The Use of Anthropogenic Linear Features by Wolves in Northeastern Alberta

by

Melanie Dickie

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Department of Biological Sciences
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ABSTRACT

Predation by grey wolves (*Canis lupus*) has been identified as an important cause of boreal woodland caribou (*Rangifer tarandus caribou*) mortality. Wolves have been hypothesized to use human-created linear features such as seismic lines, pipelines and roads to increase ease of movement resulting in higher kill rates. I tested if wolves select linear features and if they increase movement rates while travelling on linear features in northeastern Alberta and northwestern Saskatchewan using fine scale analyses with 5-minute GPS (Global Positioning System) locations from twenty-two wolves in 6 packs. In addition, I examined how the abundance and physical properties of linear features affects wolf selection of, and movement on, these features. Wolves selected all linear feature classes except for low-impact seismic lines in summer and trails in winter, with the magnitude of selection depending on season. In summer, compared to the surrounding forest, wolves travelled slower on low-impact seismic lines but 2 to 3 times faster on all other linear feature classes. In winter wolves travelled 2 to 3 times faster on conventional seismic lines, pipelines, roads and railways, but slower on low-impact seismic lines and transmission lines. In addition, increased average daily travelling speed while on linear features as well as increased proportion of steps spent travelling on linear features caused increased net daily movement rates, supporting that wolf use of linear features can increase their search distance. The selection of linear features by individual wolves was not related to linear feature density. In summer, linear features through uplands provided a greater increase in travelling speed relative to surrounding forest than wetlands, however this was opposite in winter. Furthermore, when on linear features, wolves selected and moved faster on linear features with shorter vegetation. Vegetation reaching a height beyond 1 m on linear features reduced movement by 23% in summer, whereas vegetation did not decrease travelling speed in winter until it exceeded 5 m. This knowledge can aid mitigation strategies by targeting specific features for reclamation and linear deactivation, such as conventional seismic lines and pipelines with vegetation regrowth less than 1 m, allowing for more effective use of conservation resources.

PREFACE

This thesis is an original work by Melanie Dickie. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Understanding wolf movement and mitigating use of seismic lines", AUP00000480, April 2013.

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INTRODUCTION

Understanding predator-prey dynamics is necessary for species and ecosystem management, and as such predator-prey dynamics has garnered much interest over the years (Holling 1959a; b; Arditi & Ginzburg 1989; Fryxell *et al.* 2007). Whether the interest stems from wanting to understand how predators affect their prey, or vice versa, it is important to understand predation rates and the factors that influence them. Predation rates can be broken into four components; the predator's 1) numerical response, how predator reproductive rates respond to prey population density, 2) functional response, how the number of prey killed per predator per unit time changes with prey density, 3) aggregative response, how the predator spatial configuration changes with prey congregation, 4) and developmental response, how the number of prey required to sustain predators changes with maturity (Solomon 1949; Holling 1959a). Understanding the functional response of predators is integral to determining predation rates. The functional response can be conceptualized as the kill rate of a predator, where the number of prey killed per predator per unit time is a function of the instantaneous search rate, handling time and prey density as described by the Holling disc equation (Holling 1959b). Specifically, the instantaneous search rate is comprised of the distance the predator can travel in a given time, the search buffer in which they can detect prey, and the proportion of encounters with prey that results in a kill (Fryxell *et al.* 2007). Comprehending how human disturbance influences the instantaneous search rate or more broadly, predation rates, is necessary in changing landscapes.

Altered predator-prey dynamics due to human-induced landscape change is thought to contribute to the decline of the boreal ecotype of woodland caribou, which are provincially and federally listed as threatened (COSEWIC 2002). Ten of 14 populations recently studied in Alberta are declining (Hervieux *et al.* 2013). Predation by wolves has been identified as an important mortality factor and likely cause of population decline (Bergerud & Elliot 1986; Seip 1992; Rettie & Messier 2000; McLoughlin *et al.* 2003; Festa-Bianchet *et al.* 2011; Pinard *et al.* 2012). Activities associated with forestry and oil and gas exploration have been linked to increased predation pressure on woodland caribou via apparent competition, which has been caused by greater spatial overlap, higher wolf populations and changes to hunting behaviour (Latham *et al.* 2011b; Hervieux *et al.* 2013). Wolves have also been hypothesized to use human created linear features such as seismic lines, pipelines and roads to increase ease of movement. As a consequence it is hypothesized that prey encounters increase, resulting in higher kill rates (Bergerud, Jakimchuk & Carruthers 1984; James & Stuart-Smith 2000; Latham *et al.* 2011a; Whittington *et al.* 2011; McKenzie *et al.* 2012; DeCesare 2012; Apps *et al.* 2013).The use of linear features to facilitate travelling can become important to the location of prey, when wolves rely heavily on searching large areas to increase encounters with prey (Mech 1970; Whittington *et al.* 2011; McKenzie *et al.* 2012). For example, an increase of the instantaneous search rate would lead to an increased kill rate until predators are saturated by handling time (Holling 1959b). Therefore, it is important to understand how linear features affect wolf movement in behaviour to properly manage woodland caribou.

Evidence that linear features facilitate movement and consequently influence encounter rates is increasing (Latham *et al.* 2011a; Whittington *et al.* 2011; McKenzie *et al.* 2012). However, few studies attempt to make direct links between caribou predation events and linear features (James & Stuart-Smith 2000; James *et al.* 2004; Environment Canada 2011; Latham *et al.* 2011a). Previous studies on wolf movement related to linear features did not explicitly test whether short-term increased movement rates translated into more area searched over longer temporal scales (Latham *et al.* 2011a; McPhee, Webb & Merrill 2012). However, increased short-term movement rates may not lead to increases to the instantaneous search rate (Holling 1959b). For example, wolves may increase movements on linear features to travel distances quickly, but then devote more time to other behaviours such as resting or reproduction instead of increasing overall movements or consumption of prey (Mech & Boitani 2003; Giuggioli, Potts & Harris 2011). The Holling disc equation assumes predators have two basic behaviours; handling prey and hunting for prey (Holling 1959b). However, if linear features increase travelling speeds, but wolves then use the time they would otherwise be moving for other behaviours not included in the Holling disc equation, such as resting or socialization, increased movement rates may not increase predation rates. Without explicitly testing predation rates, a link between short-term movements and daily movement gets us one step closer to understanding the possible influence of linear features on wolf predation.

Furthermore, little effort has been made to determine how differences in linear feature abundance affect wolf selection and movement. The abundance and spatial arrangement of resources have been found to influence selection (Mysterud & Ims 1998). The abundance and spatial arrangement of linear features on the landscape varies, and therefore has the potential to influence selection. When linear features are abundant, selection for each individual feature may be weak because there are many options for movement. Conversely, if linear features are rare on the landscape, but provide a benefit to wolf movement, they may be more strongly selected. Areas of dense linear features are also associated with areas of high human use, which are avoided by wolves (Hebblewhite & Merrill 2008). Some features such as railways and transmission lines are rare, whereas other features such as conventional seismic lines and pipelines are abundant. If specific feature classes provide greater benefits to movement than others, not only will selection be stronger, but stronger selection would be expected when they are rare. Consequently, it is important to consider linear feature densities when evaluating the response of wolves to various linear features.

In addition to abundance, physical structure of linear features may affect linear feature selection by wolves as well as wolf movement on these features. First, the habitat linear features traverse may affect wolf movement. For example, uplands and wetlands have vastly different characteristics that may influence wolves. Uplands are characterised by dry substrates and often have dense vegetation (Beckingham & Archibald 1996). Dense vegetation in uplands can impede wolf movement; however dry conditions provide stable substrates. Conversely, the high water content and hummocks in wetlands offer less stable substrates than uplands, which could slow wolf movements. However, wetlands have relatively sparse vegetation (Beckingham & Archibald 1996), and could therefore provide less movement resistance. Linear features in uplands may be beneficial to wolves by removing dense vegetation, thereby decreasing movement resistance. Linear features in wetlands may provide flatter terrain for wolves due to flattening of hummocks, however may not provide as strong of benefit to movement as in uplands due to sinking and already sparse canopies. Furthermore, benefits of linear features in uplands and wetlands to wolf movement may be different in the winter than summer. In winter, snow can be limiting to movement (Fuller 1991). Therefore, the benefit of moving on linear features through uplands may be negated due to increased snow depths on linear features relative to surrounding forest, as full canopies in uplands provide refuge from deep snow. Conversely, linear features through wetlands may provide less resistance to movement than the surrounding forest. Sinking is no longer an issue in winter due to freezing, and so flat terrain from the process of creating linear features may provide stable substrates for movement. Understanding how linear features interact with the habitat they traverse should be considered when evaluating the effect of linear features on wolves, as well as when planning restoration activities.

Another physical attribute of linear features that may lead to differential wolf selection of linear features, as well as to movement differences, is vegetation regeneration. If vegetation impedes movement, linear features with less vegetation regrowth may have greater use compared to those with an advanced state of regeneration. A number of factors may contribute to the regeneration of linear features. Linear features through upland forests such as trembling aspen (*Populus trembuloides*) and white spruce (*Picea glauca*) dominated forests have been found to regenerate more quickly than linear features through wetlands (Lee & Boutin 2006). In addition, re-use of linear features can slow or restart the successional trajectory (Lee & Boutin 2006). Furthermore, the methods used to create linear features can affect their ability to regenerate. Historically, linear features were created using bulldozers; however, through time efforts have been made to reduce the width of linear features as well as using different techniques to minimize ground disturbance to promote regrowth (Lee & Boutin 2006). These factors can combine to produce revegetation differences among linear features, as well as differences along the same linear feature. Rate of revegetation differences may influence the response of wolves to these features. It is important to consider how physical attribute differences among linear features, as well as along the same linear feature, affect wolf selection of these features and movement. Such information will help prioritize linear features for restoration as well as predicting how wolves may respond to restoration activities.

My thesis aims to meet two goals; 1) to determine if wolves select linear features of different types and if use of linear features increase wolf movement rates, and 2) determine if wolf use and travel speed on linear features is affected by linear feature density and/or vegetation on the feature.

To address if linear features affect wolf movement, and further if various linear feature classes differ in their effect, I ask three questions; i) do wolves select linear features ii) do wolves travel faster on linear features, and iii) does increased use of linear features increase daily movements? If linear features function to increase the effectiveness of wolves at finding their prey by increasing movement, I predict that wolves select linear features, move faster on linear features and increase overall daily movements by using linear features. I also predict that differences among linear feature classes will lead to varying magnitudes of effect on wolf selection and movement. I use fine-scale analyses to directly compare movements along linear features to movements in the forest, and determine if these fine-scale movements translate to larger time-scales.

To address if differences in abundance and physical structure of linear features affect wolf selection and movement, I ask three questions; i) does wolf selection of linear features depend on linear feature density within their home range, ii) does wolf travelling speed on linear features differ between uplands and wetlands, and iii) does vegetation regrowth impact wolf selection and movement on linear features? Specifically, I predict wolves will increase the magnitude of linear feature selection when linear feature density is low because they will seek out linear features when they are rare on the landscape, increased travelling speed on linear features depends on whether the linear features is through uplands or wetlands because cleared canopies in uplands will be beneficial while wetlands will continue to impede movement and wolves will show decreased selection and movement rates on linear features with more vegetation regrowth. Previous studies have not addressed how the physical characteristics of linear features affect wolf use and selection, and how these relationships can be incorporated into management strategies.

