2000 bootstrap permutations using individual conditional logistic regression. Significant estimates are bolded.

significantly faster on LFs than off ($\beta = 0.727$, $SE = 0.025$ in summer and $\beta = 0.293$, $SE = 0.037$ in winter, $P < 0.001$). This pattern was again nuanced by seasonal differences, when during summer LFs in uplands increased wolf traveling speed more than LFs in wetlands ($\beta = -0.144$, $SE = 0.076$, $P < 0.001$; Fig. 3). In winter however, the pattern was opposite, with faster speeds on LFs in wetlands ($\beta = 0.286$, $SE = 0.070$ in winter, $P < 0.001$; Fig. 3). Wolves traveled 2.1× faster (7.7 km/h) on LFs in uplands and 1.8× faster (5.0 km/h) on LFs in wetlands in summer (Fig. 3), but 1.3× faster (0.4 km/h) on LFs in uplands and 1.8× faster (0.8 km/h) on LFs in wetlands (Fig. 3; Appendix S6). Individuals within the same pack showed more variation ($SD_{sum} = 0.044$; $SD_{win} = 0.030$) than among packs ($SD_{sum} = 0.002$; $SD_{win} = 0.027$).

DISCUSSION

A primary objective of habitat restoration is to return vegetation structure to its pre-disturbance state but the end point of this objective may not be indicative of when habitat is functionally restored (Palmer et al. 1997, Wortley et al. 2013). Here, we focused on an ecological process contributing to population declines of boreal caribou to assess the functional recovery of LFs. Specifically, we evaluated how wolf movement behavior on LFs changed as a function of vegetation structure. As predicted, wolf selection of LFs decreased with increasing vegetation height and wolf movement rates decreased as vegetation complexity increased. These relationships, however, were complex, often showing non-linearity and being affected by seasonality. A general conclusion was that relatively small and early changes in vegetation structure (e.g., height >0.50 m) caused a substantial drop in wolf movement rates on LFs

(1.5 km/h faster on LFs compared to 4.4 km/h faster), suggesting that in the context of habitat restoration for caribou, the functional recovery of LFs may occur at faster rates than the return of historic vegetation structure.

Previous research has demonstrated wolf selection for LFs and its influence on movement (James and Stuart-Smith 2000, Latham et al. 2011a, McKenzie et al. 2012, Dickie et al. 2017); however, these studies assume that wolves respond to all LFs equally (except see Dickie et al. 2017). Our results suggest that wolf selection for LFs is mediated by vegetation structure, presumably due to its influence on movement efficiency. Wolf movement rates were highest on relatively open LFs and, consequently, wolves showed the strongest selection for these LF types. Increasing vegetation height, cover, and roughness resulted in lowered movement rates and lowered LF selection by wolves. Despite a large drop in movement rate once vegetation height on LFs exceeded 0.50 m (66% reduction), especially in uplands, wolves still showed relative selection for LFs across all indices of vegetation structure and land-cover types, perhaps indicating that even small gains in efficiency can influence wolf movement behavior. Wolf movement rates on LFs remained higher than in non-LF forest in both seasons until 34% of the LF's vegetation exceeded 4.86 m. From a foraging perspective, any gain in movement efficiency afforded by LFs likely translates into higher search rates, potentially leading to higher encounter rates with prey and thus higher predation rates (Bergerud et al. 1984, James and Stuart-Smith 2000, Latham et al. 2011a, Whittington et al. 2011, DeCesare 2012, McKenzie et al. 2012, Apps et al. 2013, Dickie et al. 2017).

Differences in wolf selection for LFs between seasons and land-cover types are also likely due to