MATERIALS AND METHODS

STUDY SITE

My study took place in the Wood Buffalo region of northeastern Alberta near the town of Conklin (55°35`N, 111°00`W), and extends into northwestern Saskatchewan (Fig. 1). The 18 000-km^2 study area contains boreal forest with a natural mosaic of peatlands, uplands, marshes and swamps, including black spruce bogs and black spruce-tamarack fens (Latham *et al.* 2011a). The area is relatively flat with an elevation of approximately 550 m. In addition, there are various small lakes and rivers within the study area. Trembling aspen, white spruce, jack pine (*Pinus banksiana*) and balsam fir (*Abes balsamea*) dominate the upland boreal forests. Lowlands are dominated by black spruce (*Picea mariana*), tamarack (*Larix laricina*), Labrador tea (*Ledum groenlandicum*), dwarf birch (*Betula spp.*), willows (*Salix spp.*), sedges (*Carex spp.*) and peat moss (*Sphagnum spp*). Terrestrial and arboreal lichens are present in both lowlands and uplands. The mammalian community consists of white-tailed deer (*Odocoileus virginianus*), woodland caribou, moose (*Alces alces*), wolves, black bears (*Ursus americanus*), Canada lynx (*Lynx canadensis*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), beaver (*Castor canadensis*), snowshoe hare (*Lepus americanus*) and other small mammals. The main prey species for wolves are moose and white-tailed deer, however, beaver, woodland caribou and snowshoe hare are also in their diet (Latham *et al.* 2011b). The study area encompasses the Cold Lake caribou range as well as the East Side Athabasca Range (ESAR).

Features associated with energy and forestry industries are extensive. Linear features are cutlines that create a network of disturbances throughout northeastern Alberta; including transmission lines, features used for transportation such as roads, trails and railways, as well as features for oil and gas exploitation such as pipelines, conventional seismic lines and low-impact seismic lines. In Northern Alberta, the first step to locating oil and gas reserves involves creating conventional seismic lines. To locate oil and gas reserves, small explosive charges combined with receivers are used to profile the underlying rock and hydrocarbon layers. To perform seismic exploration, long and straight cutlines are created through the forest. Historically conventional seismic lines were constructed to be wide enough for relatively large machinery; however there has been a trend to reduce lines to approximately 5 m wide to reduce costs and environmental impacts. In addition, new technologies have been developed to obtain more accurate, three-dimensional hydrocarbon locations. This technology requires a network of closely spaced receiver and transmitter lines. With the need to obtain more accurate hydrocarbon locations as well as the implementation of Steam Assisted Gravity Drainage extraction techniques, low-impact seismic lines began to be implemented. Low-impact seismic lines are spaced in grids, with each cutline being approximately 50 m apart. These features are much narrower than conventional seismic lines, and tend to meander through the forest. Once hydrocarbons are found, other linear features, such as pipelines, roads and transmission lines are used to extract oil and gas, gain access to facilities involved in the extraction and processing of oil and gas, and provide power to these facilities. Differences among linear feature classes, as well as when and how linear features were created, have lead to a patchy landscape in northern Alberta.

Linear features are ubiquitous through northern Alberta, and have therefore garnered much interest over time from managers and government agencies (James & Stuart-Smith 2000; COSEWIC 2002; Latham *et al.* 2011a; McKenzie *et al.* 2012). Reporting of human disturbances usually includes features associated with oil and gas exploration (COSEWIC 2002; Environment Canada 2011, 2012); however, reports of linear features, such as those by the Government of Alberta, often do not include information on low-impact seismic lines. Therefore, to be consistent with other reports of linear feature densities, I provide information on overall linear feature densities, excluding low-impact seismic, as well as low-impact seismic separately. Not including low-impact seismic lines, the Cold Lake and ESAR caribou ranges have average linear feature densities of 1.70 km/km^2 and 1.99 km/km^2 respectively. In addition to the base linear feature densities, Cold Lake caribou range and ESAR contain approximately 12 521 km and 18 586 km of low-impact seismic lines, respectively.

WOLF CAPTURE AND COLLARING

Wolves were captured by Wildlife Infometrics and Bighorn helicopters under the Regional Industry Caribou Collaboration (RICC). All wolves were captured and handled in accordance with approved animal care through the University of Alberta (AUP00000480, 2013) and Government of Alberta (Permit 53657 and 54559). The capture crew attempted to collar two to four wolves per pack per year in every pack within the lease rights of industrial partners in the RICC. Twenty-two Iridium GPS collars (Lotek Wireless, Aurora, Ontario, Canada) were deployed on wolves in six packs over the winters of 2013 and 2014. Capture crew were unable to successfully collar individuals from at least three packs of interest. As such, the area of inference is defined by wolf territories (Fig. 1). Collars were programmed to provide locations on a cycle of five minutes for two days, then hourly for four days during from April 15 to July 15 (defined as summer). In addition, collars were programmed to provide 5-minute locations from January 1 to March 30 (defined as winter).

LINEAR FEATURES

Linear features were visually classified by the Alberta Biodiversity Monitoring Institute, and supplemented when necessary following the same specifications. Digitizing was performed using 2012 SPOT imagery (2-m resolution) as well as Valtus Views (0.5-m resolution), when available, at a 1:15 000 scale. Linear features were classified as conventional seismic lines, low-impact seismic lines, trails, roads, pipelines, transmission lines and railway based on modified specifications of the Government of Alberta. Linear features were classified as low-impact seismic lines if they were less than 5 m wide. Low-impact seismic lines also tended to be sinuous and were laid out as a grid. Features were classified as conventional seismic lines when they were 5 to 10 m wide and tended to be long and straight. Features were classified as trails if they were cutlines with no visible road surface that were not long and straight, nor in a grid. Trails generally had an approximate width of 10 m, but could be anywhere between 5 m and 15 m wide. Tire tracks with grass growing in the centre were often visible. In addition, forestry roads that were within forestry cutblocks were classified as trails. Seismic lines and trails were stopped at the edge of any natural or man-made clearing with a width equal to or greater than 20 m. Features were classified as pipelines based on supplementary data provided by the Government of Alberta, originating from Digital Integrated Dispositions (DIDs). Pipeline right-of-ways range from 10 m to 100 m wide. If pipelines contained more than one pipe, they were drawn as one corridor. If the pipeline paralleled a road, it was placed on the most obvious side of the right of way. Linear features were classified as roads when road surfaces were visible. This included winter roads, gravel roads, as well as major paved highways. Road width varied between 10 m and 60 m. Only roads, including driveways, exceeding 50 m were classified. Features were classified as railways when they showed visible tracks. Transmission lines were classified using supplementary data originating from DIDs. Transmission lines tended to be wide, but ranged from 5 m to 65 m wide, and were easily identified with imagery. Transmission lines running along roadsides or to small facilities were not captured. When multiple linear features followed the same corridor the features were classified individually as long as they were visibly separated at a scale between 1:5000 and 1:10000. When seismic lines or trails shared the same corridor as wider features, the shared corridor was assigned to the widest linear feature class.

Digitizing linear features using remote sensing imagery created one-dimensional lines, but did not represent the width of each feature class. Therefore, I converted the one dimensional line features into polygons by assigning a buffer according to their average width in the landscape (Table 1). Three linear features of each class were randomly chosen within each wolf pack's 100 % minimum convex polygon (MCP) and the width measured to the nearest 2.5 m, corresponding to the cell size of SPOT imagery. MCPs were calculated using only 5-minute GPS locations using ArcGIS 10.1 (ESRI, 2013). If there were no linear features of a given feature class in a pack's MCP, that feature class was not represented for that pack. The average width of the feature class was then rounded to the nearest 2.5-m increment, again to match the resolution of imagery used for digitizing. A buffer equal to the width of that linear feature class was then assigned to each linear feature class, on both sides. While this approach created linear feature polygons twice the width of the average linear feature on the landscape, it accounted for errors in the digitization process such as lines being drawn on the edge of the linear feature instead of in the middle. Also, while some features were buffered by greater than their width, variation in the widths of linear features meant that linear features were sometimes wider than the applied buffer. Other methods used to assign GPS locations to linear features by buffering according to their width have included an additional term to encompass error in the GPS locations provided by collars (McKenzie *et al.* 2009). However, by not including additional area for GPS-collar error and maintaining a narrow buffer I decreased the chance that wolf locations in the forest edge were misclassified as being on linear features. This is a conservative approach that minimized the chance of detecting wolf selection on linear features, or Type I error.

WOLF SELECTION AND MOVEMENT ON LINEAR FEATURES

DO WOLVES SELECT LINEAR FEATURES?

I evaluated the relationship between linear feature class and wolf selection by comparing GPS locations to random locations. Because I was interested in fine scale movement of wolves, and linear features such as low-impact seismic lines were patchy within the study area, it was important to constrain the characterisation of availability for each used location. Specifically, I compared each used location obtained with a 5-minute fix rate to 10 available locations within a radius set to the 90th percentile of the maximum step length; 0.274 km (i.e.. the 90th percentile maximum distance between two consecutive 5 minute locations). Each GPS and random location was assigned a linear feature class or was designated as being in the surrounding forest. Linear feature class was assigned to locations that were completely contained within a linear feature`s buffer. If the location fell where multiple linear feature classes overlapped, the location was classified as the feature class with the largest buffer width. If the location did not fall within the buffer of any linear feature, it was classified as forest.

I also included landcover as a covariate to control for selection differences among landcover types. I extracted the landcover category in which the location fell based on Alberta Vegetation Inventory (AVI) and Saskatchewan Forest Inventory (SFI). Landcover was classified as deciduous, coniferous, mixedwood, wetland and other using ecosite characteristics (Beckingham & Archibald 1996), and was independent of the linear feature layer. The landcover of large scale human-modified areas (for example a ranch or oil and gas facilities) was classified as other; these features were rare. If the location fell in an area with unknown landcover classification due to lack of AVI or SFI coverage, that location was excluded from the analysis.

Each wolf was modelled separately using conditional logistic regression using the survival package in R (Therneau 2014) to determine if wolves selected or avoided linear features compared to surrounding forest, and if the magnitude of selection differed among each linear feature class. Including linear feature class and landcover class as two separate categorical variables allowed me to estimate selection coefficients for each linear feature class more accurately, because variation due to landcover was controlled for. Coniferous forest and non-linear feature forest were set as the landcover and linear feature reference categories, respectively, because they were the most common categories (Boyce *et al.* 2003). The interaction among linear feature class and landcover class was of interest; however models with interactions failed to converge. For each landcover category and linear feature class individual coefficients were averaged across individual wolves. Coefficients were weighted by the inverse square of the standard error to give individuals with more precise estimates more weight. A bootstrap analysis with 2000 permutations was used to calculate 95% confidence intervals (Canty & Ripley 2015). I define selection as features that are used more than their availability on the landscape, and avoidance as used less than their availability. Summer and winter seasons were analysed separately (Latham *et al.* 2011a). Two wolves did not have sufficient winter data, and were removed from analyses.

DO WOLVES TRAVEL FASTER ON LINEAR FEATURES?

To determine if linear features facilitated wolf movement, I evaluated the relationship between linear feature class and wolf travelling speed. Successive GPS locations in time for each individual were connected to create steps using ArcGIS 10.1 (ESRI, 2013). Travelling speed was then calculated as the distance between two successive GPS locations divided by the time between locations, and converted to km/hr. I limited travelling speed analyses to steps between 5-minute locations to keep sampling frequency consistent. Steps longer than a 5-minute period due to missed fixes were not included in analyses. The log of travelling speed revealed a bimodal distribution suggesting two types of movement (Fig. 2); slow and fast. I calculated a breakpoint of 0.21 km/hr using the segmented package in R (Muggeo 2014). I assumed that short step lengths, i.e. less than 0.21 km/hr corresponded to resting and feeding bouts while longer step lengths, i.e. greater than or equal to 0.21 km/hr corresponded to travelling movements. Because I was interested in how linear features affect the latter, step length analyses were restricted to movements greater than or equal to 0.21 km/hr.

I classified each step as on or off a linear feature, and if on a linear feature, which linear feature class the step was on. A step was classified as on a linear feature of a specific class if a 5-minute step was completely contained within a linear feature's buffer. If a step intersected a linear feature buffer but was not completely contained within, or was not within any linear feature's buffer, the step was classified as being in non-linear feature forest. This approached allowed me to identify travelling movements along linear features as opposed to crossing linear features.

I compared travelling speeds as a function of linear feature class using a generalized mixed-effects model with a random intercept included for each wolf, nested within pack with the lme4 package in R to (Bates *et al.* 2014). I transformed travelling speed using the natural logarithm because it was non-normally distributed and set non-linear feature forest as the reference category for linear feature class. P-values are not easily calculated with mixed-effects models, so I approximated p-values using the lmerTest package with a Satterthwaite approximation (Kuznetsova, Brockhoff & Bojesen 2014). Summer and winter seasons were analysed separately.

DOES INCREASED USE OF LINEAR FEATURES INCREASE DAILY MOVEMENTS?

Increased travelling speed on linear features may not translate to increased overall daily movement if wolves spend more time resting. Therefore, I evaluated whether overall daily wolf movements were increased by 1) increased travelling speed on linear features and 2) increased time spent on linear features.

To determine if increased speed while travelling on linear features causes increased daily movements, I evaluated the relationship between the total distance each wolf moved in a day and the average travelling speed while on linear features for each wolf, for each day. I calculated the total distance wolves moved, regardless of movement type, for each day containing 5-minute GPS locations. A day was defined as a 24-hour period from the time collars began transmitting 5-minute GPS locations. I used days only in which there were a minimum of 200, 5-minute steps in analyses to minimize the effect of missed fixes on calculating total distance or average travelling speed. I calculated the average travelling speed while on linear features, and included only 5-minute steps. I classified steps as on linear features when they were completely contained within any linear feature class' buffer. Because I was interested in travelling movements along linear features, I included movements with travelling speeds greater than or equal to 0.21 km/hr only.

In addition, I evaluated the relationship between total daily distance moved and the proportion of travelling steps that were on linear features for each wolf, for each day to test if wolves searched more area in a day when they spent more time travelling on linear features. The proportion of travelling steps on linear features was calculated as the number of travelling steps, i.e. steps with travelling speeds greater than or equal to 0.21 km/hr, that were completely contained within a linear feature's buffer divided by the total number of steps taken in that day, regardless of movement type and location.

I evaluated the relationship between daily distance moved and 1) travelling speed on linear features and 2) proportion of travelling steps on linear features using two separate generalized mixed-effects models with a random intercept included for each wolf, nested within pack with the lme4 package in R to (Bates *et al.* 2014). I calculate p-values using the lmerTest package with a Satterthwaite approximation (Kuznetsova, Brockhoff & Bojesen 2014). Summer and winter seasons were analysed separately, and each independent variable was transformed using the natural logarithm to normalize distributions.

EFFECT OF LINEAR FEATURE ABUNDANCE AND PHYSICAL STRUCTURE ON SELECTION AND MOVEMENT

DOES WOLF SELECTION OF LINEAR FEATURES DEPEND ON LINEAR FEATURE DENSITY WITHIN THEIR HOME RANGE?

To determine if wolf selection of linear features depends on linear feature density, I evaluated the relationship between each wolf's raw selection coefficient from the models above and the linear feature density in their home range. I did this using two approaches; with all linear feature classes combined and with each linear feature class separate.

First, I evaluated whether overall linear feature density drives the average selection of linear features by regressing average wolf selection of linear features against the overall linear feature density, excluding low-impact seismic lines, in each wolf's home range. Average selection of linear features was calculated for each wolf by averaging their linear feature selection across linear feature classes. I calculated the average overall linear feature density using a moving window with a 1-km radius for each wolf's 100% MCP. I did not include low-impact seismic lines when reporting the overall linear feature density to keep densities comparable to other studies and because it drove linear feature density up for the few wolves that were exposed to low-impact seismic lines. However, inferences remained the same when low-impact seismic lines were included in average overall linear feature density. Summer and winter seasons were analysed separately.

Second, I evaluated whether wolf selection of each linear feature class was related to the density of that linear feature class by conducting a linear regression between wolf selection coefficients of each linear feature class and the density of that linear feature class within each wolf`s home range for each linear feature class separately. The selection of each linear feature class for each wolf was obtained from the resource selection models described above, in which I determined the magnitude of wolf selection for each linear features class, for each individual. I calculated the average linear feature density for each linear feature class separately using a moving window with a 1-km radius for each wolf's 100% MCP. MCPs were calculated using only 5-minute GPS locations. Summer and winter seasons were analysed separately.

DOES WOLF TRAVELLING SPEED ON LINEAR FEATURES DIFFER BETWEEN UPLANDS AND WETLANDS?

To determine if wolf movement on linear features are affected by whether the linear feature is through uplands or wetlands, I evaluated the relationship between wolf travelling speed and whether linear features were through uplands or wetlands. As above, I calculated the travelling speed (km/hr) for steps connecting successive 5-minute GPS locations. I included only steps with travelling speeds greater than, or equal to 0.21 km/hr in the analysis. I classified steps as on or off linear features using buffered linear features derived from hand digitized imagery. Steps were classified as on linear features if they fell completely within any linear feature's buffer, regardless of feature class. Any steps that were not completely contained within a linear feature buffer were classified as off linear features. In addition, I classified steps as within uplands or wetlands. I first calculated the proportion of each step that fell within uplands and wetlands using ecosite characteristics (Beckingham & Archibald 1996) derived from AVI and SFI. Because I was interested in directly comparing travelling movements in uplands from those in wetlands, I restricted analyses to steps that were completely in either uplands or wetlands.

I conducted a mixed-effects generalized linear model with individuals nested within pack included as a random term to determine if wolf travelling speed was different between uplands and wetlands, if wolves travelled faster on than off linear features, and how linear features interacted with uplands and wetlands. Uplands and off linear features were set as the reference categories. I transformed travelling speed using the natural logarithm to normalize the distribution. I approximated p-values using the package lmerTest with a Satterthwaite approximation in R (Kuznetsova, Brockhoff & Bojesen 2014). Summer and winter seasons were analysed separately.

DOES VEGETATION REGROWTH AFFECT WOLF SELECTION AND MOVEMENT ON LINEAR FEATURES?

I evaluated the relationship between wolf selection and vegetation height while on linear features by comparing GPS locations on linear features to random locations on linear features. Again, I created 10 available locations for each GPS location within a radius set to the 90th percentile of the maximum 5-minute step length; 0.274 km. Each GPS and random location was assigned a vegetation height, linear feature class and land cover type. Including linear feature class and landcover class allowed me to estimate height selection coefficients more accurately, because variation due to landcover and feature class was controlled for.

Vegetation height on linear features was obtained and processed using Light Detection and Ranging (LiDAR) as part of a larger RICC project. In August 2012, LiDAR was flown in 0.7-m swaths to gain an up-to-date inventory of the anthropogenic footprint with vegetation heights at a 1 m resolution. Vegetation height data on linear features were available for a subset of wolves in a 4 300-km^2 area only. LiDAR was ground truthed using a stratified random design to measure vegetation height across each type of human disturbance footprint. I extracted the vegetation height value for each GPS and random location based on the pixel in which the location fell.

Because the effect of vegetation height on wolf selection of linear features could differ among linear feature classes, I included linear feature class as a covariate. However, linear features hand digitized and buffered using imagery did not perfectly overlap with LiDAR-derived linear feature polygons. Discrepancies in the overlap between linear feature layers were usually due to inaccuracies in hand digitized linear features. Therefore, I overlaid the two data sets to obtain linear features with known linear feature classes, as well as vegetation heights. GPS and random locations that did not fall within both data sets were removed from analyses. In addition, each GPS and random location was assigned a linear feature class. Linear feature class was assigned to locations that were completely contained within a linear feature's buffer. If the location fell within overlapping buffers, the location was classified as the feature class with the largest buffer width.

Lastly, I included landcover as a covariate because the effect of vegetation height on wolf selection of linear features could differ among landcover types. Landcover was derived from AVI and the Saskatchewan Forest Inventory as described above and categorized as coniferous, deciduous, or mixedwood forest, wetland, or other. I extracted the landcover category in which the GPS or random location fell. If the location fell in an area with unknown landcover classification, that location was excluded from the analysis.

I modelled each wolf separately using conditional logistic regression to determine if wolves selected shorter vegetation heights while on linear features. Coefficients were averaged across individuals, and weighted by the inverse square of the standard error so that individuals with more precise estimates were given more weight. A bootstrap analysis with 2000 permutations was used to calculate 95% confidence intervals (Canty & Ripley 2015). The most common linear feature class and land cover type, conventional seismic lines and coniferous forest respectively, were used as reference categories. Summer and winter seasons were analysed separately.

To determine if vegetation height on linear features affects wolf movement, I evaluated the effect of vegetation height on wolf travelling speed while wolves were on linear features. Using GPS locations within the area in which LiDAR and hand-digitized linear feature boundaries overlapped, I calculated the length of each step connecting successive 5-minute locations and divided by time to calculate speed. I then converted speed to km/hr. I excluded steps with travelling speeds less than 0.21 km/hr because I was interested specifically in travelling movements. I extracted the linear weighted mean vegetation height for each step, and assigned steps into height categories based on their linear weighted mean. I did not analyse height as a continuous variable for two reasons; 1) evaluating the raw data demonstrated that the relationship between travelling speed and height was non-linear and 2) because I was interested in movement behaviour switches when vegetation height increased. Specifically, I categorized vegetation height as < 1 m (cleared linear features), 1 - 2 m (linear features with minimal revegetation), 2 - 5 m (linear features with moderate revegetation) and > 5 m (linear features with high revegetation).

I used a mixed-effects generalized linear model with individuals nested within their packs to evaluate the relationship between travelling speed and vegetation height category with the lme4 package in R (Bates *et al.* 2014). I estimated p-values using the package lmerTest with a Satterthwaite approximation in R (Kuznetsova, Brockhoff & Bojesen 2014). Summer and winter seasons were analysed separately.

A CASE FOR THE INDEPENDENCE OF WOLVES

Obtaining population level inferences from individuals while accounting for autocorrelation at the individual level is commonly accomplished by one of two analytical methods; mixed-effects models or modelling individuals and averaging coefficients across individuals (Boyce 2006; Hebblewhite & Merrill 2008; Sawyer, Kauffman & Nielson 2009; Northrup *et al.* 2012; Squires *et al.* 2013). For selection analyses I opted to obtain population level selection inferences by modelling individuals separately and then averaging estimates across individuals, which is commonly used and well supported by literature (Boyce 2006; Sawyer, Kauffman & Nielson 2009; Northrup *et al.* 2012; Squires *et al.* 2013). However, there can be issues with averaging individuals when individuals are non-independent. Studies of territorial animals such as wolves have dealt with non-independence among individuals within the same pack by limiting sampling to one wolf per pack, per year (Latham *et al.* 2011a; McKenzie *et al.* 2012; DeCesare 2012).