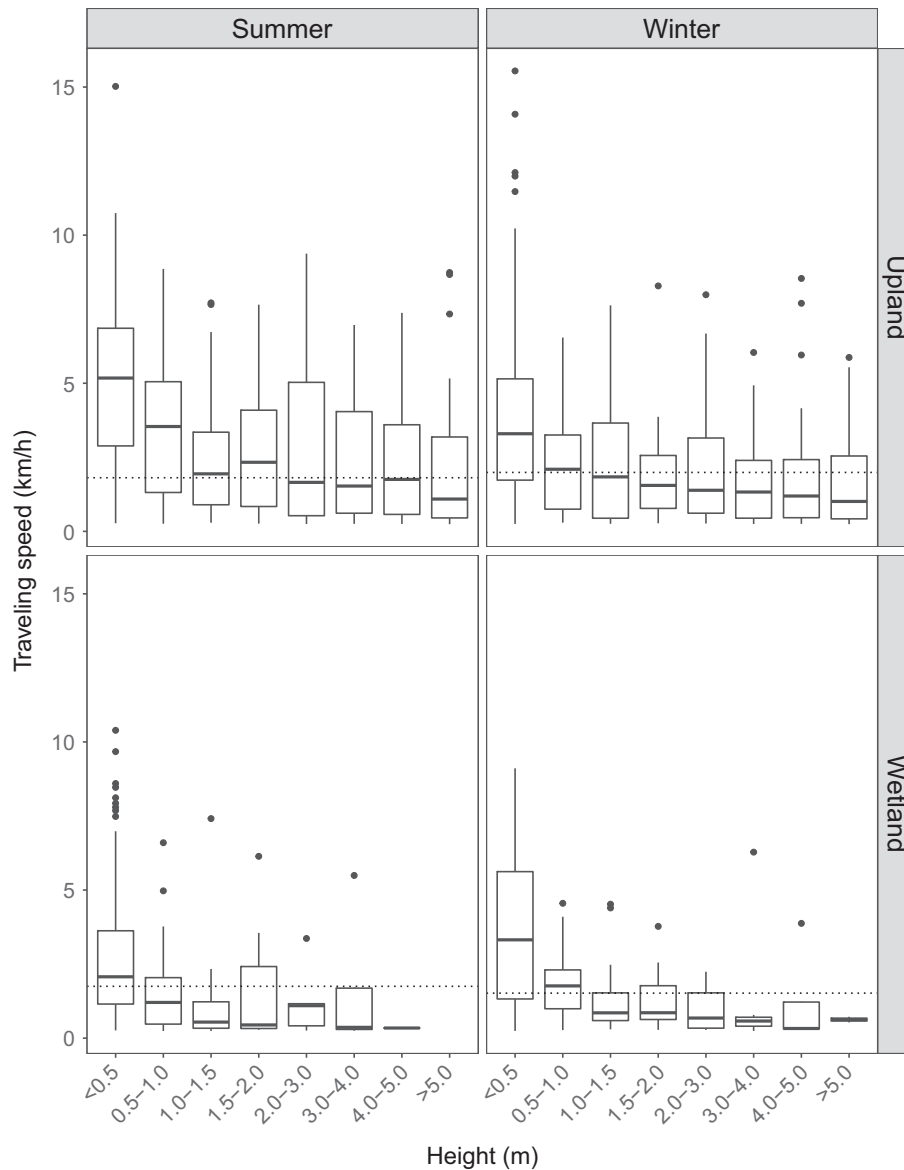


Fig. 1. Wolf traveling speed (km/h) as a function of vegetation height (m) in summer and winter, stratified as uplands and wetlands. Speed was calculated using straight lines interpolated from five-minute Global Positioning System locations. Height was calculated using least cost paths on linear features (LFs; $n = 717$ in summer and 632 in winter) and in forest ($n = 717$ in summer and 632 in winter), and binned into categories. Steps were stratified as upland ($n = 529$ on LFs and 349 on non-LF forest in summer, $n = 321$ on LFs and $n = 376$ on non-LF forest in winter) or wetland ($n = 78$ on LFs and $n = 220$ on non-LF forest in summer, $n = 121$ on LFs and $n = 119$ on non-LF forest in winter) if $\geq 75\%$ of the step intersected that land-cover type. The dotted horizontal line represents average wolf traveling speed in forests (summer = 1.81 km/h in uplands and 1.75 km/h in wetlands; winter = 1.99 km/h in uplands and 1.52 km/h in wetlands). The upper and lower bounds of the boxplots correspond to the first and third quartiles of the median, that is, the 25th and 75th percentiles. Whiskers extend to the highest value within the inter-quartile range (distance between the first and third quartiles) multiplied by 1.5. Data displayed as points outside of the boxplot correspond to outliers identified by a Tukey test.