However, I argue that issues associated with the violation of independence from analysing two to four individuals per pack is minimal in my study design of fine scale selection in relation to issues with constraining availabilities.

For resource selection analyses, where used locations are compared to available locations, it was crucial that I restrict availabilities to each used location. This is because I was interested in fine-scale behavioural responses to linear features, which are often patchily distributed. For example, if a dense area of low-impact seismic lines was present in a small portion of the home range, these features should not be considered as available if they were at distances exceeding what could be biologically feasible for the wolf's next step. Therefore, the use of conditional logistic regression was important for my study design. Mixed-effect 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, Fortin & Courbin 2010). Because I was concerned about the possibility of non-independence affecting my selection analyses, I tested if packs had significantly different average selection estimates, and whether the variance among packs was higher than residual variance (Appendix 1). The results from these analyses gave me confidence that issues associated with non-independence of wolves were minimal, and the benefits of conditional logistic regression outweighed the costs of averaging individuals.

For movement analyses, where I analysed the effect of various habitat characteristics on travelling speed, using conditional models was not an issue. Constraining availabilities was a concern only for comparing used and available locations, not step lengths. Therefore, I opted to obtain population level inferences by using mixed-effects models with individuals nested within their packs (Hebblewhite & Merrill 2008). Because I was concerned about the possibility of non-independence affecting my analyses, I used this opportunity to test the variation among individuals within and amongst packs. Mixed-effects models with individuals nested in packs showed very low variation among packs, and typically yielded more variation among individuals within the same pack, than among packs. I also tested whether inferences were sensitive to the two different modeling approaches. Inferences remained consistent whether I modelled individuals separately and averaged coefficients or performed mixed-effects models with individuals nested within packs. As such, I am confident that including 2-4 individuals within the same pack did not violate the assumption of independence, and did not impede my ability to make population level inferences.

RESULTS

WOLF SELECTION AND MOVEMENT ON LINEAR FEATURES

DO WOLVES SELECT LINEAR FEATURES?

I obtained 145 888 GPS locations from 20 wolves in 6 packs during the summer of 2013 and 2014 and 79 633 locations from 11 wolves in 6 packs during the winter of 2014.

The study area has an abundance of linear features, with individuals exposed to an average linear feature density within their home range between 0.52 to 3.57 km/km^2 excluding low-impact seismic lines. However, each linear feature class covered approximately only 5% of the landscape. The relative abundance of linear feature classes varied on the landscape, with conventional seismic lines being the most common feature class (Fig. 3). All 20 wolves were exposed to conventional seismic lines and trails. Of the wolves that were exposed to conventional seismic lines in summer nearly all selected them, with the exception of five, which were neutral to them (Table 2). Selection of trails in summer was less consistent across individuals than for conventional seismic lines; only 60% of individuals selected trails (Table 2). Most wolves were exposed to pipelines (n=19 in summer and 9 in winter) and roads (n=18 in summer and 8 in winter). Of the individuals exposed to pipelines and roads, 53% and 61% selected those linear features, respectively (Table 2). While only 6 wolves were exposed to railways in summer, 83% selected them, and no wolves avoided them (Table 2). Similar to railways, only 6 wolves were exposed to transmission lines, but 83% selected them and no wolves avoided them (Table 2). In addition, low-impact seismic lines were not present within all individual's home ranges (n=7 in summer and 4 in winter), but were in dense grids when present.

Of the wolves exposed to low-impact seismic lines in summer, 43% avoided these features and only 29% selected them (Table 2).

In addition, 82% of the wolves that were exposed to conventional seismic lines in winter selected these features (Table 2). Selection of pipelines and roads was less consistent than conventional seismic lines. Of the 9 wolves that were exposed to pipelines, 67% selected them (Table 2), whereas 75% of the 8 wolves exposed to roads in the winter selected roads (Table 2). While only 3 wolves were exposed to railways in the winter, 100% selected these features. Likewise, 2 of the 3 wolves exposed to transmission lines showed selection. All 4 of the wolves exposed to low-impact seismic lines in winter selected them more than the surrounding forest. No wolves that were exposed to low-impact seismic lines, conventional seismic lines, pipelines, railways, roads or transmission lines in winter avoided those features. Wolf selection of trails was inconsistent, with 45% of wolves showing no response, 36% selecting trails and 18% avoiding trails.

With landcover type controlled for, wolves, on average, selected each linear feature class more than the surrounding forest, with the exception of low-impact seismic, in the summer (Table 3). In summer railways were more strongly selected than other feature classes. The odds of wolves selecting railways were 6.3× higher than the surrounding forest, on average. Conventional seismic lines, pipelines, trails, roads and transmission lines were similarly selected more than surrounding forest. On average, the odds of wolves selecting conventional seismic lines, pipelines, trails, roads and transmission lines were approximately 2× higher than the surrounding forest when landcover was controlled for.

In winter wolves, on average, selected each linear feature class more than the surrounding forest, with the exception of trails once landcover was controlled for. However, the magnitude of selection was more variable among feature classes in winter than summer. In winter roads, railways and transmission lines were all strongly selected relative to other features (Table 3). On average, the odds of wolves selecting these feature types in winter was approximately 3, 4 and 8 × higher than the surrounding forest when landcover type was controlled for. The odds of wolves selecting conventional seismic lines and pipelines were approximately 2× higher than the surrounding forest on average when landcover type was controlled for. Wolves selected low-impact seismic lines more than the surrounding forest during the winter; however the magnitude of selection was smaller than for other feature classes (Table 3). On average, the odds of wolves selecting low-impact seismic lines were approximately 1.2× higher than the surrounding forest when landcover type was controlled for.

DO WOLVES TRAVEL FASTER ON LINEAR FEATURES?

I identified 49 239 5-minute travelling steps from 20 wolves in 6 packs in the summer of 2013 and 2014 and 21 826 travelling steps from 13 wolves in 6 packs in the winter of 2014. All wolves used every linear feature class that was available in their home range for travelling movements.

The magnitude of effect of linear feature class on wolf travelling speed varied among linear feature classes (Fig. 4). When landcover was controlled for, wolves travelled on average 1.25× faster on trails, 2× faster on conventional seismic lines, pipelines, railways and transmission lines, as well as 3× faster on roads compared to the surrounding forest during summer (Table 4). Conversely, wolves travelled 31% slower, corresponding to an average speed of 0.98 km/hr, on low-impact seismic lines than surrounding forest. In winter, wolves travelled 2× faster on conventional seismic lines, pipelines and railways compared to surrounding forest, as well as 3× faster on roads. Alternatively, wolves travelling on low-impact seismic and transmission lines moved 53% (a speed of 0.64 km/hr) and 48 % (a speed of 0.70 km/hr) slower than in surrounding forests, respectively controlling for landcover (Table 4).

While wolves travelled faster on linear features than the surrounding forest on average, some steps classified as in surrounding forest had fast travelling speeds as well (Fig. 4). Long movements in the surrounding forest were often associated with movements slightly off of linear features, where most, but not all, of the step was contained by the linear feature buffer. I classified these steps as in the surrounding forest instead of on linear features because it was impossible to determine if it was classification error, if it was due to GPS location errors, or if the wolf was travelling alongside linear features. However, this is a conservative approach as it would underestimate the difference between linear features and surrounding forest.

DOES INCREASED USE OF LINEAR FEATURES INCREASE DAILY MOVEMENTS?

During summer, I identified 721 wolf days from 20 wolves in 6 packs, 451 of which had over 200 GPS locations to calculate total daily distance. During the winter season, I identified 298 wolf days from 13 wolves in 6 packs, 274 of which had over 200 GPS locations to calculate total daily distance. The average travelling speed of wolves varied greatly on linear features (range: 0.22 - 15.02 km/hr), total distance moved per day (range: 0.96 - 70.4 km) and the proportion of steps spent travelling on linear features per day (range: 0.00 - 0.15).

As the average daily travelling speed on linear features increased, the total distance moved per wolf per day significantly increased in summer ($\beta = 0.112$, SE = 0.013, $P < 0.001$; Fig. 5) and winter ($\beta = 0.174$, SE = 0.020, $P < 0.001$; Fig. 5). A1-km/hr increase in wolf travelling speed while moving on linear features corresponded to a 12% and 19% increase in total distance moved per day in summer and winter, respectively. For example, if wolves were travelling on average 5 km/hr on linear features in a day, the total distance they moved in a day increased by 10 km or 14 km in summer and winter, respectively. In both seasons variation attributed to the mixed effects was minimal, however there was higher variation among individuals within the same pack (SD = 0.047 in summer, SD = 0.003 in winter) than among packs (SD < 0.001 in summer, SD < 0.001 in winter).

Increased proportion of travelling steps on linear features was related to an increase in the total distance moved per wolf per day in both summer and winter ($\beta = 10.903$, SE = 1.195, $P < 0.001$ and $\beta = 12.650$, SE=1.621, $P < 0.001$ respectively; Fig. 6). A 1% increase to the number of steps travelling on linear features increased the total distance moved per day by 11% and 13% in summer and winter, respectively. This translates to an increase of approximately 13.7 km and 20.8 km for every hour wolves spent travelling on linear features in the summer and winter, respectively. In both seasons variation attributed to the mixed effects was minimal, however there was higher variation among individuals within the same pack (SD = 0.083 in summer, SD = 0.045 in winter) than among packs (SD = 0.011 in summer, SD < 0.001 in winter).

EFFECT OF LINEAR FEATURE ABUNDANCE AND PHYSICAL STRUCTURE ON SELECTION AND MOVEMENT

DOES WOLF SELECTION OF LINEAR FEATURES DEPEND ON LINEAR FEATURE DENSITY WITHIN THEIR HOME RANGE?

I analysed the effect of linear feature density on wolf selection of linear features using two approaches. First, I evaluated the selection of linear features, averaged across linear feature classes, as a function of the average linear feature density, excluding low-impact seismic lines, in each wolf's home range. Excluding low-impact seismic lines, the average linear feature density in each wolf's home range varied from 0.52 to 3.57 km/km^2. The overall selection of linear features did not depend on the average linear feature density within the wolf's home range in summer (β = -0.007 SE = 0.016, *P* = 0.641) or winter (β = -0.005, SE = 0.016, *P* = 0.760; Fig. 7).

Next, I evaluated whether wolf selection of various linear feature classes depended on the density of that linear feature class within the wolf's home range. When each linear feature class was analysed separately, low-impact seismic lines showed the greatest density range; from 0 to 11.7 km/km^2 (Table 5). Conversely, the densities of railways and transmission lines varied little across the home ranges of wolves, with densities between 0 to 0.12 km/km^2 and 0 to 0.14 km/km^2, respectively (Table 5). When linear feature classes were evaluated separately, only low-impact seismic lines in summer showed a significant relationship between wolf selection and average density of low-impact seismic lines (β = 0.131, SE = 0.048, *P* = 0.040; Table 6). For every increase of 1 km/km^2 of low-impact seismic lines in the wolf's home range, the odds of wolves selecting low-impact seismic lines in the winter increased by 14%. All other linear feature classes showed no significant relationship between wolf selection of linear features and home range linear feature density for each class (Table 6).

DOES WOLF TRAVELLING SPEED ON LINEAR FEATURES DIFFER BETWEEN UPLANDS AND WETLANDS?

Of the travelling steps, 8197 were classified as completely within uplands (n = 27109) or wetlands (n = 11088). Of these steps, 5% were classified as on linear features.

Regardless of whether linear features were in uplands or wetlands, wolves travelled significantly faster on linear features than off linear features in both summer (β = 0.728, SE = 0.025, *P* < 0.001; Table 7; Fig. 8) and winter (β = 0.293, SE = 0.037, *P* < 0.001; Table 7; Fig. 8). When comparing movements completely within either uplands or wetlands, wolves travelled 2.07 × and 1.34× faster on linear features in summer and winter, respectively. In addition, wolves travelled significantly slower in wetlands than uplands, regardless of whether they were travelling on or off linear features in summer (β = -0.135, SE = 0.012, *P* < 0.001; Table 7; Fig. 8) and winter (β = -0.095, SE = 0.018, *P* < 0.001; Table 7; Fig. 8). Wolves travelled 13% and 9% slower in wetlands than uplands in summer and winter, respectively.

Linear features in uplands increased wolf travelling speed relative to surrounding forest more than did linear features in wetlands during summer, as shown by the interaction between linear feature and uplands vs. wetlands (Table 7; Fig. 8). However, the interaction was only marginally significant (β = -0.144, SE = 0.076, *P* = 0.057). In contrast, linear features increased speed relative to surrounding forest 1.33× more in wetlands than uplands in winter (β = 0.286, SE = 0.070, *P* <0.001; Table 7; Fig. 8). Individuals within the same pack showed more variation (SD = 0.044; SD = 0.030 in summer and winter, respectively) than among packs (SD = 0.002; SD = 0.027 in summer and winter, respectively).

DOES VEGETATION REGROWTH AFFECT WOLF SELECTION AND MOVEMENT ON LINEAR FEATURES?

I obtained 8 190 locations on linear features from 9 wolves in 3 packs from the summer of 2013 and 2014 in which there were data for both vegetation height and linear feature class In addition, I obtained 9 155 locations from 4 wolves in 3 packs from the winter months of 2014. The number of wolves collared per pack for the height analyses varied between 1 to 5 individuals per pack in summer, and 1 to 3 individuals per pack in winter. The vegetation height on linear features in which wolves were located varied greatly, with height ranging from 0 to 28 m. Tall height values, such as 28 m, often correspond to the edges of linear features. On these edges, tree crowns extended onto the linear features from surrounding forest despite having cleared understories, which artificially increases height values. These values were rare, but linear feature revegetation corresponding to large height values should be interpreted with caution.

When individual wolves were averaged for population level inferences, wolves selected areas on linear features with shorter vegetation in summer once landcover and feature class were controlled for (Table 8). However, with every 1-m increase to vegetation height, the odds of wolves selecting that area of linear feature decreased by only 4%. In addition, 8 of the 9 wolves avoided areas on linear features with increased vegetation, but only 2 were significant ($\beta = -0.059$, SE = 0.015 and $\beta = -0.056$, SE = 0.018). In winter wolves did not select areas on linear features with shorter vegetation, on average, once linear feature class and landcover were controlled for (Table 8). However, 2 of the 4 wolves showed significant selection for shorter vegetation ($\beta = -0.022$, SE = 0.008 and $\beta = -0.054$, SE = 0.021).

I identified 1 417, 5-minute travelling steps on linear features from 12 wolves in 3 packs from the summer months of 2013 and 2014 in which height data were available. In addition, I identified 1 235, 5-minute travelling steps from 4 wolves in 2 packs from the winter months of 2014. The linear weighted mean vegetation height varied greatly among wolf travelling steps, with height ranging from 0 to 28 m. In both seasons, the height category with the fewest steps was 1-2 m, whereas the rest of the height categories had relatively equal representation (Fig. 9).

Compared to linear features with vegetation heights less than 1 m, wolves moved 24% and 13% slower when vegetation reached 1 - 2 m and 2 - 5 m, respectively, in summer. In addition, wolves moved 27% slower when vegetation exceeded 5 m (Table 9, Fig. 10). However, wolves moved 20 % faster when vegetation was 1 - 2 m tall compared to linear features with vegetation heights less than 1 m in winter (Table 9, Fig. 10). In winter, wolves did not move slower on linear features with taller vegetation until they exceeded 5 m. However, wolves travelled on average 44 % slower once vegetation exceeded 5 m in winter, which is a drastic reduction compared to linear features with vegetation heights of less than 1 m (Table 9, Fig. 10). There was higher variation among individuals within the same pack (SD = 0.423 in summer, SD = 0.221 in winter) than among packs (SD = 0.088 in summer, SD= 0.141 in winter).

DISCUSSION

My research estimated how wolf resource selection and movement were affected by different types of linear features. Specifically, I predicted that if linear features function to increase the effectiveness of wolves at finding their prey, wolves would select linear features, move faster on linear features, and increase daily movements when they spent more time on linear features. I used 5-minute GPS data to directly compare movements along linear features to movements in the forest, and determine if fine-scale movements between consecutive locations translated to increased distance moved in a day. This study provides empirical evidence that wolves selected linear features, and linear features increase wolf movement. While previous studies have shown that linear features influence wolf selection and movement (James & Stuart-Smith 2000; Latham *et al.* 2011a; McKenzie *et al.* 2012), I showed that wolves travelled faster on linear features, and this increased overall daily distance travelled. Increased travelling speeds on linear features, as well as increased net daily movement, suggests that linear features function to increase wolf search rate. If increased net search rates lead to an increase in the instantaneous search rate, and wolves are not limited by handling time, linear features may increase kill rates (Holling 1959b).

The second goal of my research was to determine how managers can use linear feature variation to optimize restoration efforts. My study is the first to evaluate and discuss how wolf selection and movement on linear features was affected by abundance and physical structure to inform policy and optimize restoration activities. I predicted that wolves would increase the magnitude of linear feature selection when linear feature density was low, that whether linear features traversed uplands or wetlands would influence the relative increase in travelling speed on linear features compared to surrounding forest, and that wolves would show decreased selection and movement rates on linear features with more vegetation regrowth. I showed that wolf selection for linear features did not depend on the density within their home range, the magnitude in which linear features increased travelling speed relative to the surrounding forest depended on whether the feature traversed uplands or wetlands, wolves selected areas on linear features with shorter vegetation, and movement rates on linear features decreased with increased vegetation height. Overall these results suggest that differences in linear feature abundance and physical structure influence the response of wolves to these features. Below, I provide suggestions on how these differences can be used to optimize restoration activities.

WOLF SELECTION AND MOVEMENT ON LINEAR FEATURES

Wolves selected nearly all linear feature classes more than the surrounding forest when landcover was controlled for, suggesting an attraction to linear features (Thurber *et al.* 1994; James & Stuart-Smith 2000; Whittington, St. Clair & Mercer 2005). Differences in the magnitude of wolf selection could be associated with the physical structure of the linear feature as well as human disturbance (Thurber *et al.* 1994). Of all the linear feature classes, wolves selected railways the most compared to the surrounding forest, and transmission lines the most in winter. These features may provide easy travelling for wolves because they are long, straight and consistently cleared of obstruction. Wolves also tended to strongly select roads compared to the surrounding forest, which are also consistently cleared for human use. However higher traffic volume and human disturbance may make these features less attractive to wolves (Thurber *et al.* 1994). The selection of conventional seismic and pipelines by wolves was similar, and was less than railways. Both feature classes are long, straight corridors that are not kept cleared of obstruction, are not often used by humans, and are moderately wide. While pipelines are maintained, only part of the corridor is kept as a poorly maintained trail while the rest can be left to regenerate. Conventional seismic and pipelines may also saturate the landscape, reducing selection of each individual line. In addition, only low-impact seismic and trails were not selected by wolves, on average. Both of these features are relatively narrow and sinuous, and may make them less beneficial to wolf movement if they do not provide a direct path or hinder line-of-sight while travelling. The differential selection among features that are frequently used by humans and those that are not suggests a trade-off between the advantage of facilitating movement and avoidance of humans (Thurber *et al.* 1994; Muhly *et al.* 2011; Ciuti *et al.* 2012). While the influence of intensity of human use on wolf behaviour and habitat selection has been studied (Hebblewhite *et al.* 2005; Hebblewhite & Merrill 2008), the interaction between wolf selection of each feature and human use remains unaddressed.

In addition, linear features substantially increased travelling speed compared to the surrounding forest, suggesting linear features benefit wolf movement (Latham *et al.* 2011a; McKenzie *et al.* 2012). In both summer and winter, wolves travelled three times faster on roads than surrounding forest, and two times faster on conventional seismic lines, pipelines and railway. Wolves also travelled two times faster on transmission lines in summer. Trails and transmission lines provided less of a benefit to wolf movement. While wolves travelled faster on trails relative to surrounding forest in summer, wolf travelling speed increased by only 30 percent. In winter, wolves on average travelled at the same rate on trails as in the surrounding forest. Wolves travelled faster on transmission lines compared to the surrounding forest in the summer, but slower in winter. Lastly, wolves travelling on low-impact seismic travelled slower than in surrounding forest in both summer and winter. Linear feature classes that increase travelling speed of wolves also tended to be selected by wolves; in summer the only linear feature class that was not selected by wolves, low-impact seismic lines, was the only feature that decreased wolf movement rates. This suggests that wolves may be selecting linear features because they increase movement rates. However, wolves selected low-impact seismic lines and transmission lines even though they decreased movement rates. This suggests that there may be other mechanisms for wolf selection of linear features secondary to increased movement.

The relationship between selection and increased travelling speed was less apparent in winter than summer, and the increase in wolf travelling speed tended to be less in winter. Previous work has also found reduced effects of linear features on wolf movement in winter (Latham *et al.* 2011a). The effect of linear features on travelling speed in winter could be less important due to the effects of snow compaction and depth. Snow can influence habitat use and movement, and can provide resistance to animal movement if deep and non-compacted (Fuller 1991; Huggard 1993; Metz *et al.* 2012). Changes to prey distribution, diet differences, as well as movement behaviour differences between seasons may also change linear feature use in winter (Metz *et al.* 2011). Wolves tend to hunt large bodied prey such as ungulates in the winter (Metz *et al.* 2012), whereas in summer smaller prey, such as deer and beaver, constitute a higher proportion of their diet (Latham *et al.* 2011b). If wolves are eating smaller meals more frequently, facilitated movement via linear features may become more important as the ratio of search time to handling time increases, placing a premium on speed to find prey. In addition, linear features may provide wolves with a path of lower resistance during directional movements to and from the den during the denning period (i.e. summer). In contrast, in winter wolves may be concentrating their efforts on hunting or moving among habitats with high prey availability in an attempt to conserve energy (Metz *et al.* 2012).

When evaluating the relative importance of various linear feature classes on wolf selection and movement, it is important to consider how ubiquitous these features are across the landscape. First, even if wolf selection and movement was strongly influenced by a specific linear feature class, it may not have broad-scale implications to prey populations if that feature class is rare. For example, while wolves strongly selected railways and transmission lines, only wolves from two packs were exposed to these features. Conversely, conventional seismic lines, pipelines, roads and trails were available to all wolves, and may have an overall larger effect on wolf movement. Second, analysing a small sample of wolves decreases the confidence associated with making inferences about these features. Inferences pertaining to abundant landscape features, such as conventional seismic, pipelines, trails and roads are more robust than those that are rare.

My results also suggest that wolf use of linear features is linked to the instantaneous search rate of predators. Both average travelling speed while moving on linear features and increased proportion of travelling steps on linear features increased net daily distance moved. All else being equal, an increase to the instantaneous search rate could increase encounter rates with prey. Therefore, linear features have the potential to increase kill rates (Holling 1959b; Fryxell *et al.* 2007). While increased travelling speed associated with linear features has been shown before (James & Stuart-Smith 2000; Latham *et al.* 2011a; McKenzie *et al.* 2012; McPhee, Webb & Merrill 2012) my study is the first to directly link increased short-term movements to daily search rates.