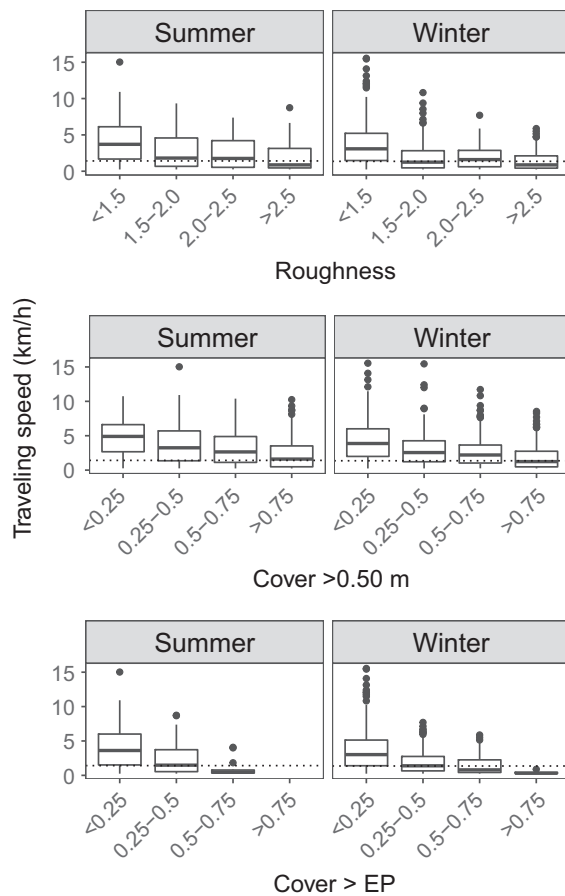


Fig. 2. Wolf traveling speed (km/h) as a function of vegetation roughness, cover above 0.50 m, and cover above the height equal point in summer and winter. Speed was calculated using straight lines interpolated from five-minute Global Positioning System locations. Vegetation roughness and cover were calculated using least cost paths on linear features ($n = 717$ in summer and 632 in winter) and in forest ($n = 717$ in summer and 632 in winter), and binned into categories. The dotted horizontal line represents average wolf traveling speed in forests (1.42 km/h in summer 1.36 km/h in winter) obtained from Dickie et al. (2017). The upper and lower bounds of the boxplots correspond to the first and third quartiles of the median, that is, the 25th and 75th percentiles. Whiskers extend to the highest value within the inter-quartile range (distance between the first and third quartiles) multiplied by 1.5. Data displayed as points outside of the boxplot correspond to outliers identified by a Tukey test.

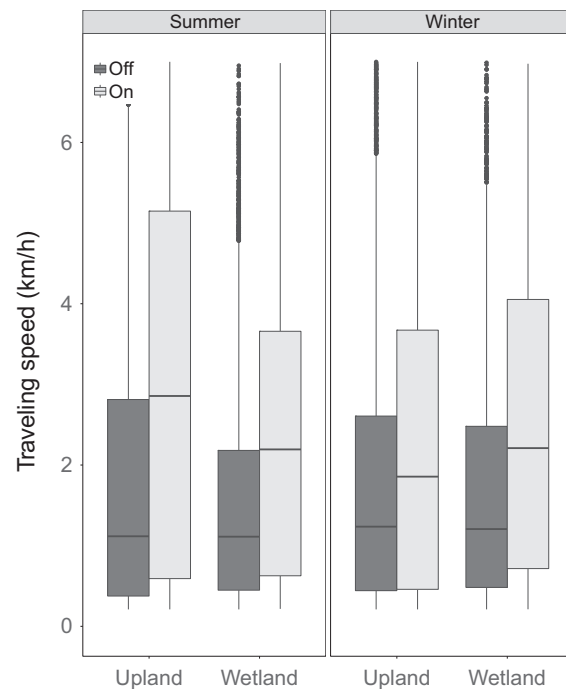


Fig. 3. Average traveling speed (km/h) of wolves on and off linear features in uplands and wetlands in summer ($n = 20$ wolves from six packs) and winter ($n = 11$ wolves from six packs). Traveling steps connecting successive five-minute Global Positioning System locations were classified as upland or wetland only if the entire step traversed the given land-cover type. The upper and lower bounds of the boxplots correspond to the first and third quartiles of the median, that is, the 25th and 75th percentiles. Whiskers extend to the highest value within the inter-quartile range (distance between the first and third quartiles) multiplied by 1.5. Data displayed as points outside of the boxplot correspond to outliers identified by a Tukey test.

variation in relative movement efficiency. Wolves showed lowered selection for LFs in winter than in summer; gains in movement efficiency on LFs during winter are likely to be minimal because snow, a constraint on wolf movement in winter (Fuller 1991), may be similar in height to, or even higher than, non-LF forest. Additionally, wolves selected LFs more strongly in uplands than in wetlands, again reflected by higher movement rates on LFs in uplands relative to non-LF forest. If dense

vegetation limits movement, LFs through upland forests may provide more of an increased movement efficiency for wolves compared to LFs in sparsely vegetated wetlands (Beckingham and Archibald 1996). Our findings on land-cover type differ from similar analyses conducted on black bears (Tigner et al. 2014), which is likely due to different foraging strategies between bears and wolves. Wolves are considered to be coursing predators with more directed movements compared to bears (Mech and Peterson 2003), which tend to forage in a grid-like pattern (Gunther and Renkin 1990). Moreover, as omnivores, bears may actively forage on LFs in uplands, which may have a higher abundance of preferred plants (Latham et al. 2011b).