However, increased daily distance travelled does not provide a direct link to kill rates. Increased distance move could result in three possible outcomes. First, linear features may facilitate movement leading to increased instantaneous search rate, thereby increasing kill rates as expected by the functional response (Holling 1959b). While this has been suggested using simulations (McKenzie *et al.* 2012), it has yet to be tested empirically. Alternatively, linear features may facilitate movement, thereby increasing instantaneous search rate without increasing kill rates if prey saturate the landscape and wolves are on the asymptote of the type II functional response (Holling 1959b). Instead of increasing kill rates, wolves may conserve energy or devote time to other behaviours (Mech & Boitani 2003; Giuggioli, Potts & Harris 2011). Lastly, linear features may facilitate movement allowing wolves to become more efficient at behaviours such as territory monitoring, travelling to and from rendez-vous sites, among habitat patches, or to and from den sites, without directly influencing hunting behaviours (Mech & Boitani 2003; Tsunoda *et al.* 2009; Giuggioli, Potts & Harris 2011). Previous work attempting to make a link between search area and kill rates found that daily kill rate was not related to daily area in which packs traveled, however their definition of daily area searched was extremely course (Hayes *et al.* 2000). Without visiting clusters of GPS locations and conducting kill site investigations, it is not possible to directly investigate the relationship between linear features and kill rates. I suggest that the results from my study, along with simulations (McKenzie *et al.* 2012), call for a detailed kill site investigation to relate the time spent on linear features to wolf kill rates in summer and winter seasons (Webb, Hebblewhite & Merrill 2008; Merrill *et al.* 2010).

The effect of linear features on wolf movement and hunting behaviours could be confounded with prey densities. Prey abundance and densities across the landscape could be influenced by the density of linear features or other human disturbances associated with oil and gas exploration. For example, recently disturbed areas may increase early-seral food availability, thereby increasing deer and moose densities (Serrouya *et al.* 2011). If prey densities are high in areas of high human disturbance, increases in the instantaneous search rate of wolves could be compounded by increases in prey densities in areas of high linear feature densities, as suggested by previous simulations (McKenzie *et al.* 2012). Alternatively, prey density may be low in areas of dense linear features, for example because of increased mortalities or avoidance of human activity (see Fahrig & Rytwinski 2009 for review). If prey densities are low in areas of high disturbance, increases in per capita kill rates due to increased search rates may be minimal compared to decreased kill rates due to low prey densities. However, linear features as well as other disturbances related to oil and gas exploration make up a small proportion of the overall landscape in northern Alberta, thereby having minimal affects on overall food availability. As such, large scale responses to linear feature densities are unlikely to occur. While it has been noted that the abundance of white-tailed deer has increased with increasing human disturbance (Latham *et al.* 2011b; Fisher et al, *unpublished data*), this has been contributed to northern range expansion due to climate change (Dawe, Bayne & Boutin 2014). Furthermore, when prey densities are low the instantaneous search rate is more important than at high densities, because handling time is not limiting (Holling 1959b). Prey densities are a key component of per capita kill rates (Holling 1959b), and should be considered when making inferences about the effect of linear features.

In addition to changes in prey densities, prey could respond to linear features by selecting or avoiding linear features within their home ranges, influencing prey distribution. Some prey species such as moose have been found to select linear features such as roads (Rea 2003; Berger 2007). If prey place home ranges close to linear features, or select linear features within their home range, local prey densities would be inflated near these features. Kill rates may therefore increase disproportionately because of high wolf selection along these features. Conversely, some prey such as woodland caribou have been found to avoid human disturbances such as linear features (James & Stuart-Smith 2000; Dyer *et al.* 2001). If prey avoid linear features, local prey densities would be deflated near linear features relative to surrounding undisturbed forest. Therefore, increased wolf selection and movement of linear features may result in concentrated hunting efforts in these small areas, leading to no increases in kill rates if wolves miss their prey. However, as suggested by Dyer *et al.* (2001), even if prey such as caribou avoid linear features, predation rates may increase if prey species that are more dominant in wolf diets, such as moose and deer (Latham *et al.* 2011b), select linear features. This is because increased kill rates of more dominant prey may lead to an increase in reproductive output, or numerical response (Holling 1959a), leading to higher wolf densities. Furthermore, as the density of linear features increases, it becomes increasingly difficult for prey to avoid these features. It is crucial to determine how linear features affect both the density and distribution of prey species, and how these changes interact with linear feature use by wolves. As such, the inclusion of prey densities of multiple prey species in future kill-rate analyses is necessary.

EFFECT OF LINEAR FEATURE ABUNDANCE AND PHYSICAL STRUCTURE ON SELECTION AND MOVEMENT

Contrary to my prediction, line density was not related to the linear features selection, suggesting the preference of linear features was not conditional on their availability (Mysterud & Ims 1998). The lack of a relationship between selection and linear feature density held true for all linear feature classes separately, as well as all linear features considered together. Wolf selection of linear feature features depended on linear feature density for only low-impact seismic lines in summer. However the significant effect was largely driven by one wolf who strongly avoided low-impact seismic lines which were rare in the wolf's home range. This may suggest that wolves do not seek out linear features when they are rare, but instead take advantage of them when present. In addition, wolves may use specific linear features they are familiar with as travel corridors. Previous work has suggested that a functional response to human activity by wolves is possible (Whittington, St. Clair & Mercer 2005; Hebblewhite & Merrill 2008). However, my results support the suggestion by Hebblewhite and Merrill (2008) that the density of linear features may be less important than the level of human activity on those features. Additionally, my study area has high linear feature density, with few wolves being exposed to low overall linear feature densities, which may hamper my ability to identify strong selection at low densities.

While wolves moved faster on linear features than in surrounding forests, the effect of linear features on wolf travelling speed depended on whether the linear feature traversed uplands or wetlands. In addition, this interaction differed by season. In summer, linear features in uplands increased movement rates relative to surrounding forest more than linear features in wetlands. If the limiting factor to movement is dense vegetation, linear features through upland forests would be more beneficial to travelling wolves compared to features in sparsely vegetated wetlands (Beckingham & Archibald 1996). Limitations to movement in wetlands is more likely due to unstable substrates because of wetness (Beckingham & Archibald 1996). It is unlikely that linear features change wetness in a way that would influence wolves; however linear features may provide a benefit to movement due to flattening of terrain. During the winter, linear features in wetlands increased movement rates relative to surrounding forest more than did linear features in uplands. This was largely caused by decreased travelling speeds on linear features in uplands. Linear features in uplands may be less beneficial in winter than they are in summer due to snow constraints on wolf movement (Fuller 1991). Dense canopies provide refuge from deep snow, and areas in uplands with less vegetation cover, such as linear features, may be detrimental to movement. The benefit of wetlands to movement in the winter likely stems from flattened terrain from the construction process, thereby providing more stable paths with little vegetation impediment. These results suggest that the habitat in which linear features are created in should be considered when planning restoration activities. Managers may be able to optimize restoration by targeting features that provide more of a benefit to wolf movement depending on their conservation goals.

As predicted, wolves on average selected areas on linear features with shorter vegetation. All but one wolf selected areas on linear features with shorter vegetation, however only two wolves showed significant selection. Average wolf travelling speed also decreased with increased vegetation height in summer. In addition, while wolves still travelled on linear features with taller vegetation, they moved slower on them. These results suggest that the revegetation of linear features reduces the benefit of linear features to wolf movement. Contrary to predictions, in winter wolves did not select areas on linear features with shorter vegetation on. Wolves also did not move slower on linear features until vegetation height exceeded 5 m in winter, and they even moved faster on linear features with minimal vegetation heights (1 - 2 m). The lack of evidence for wolves selecting shorter vegetation in winter suggests that difficulties associated with snow conditions may outweigh the benefits of travelling on linear features. Travelling on sections of linear features with some vegetation regrowth, rather than non-vegetated linear features, may improve movement through snow. This is consistent with changes in wolf behaviour and hunting due to snow (Nelson & Mech 1986; Fuller 1991; Huggard 1993). However, results also suggest the barriers to movement imposed by vegetation exceeding 5 m were greater than the cost of travelling in poor snow conditions.

While I have shown vegetation height has the capacity to influence wolf selection and movement, I expected selection and movement to decrease more substantially. The odds of wolves selecting that area of the linear feature decreased by only 2% when height increased by 1 m. In addition, most linear features increased movement rates by 2-3×, but only vegetation exceeding 5 m in winter slowed wolf movements to speeds similar to that of surrounding forests. Vegetation regeneration in my study area may have been insufficient to detect large changes to wolf selection and movement. Less than a third of wolf movements were classified as occurring on features with greater than 5 m in summer and winter, respectively. Linear features in northern Alberta are persistent on the landscape, and recovery of linear features can depend heavily on many factors (Lee & Boutin 2006). If managers want to restore linear features to a point in which they no longer provide movement benefits to wolves, it is important to understand the current state of the regeneration on the landscape. How habitat, feature construction, and linear feature age relate to regrowth of linear features to a level in which wolves no longer use them should also be considered.

Increasing technologies, including GPS collars with longer battery lives that send data remotely and high resolution imagery such as LiDAR, have opened promising doors for management. However, even the fine-scale data sets used in this study had issues that impeded my ability to draw conclusions about wolf selection and movement on linear features. First, while LiDAR has the ability to map vegetation data with accuracy and precision never seen before, the scale of these data does not often match with other data. I used 5-minute wolf relocations to measure habitat use and movement, which is an improvement over fix rates in previous studies (Merrill *et al.* 2010; Latham *et al.* 2011a; McPhee, Webb & Merrill 2012; but see McKenzie *et al.* 2012). However, the inability to know precise movement paths and possible GPS-location error hindered my ability to make inferences using LiDAR. In addition to the mismatch of data resolution, there were issues with characterising data obtained from LiDAR. I used LiDAR to estimate canopy heights on linear features. While the data were ground truthed, and small differences in vegetation heights could be measured, crown closure at forest edges may have been problematic in defining linear feature boundaries. For example, if wolves travelled on the edge of linear features vegetation heights could be artificially increased if branches hung over from surrounding forest. In addition, areas with tall vegetation may have small trails underneath, allowing easy movement along the feature, which may go undetected. While more sophisticated data processing and analysis can deal with some of these issues, they should be considered when making inferences or designing future studies.

Remote sensing methods such as LiDAR also have a trade-off between providing high resolution data and providing data for a large extent. Landscape patterns and processes, such as vegetation heterogeneity, operate at multiple scales, and how we choose to measure these patterns and processes can influence our inferences (Schneider 2001; Turner, Gardner & O`Neill 2001; Wu 2004). While LiDAR provided fine-grain data that allowed fine-scale selection and movement analyses, vegetation data were only available for a small number of wolves. This impeded my ability to make population level inferences similar to those in other analyses. However, other studies on the effect of linear features on wolf movement have been restricted to a similar number of individuals (McKenzie *et al.* 2012). While using individual models allowed me to examine whether individuals selected areas on linear features with shorter vegetation, and whether individuals were consistent in their selection, averaging individual models and bootstrapping confidence intervals with small sample sizes can be problematic (Chernick 2007). Care is needed when interpreting these fine-scale analyses and it is important to consider individual responses when making inferences about populations.

My study uses vegetation height as a proxy for vegetation regrowth. However, if vegetation impediment is the mechanism for increased movement on linear features, other factors such as vegetation cover and stem density are more likely to be important to wolf movement. To my knowledge this is the first study that has evaluated the relationship between vegetation and movement on linear features, however more work needs to be conducted to determine the mechanistic barriers to movement. LiDAR has the potential to answer some of these questions, and should be used to its full potential in subsequent studies.

MANAGEMENT IMPLICATIONS

My results have implications for the optimization of linear feature restoration to mitigate the effects of linear features on wolf movement. Fine-scale movements in relation to different linear feature classes have not been previously addressed. If managers aim to functionally restore linear features from the perspective of wolf use and movement, it is important to note that wolves do not select all linear features equally, and not all linear features affect wolf movement equally. While railways, transmission lines and roads were selected the most by wolves and strongly increased travelling speed, it is unrealistic to mitigate these features. Of the features that can realistically be restored, i.e. trails, pipelines, conventional seismic lines and low-impact seismic lines, my results suggest that conventional seismic lines and pipelines should be prioritized. Both these feature classes were strongly selected by wolves, though conventional seismic lines were selected more consistently by individuals. In addition, both of these features increased travelling speed in summer and winter. Conversely, low-impact seismic lines and trails were inconsistently selected, and did not always increase movement. While railways, transmission lines and roads cannot realistically be removed from the landscape, they should be considered during the restoration process. Intensive restoration activities in proximity to permanent linear features may be sub-optimal if wolves are still able to use features that strongly influenced selection and movement.

My results also suggest that the abundance of linear features and whether linear features traverse through uplands or wetlands can further optimize linear feature restoration. While the density of linear features did not affect wolf selection of linear features, no pristine landscapes were present in this study area. Thus, I recommend that low-density areas should be targeted first. By targeting low-density areas, the same amount of effort by managers will functionally restore an entire section of the landscape, rather than lowering only the density of linear features. In addition, whether linear features traverse through uplands or wetlands should be considered depending on management goals. If managers are primarily concerned about woodland caribou calf mortality, which occurs in the summer season, linear features in uplands should be targeted for reclamation activities. While caribou are not found in uplands, targeting upland linear features would slow their overall movements, decreasing net daily movement. Conversely, management could strive to decrease overall wolf kill rates in winter, when adult ungulates are vulnerable due to snow and limited foraging (Nelson & Mech 1986; Fuller 1991). In this case, targeting linear features in wetlands would be optimal, because they provide increased benefits to travelling speed relative to upland linear features.

While federal recovery guidelines have specified a threshold of 65% undisturbed habitat in individual caribou ranges (Environment Canada 2012), there are no criteria to define what constitutes a restored linear feature. My study suggests that to functionally restore linear features from the perspective of wolves, linear features should be restored to a height beyond 5 m to reduce wolf travelling speed in both seasons. Minimal vegetation (1 - 2 m tall) decreased wolf movement by 23% in summer, and wolf movement further decreased by only 4% when vegetation exceeded 5 m. However, in winter the travelling speed of wolves increased when vegetation was 1 - 2 m tall compared to 0 - 1 m. Vegetation heights exceeding 5 m were required to slow wolf movements, however travelling speeds decreased to nearly the same as average travelling speed in surrounding forests. This study provides recommendations for restoring linear features for wolf use and movement; however it is important to consider when linear features become functionally restored habitat for woodland caribou.

Table 1: Average width (m), standard error and buffer distances (m) used to buffer linear features based for each linear feature class. Linear features were measured to the nearest 2.5 m. Buffers were applied to either side of hand digitized linear features.

Class	**Average (m)**	**SE**	**Buffer (m)**
Low-impact Seismic	7	1.00	7.5
Conventional Seismic	10	0.54	10
Trail	12	0.70	12.5
Pipeline	20	2.94	20
Road	30	6.87	30
Railway	30	4.65	30
Transmission Line	37	6.43	37.5

Table 2: The percent of wolves that selected, avoided, or were neutral to each linear feature class in summer and winter. The total number of individuals analysed for each feature class are shown for reference. Conditional logistic regression was used to model the odds of selecting each linear feature class compared to surrounding forest, while controlling for landcover. The reference categories for landcover and linear features class were coniferous forest and off linear features (i.e. surrounding forest), respectively. Avoidance or selection was defined as estimates with confidence intervals that did not overlap zero.

	Summer				Winter			
Feature Class	**Select (%)**	**Neutral (%)**	**Avoid (%)**	**Total (#)**	**Select (%)**	**Neutral (%)**	**Avoid (%)**	**Total (#)**
Low-impact seismic	29	29	43	7	100	0	0	4
Conventional seismic	75	25	0	20	82	18	0	11
Pipeline	53	42	5	19	67	33	0	9
Trail	60	35	5	20	36	45	18	11
Railway	83	17	0	6	100	0	0	3
Road	61	39	0	18	75	25	0	8
Transmission line	83	17	0	6	67	33	0	3

Table 3: Mean wolf selection coefficients and bootstrapped 95% confidence intervals of landcover and linear features for summer and winter. Individuals were modelled separately using conditional logistic regression and then averaged for each covariate for population level inferences. Individual coefficients were weighted by their standard error. The number of individuals used to average each coefficient is displayed as N. Reference categories for landcover and linear features class were coniferous forest and off linear features (i.e. surrounding forest) respectively.

Variable	Summer				Winter			
	N	Estimate	CI (-/+)		N	Estimate	CI (-/+)	
Deciduous	20	0.002	-0.353	0.295	11	0.015	-0.148	0.225
Mixedwood	20	-0.087	-0.359	0.166	11	0.278	-0.021	0.522
Other	20	-0.780	-1.251	-0.405	11	-0.148	-0.388	0.049
Wetland	20	-0.122	-0.466	0.149	11	0.176	0.036	0.378
Conventional Seismic	20	0.609	0.391	0.830	11	0.729	0.512	1.021
Low-impact Seismic	7	0.016	-0.151	0.144	4	0.157	0.128	0.232
Pipeline	19	0.474	0.239	0.682	9	0.614	0.505	0.816
Railway	6	1.837	1.305	2.179	3	1.429	1.134	2.098
Road	18	0.736	0.304	1.405	8	1.065	0.542	1.548
Trail	20	0.813	0.399	1.056	11	0.308	-0.145	0.765
Transmission Line	6	0.750	0.402	1.191	3	2.064	0.825	2.194

Table 4: The effect of linear feature class on wolf travelling speed (km/hr) compared to off linear features (i.e. surrounding forest) for summer and winter. Model estimates, standard error (SE) and p-values are shown for nested mixed-effects models. Satterthwaite approximation was used to calculate p-values.

Variable	Summer			Winter		
	Estimate	SE	p-value	Estimate	SE	p-value
Intercept	0.348	0.046	<0.001	0.308	0.081	0.015
Conventional Seismic	0.770	0.034	<0.001	0.532	0.039	<0.001
Low-impact Seismic	-0.370	0.074	<0.001	-0.755	0.063	<0.001
Pipeline	0.671	0.044	<0.001	0.558	0.042	<0.001
Railway	0.771	0.059	<0.001	0.625	0.021	<0.001
Road	0.955	0.039	<0.001	0.993	0.059	<0.001
Trail	0.227	0.010	0.029	-0.132	0.026	0.618
Transmission Line	0.838	0.073	<0.001	-0.663	0.021	<0.001

Table 5: Mean, minimum and maximum linear feature density (km/km^2), averaged across individual wolves, of each linear feature class for each season. First, the average home range linear feature density was calculated for each linear feature class, for each wolf, using a moving window with a 1-km radius for each wolf's 100 % MCP. The average home range linear feature densities were then averaged across individual wolves that had the linear feature class within their home range.

Feature class	Summer			Winter		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Low-impact seismic	5.050	0.000	13.388	8.882	2.023	11.705
conventional seismic	1.122	0.336	1.811	1.135	0.683	1.590
Pipeline	0.365	0.013	0.875	0.340	0.013	0.763
Trail	0.184	0.019	0.434	0.267	0.034	0.551
Railway	0.080	0.047	0.120	0.103	0.068	0.132
Road	0.153	0.003	0.433	0.199	0.053	0.292
Transmission line	0.096	0.075	0.143	0.069	0.045	0.100

Table 6: The relationship between linear feature selection and density (km/km^2) within each individual wolf's home range, separated by linear feature class. Individual selection coefficients were derived from conditional logistic regressions with coniferous forest and off linear features (i.e. surrounding forest) as reference categories for landcover and linear features class, respectively. Linear feature densities were calculated for each linear feature class separately, for each wolf's 100% MCP.

	Summer			**Winter**		
Feature class	**Estimate**	**SE**	**p-value**	**Estimate**	**SE**	**p-value**
All features combined	-0.007	0.302	0.641	-0.005	0.016	0.760
Low-impact seismic	0.131	0.048	0.040	-0.023	0.006	0.069
Conventional seismic	-0.401	0.295	0.190	-0.081	0.536	0.883
Pipeline	0.121	0.549	0.828	-0.026	0.552	0.964
Trail	-0.074	1.100	0.947	1.005	1.553	0.534
Road	-2.476	1.677	0.159	-4.778	2.251	0.078
Railway	-5.645	13.356	0.694	-13.158	5.928	0.269
Transmission line	-4.215	12.010	0.743	17.826	20.263	0.541

Table 7: Average travelling speed (km/hr) of wolves on and off linear features, compared between uplands and wetlands, in summer and winter. Off linear features (i.e. in surrounding forest) and upland were set as reference categories. Model estimates standard error (SE) and p-values are shown for nested mixed-effects models. Satterthwaite approximation was used to calculate p-values.

	Summer			**Winter**		
Variable	**Estimate**	**SE**	**p-value**	**Estimate**	**SE**	**p-value**
Intercept	1.974	0.052	<0.001	0.119	0.085	0.252
Linear Feature	0.727	0.025	<0.001	0.293	0.037	<0.001
Wetland	-0.135	0.012	<0.001	-0.095	0.018	<0.001
Linear Feature* Wetland	-0.144	0.076	0.057	0.286	0.070	<0.001

Table 8: Wolf selection coefficients of landcover, linear feature class and vegetation height (m) for summer and winter derived from conditional logistic regression. Model estimates were weighted according to their standard error and averaged across individual wolves for each covariate separately to gain population inferences. Sample size (N) and 95 % confidence intervals (CI) derived from bootstrapping are shown. Coniferous forest and conventional seismic lines were set as the landcover and linear feature reference categories, respectively. The analysis was restricted to locations in which feature class and height data were available.

	Summer				Winter			
Variable	Estimate	N	CI (-/+)		Estimate	N	CI (-/+)	
Intercept	0.866	9	0.668	1.051	0.516	4	0.229	0.891
Wetland	-0.190	9	-0.370	0.071	0.230	4	-0.028	0.384
Other	-0.504	9	-0.659	-0.215	-0.156	4	-0.589	0.093
Deciduous	0.180	9	-0.302	0.557	0.408	4	0.203	0.575
Mixedwood	0.479	9	-0.124	0.873	0.177	4	0.012	0.294
Height	-0.044	9	-0.055	-0.028	-0.007	4	-0.026	0.007
Low-Impact Seismic	-1.091	8	-1.279	-0.960	-0.689	4	-0.898	-0.509
Trail	-0.777	8	-1.444	-0.023	-0.680	4	-1.243	-0.129
Pipeline	-0.592	9	-0.836	-0.314	-0.609	4	-0.913	-0.290
Railway	-0.603	3	-0.823	0.033	-	0	-	-
Road	-0.754	9	-0.813	-0.677	-0.377	4	-0.680	-0.156
Transmission Line	-0.940	3	-1.588	-0.650	-	0	-	-

Table 9: The effect of mean vegetation height (m) on wolf travelling speed (km/hr) in summer and winter. Vegetation heights were broken into four categories; < 1 m (cleared linear features), 1 - 2 m (linear features with minimal revegetation), 2 - 5 m (linear features with moderate revegetation) and >5 m (linear features with high revegetation). Model estimates, standard error (SE) and p-values are shown for nested mixed-effects models. Satterthwaite approximation was used to calculate p-values.