To fully link wolf use of LFs to caribou declines, more research is needed on the resulting increases in kill and predation rates on caribou in areas where wolf use or availability of LFs is higher. Without a direct link, we must consider competing hypotheses linking LFs and caribou declines. Mechanistically, LFs may increase caribou predation rates by increasing predator hunting efficiency via movement rates or by increasing spatial overlap between predators and caribou by increasing predator use of wetlands, thereby increasing encounter rates (James et al. 2004). In addition, habitat change caused by linear features may increase the amount of early-seral vegetation, increasing moose and deer populations and therefore wolf numbers (Serrouya et al. 2011, Courbin et al. 2014). Related, conversion of forest into early-seral vegetation may indirectly reduce habitat available for woodland caribou via avoidance of human infrastructure (Polfus et al. 2011). However, given the small amount of the landscape directly affected by LFs, it is unlikely that changes in habitat structure affect resource availability enough to cause these numerical responses in the absence of forestry. Lastly, while wolves are often cited as the primary driver of caribou declines in the Canadian boreal, black bears and other predators of caribou adults and calves are understudied (but see Tigner et al. 2014).

Policy and management implications

Linear features constitute a large proportion of the buffered disturbance footprint within western ranges of boreal caribou, and thus, these features have been a focus of restoration efforts

(Pyper et al. 2014). Defining LF restoration criteria therefore has significant implications for prioritizing where restoration efforts should be focused, estimating disturbance densities within caribou ranges, and the subsequent effect such estimates have on industrial activities conducted within caribou range (Environment Canada 2012). Our analyses are a crucial first step for developing functional recovery criteria for LF and can help with optimizing restoration activities. Our results demonstrate that the relative gain in wolf movement efficiency afforded by LFs depends on the structure of vegetation recovery on lines and that this relationship is non-linear. We show that most of the movement efficiency afforded to wolves by LFs is mediated when vegetation exceeds 0.50 m and increasing vegetation height above this threshold resulted in only small reductions in movement rates. If decreasing rates of wolf movement equate to decreased encounters with caribou, then the largest effect on caribou predation rates may also occur when vegetation height exceeds 0.50 m.

We emphasize that a vegetation height of 0.50 m should not be viewed as a threshold for determining when LFs no longer contribute to elevated rates of caribou predation or when habitat is recovered sufficiently to stabilize caribou populations. Identifying such a threshold would require linking wolf movement behavior on LFs to kill rates and ultimately to population growth rates of caribou. Such data, however, are expensive, time-consuming, and difficult to collect. Rather, we suggest that a vegetation height of 0.50 m provides a reasonable criterion for prioritizing LFs for restoration within caribou range. For example, LFs with <0.50 m of vegetation should be prioritized for active management prescription, while natural vegetation exceeding 0.50 m is lower priority, allowing for better allocation of limited conservation resources.

A further key outcome of our study is that we provide managers with relatively simple indices (e.g., vegetation height, cover, and roughness) for objectively evaluating LF recovery using data that can be obtained remotely. These are minimum indices when using LCPs to remotely evaluate LF regeneration (i.e., representative of the area on the LF with the shortest and most sparse vegetation) and should not be interpreted as overall LF vegetation height and cover. We caution, however, that these are not the only indices for assessing effects

of LF structure on wolf movement behavior. Other characteristics, such as width, may also be important in determining predator selection for, and movement on, LFs (Tigner et al. 2014). Understanding the effects of line width on wolf movement behavior is particularly relevant given that industry practices within caribou range are now emphasizing exploration via LIS, which can be as narrow as 1.5 m and highly tortuous.

Finally, we initially stressed that habitat restoration should be linked to ecological function, and here, we focused on one of the ecological processes linking LFs to caribou population declines. But for woodland caribou, implementing a comprehensive strategy for population recovery is a complex task because changing relationships among three trophic levels (vegetation, ungulates, and predators) have been implicated in caribou declines. These complex relationships necessitate the monitoring of multiple indices, including the abundance of predators and other ungulate prey, to effectively assess the functional restoration of caribou habitat and ultimately population recovery. Even active habitat restoration can take many years to have demonstrable effects on abundance of non-caribou ungulates, predators, and ultimately population growth rates of caribou. Meanwhile, abundant populations of alternate prey and predators will continue to cause the extinction of local caribou subpopulations (Hebblewhite et al. 2010, Serrouya and Wittmer 2010). While linear disturbances contributed to declining caribou demography rates more so than polygonal disturbances such as mines and well sites (Environment Canada 2011), the alternate prey mechanism of decline may also result in a time-lag between action and measurable effects in primary prey as well as caribou populations. Therefore, if conserving caribou is to be realized, active habitat restoration should be coupled with the management of alternate prey (Serrouya et al. 2015) and predators (Hervieux et al. 2014) until the habitat recovers (Serrouya et al. 2011).

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