Variable	**Summer**			**Winter**		
	Estimate	**SE**	**p-value**	**Estimate**	**SE**	**p-value**
Intercept	1.436	0.141	0.001	0.911	0.150	0.014
1 - 2 m	-0.269	0.087	0.002	0.178	0.871	0.042
2 - 5 m	-0.142	0.069	0.041	0.143	0.073	0.052
>5 m	-0.312	0.074	< 0.001	-0.571	0.077	<0.001

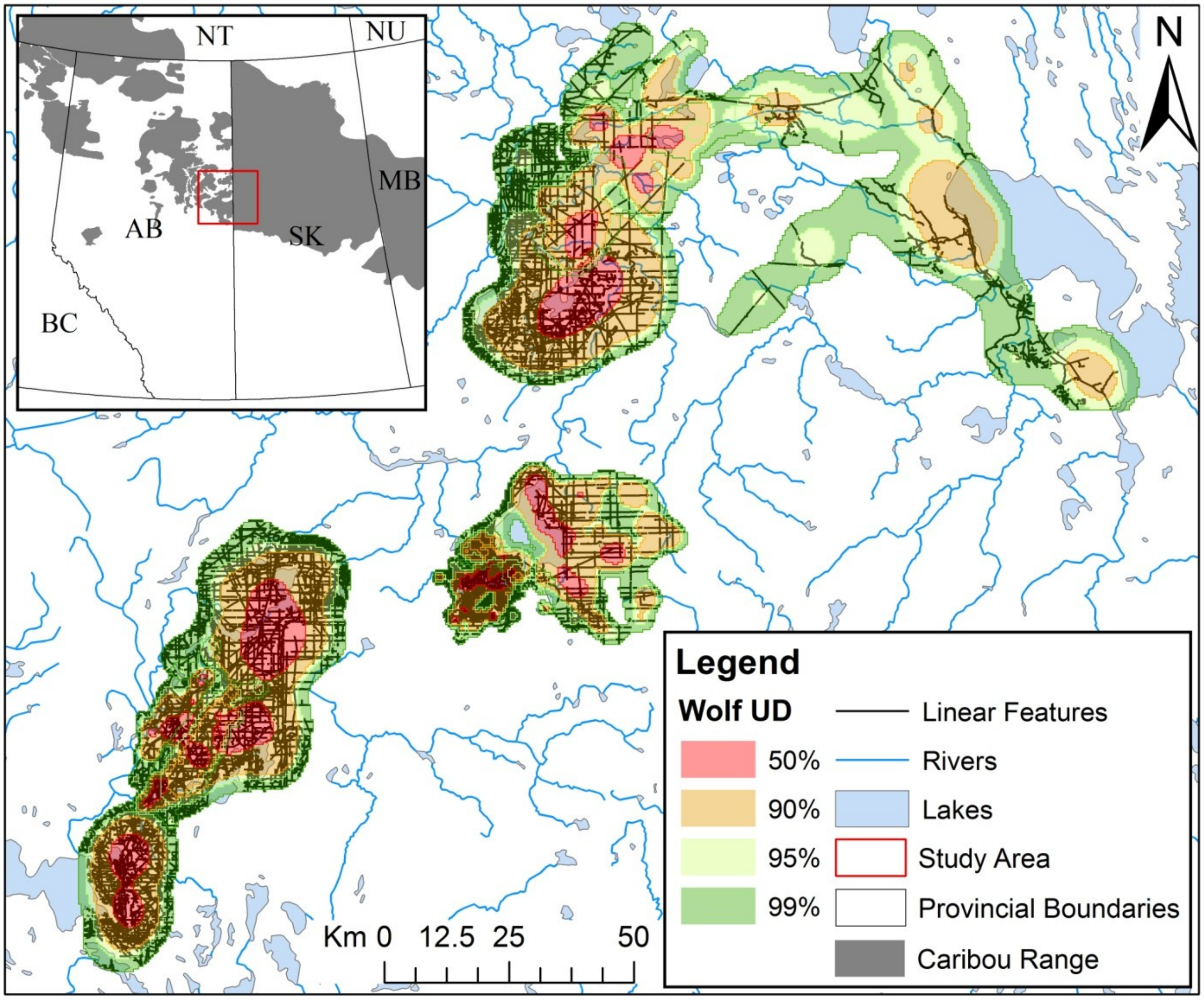

Figure 1: Wolf utilization distributions (50%, 90%, 95% and 99%) from 22 wolves in 6 packs and anthropogenic linear features in northeastern Alberta and northwestern Saskatchewan. For reference, an outline of the general study area, provincial boundaries and caribou ranges are included on a large-scale map of Canada.

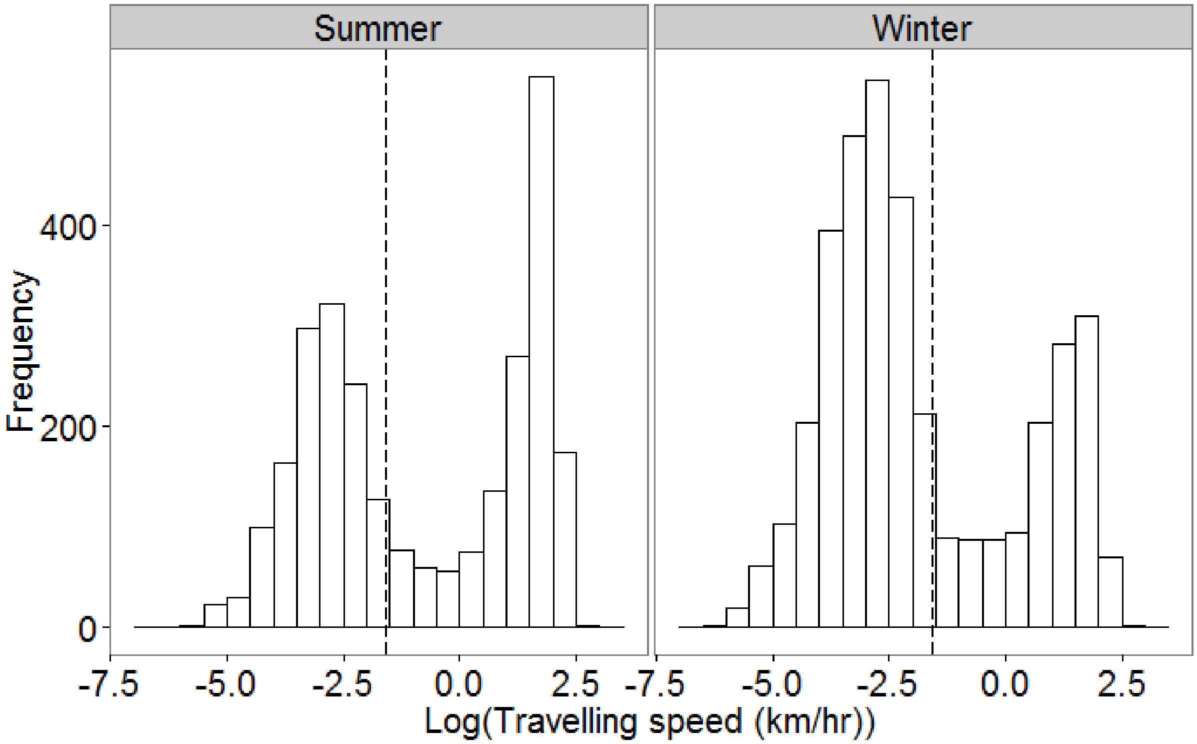

Figure 2: Histogram of log travelling speed (km/hr) of wolves in summer and winter using a 5-minute fix rate. A dotted vertical line represents the calculated breakpoint of 0.21km/hr, corresponding to approximately -1.58. Steps to the left were classified as resting or feeding, whereas steps to the right of the dotted line were classified as travelling movements. Data from 20 wolves from 6 packs in summer and 13 wolves from 6 packs in winter were included.

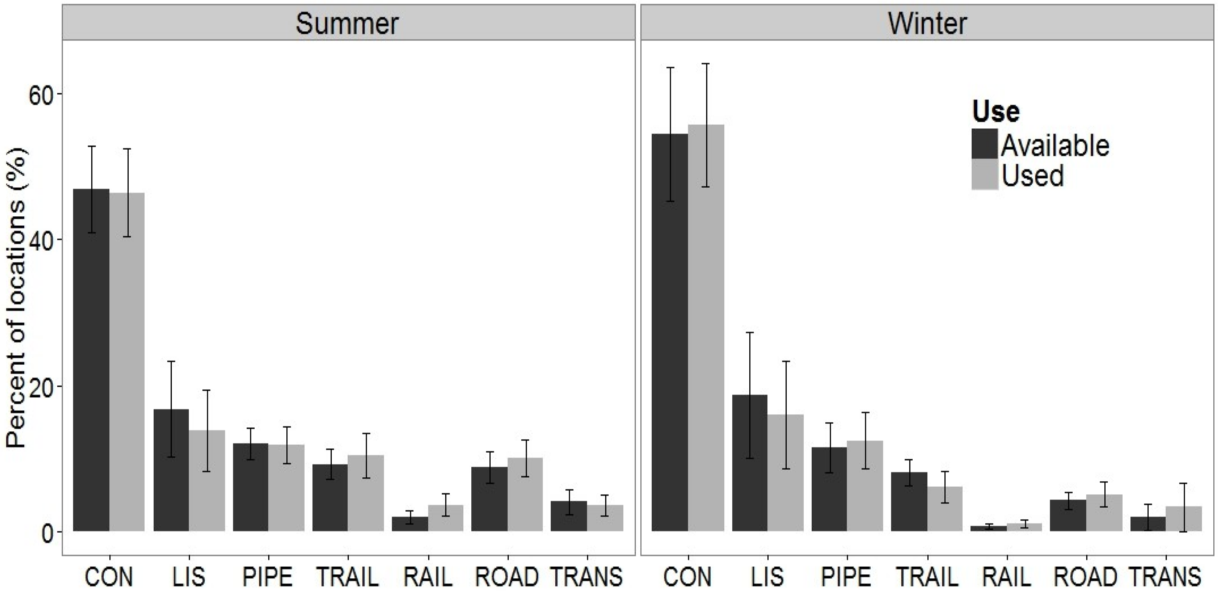

Figure 3: The average percent of used wolf and available locations (%), restricted to linear features in the summer and winter of 2013 and 2014. Available locations were drawn for each GPS location within buffers corresponding to the 90th percentile maximum step length using a five minute fix rate. The proportion of used and available locations, when on linear features, in each class was calculated for each wolf, and then averaged across wolves. Error bars represent standard error of the mean. CON = conventional seismic lines, LIS = Low impact Seismic, PIPE = pipeline, RAIL = railway, ROAD = Roads, TRAIL = trails, TRANS = transmission lines. Data from 20 wolves from 6 packs in summer and 13 wolves from 6 packs in winter were included.

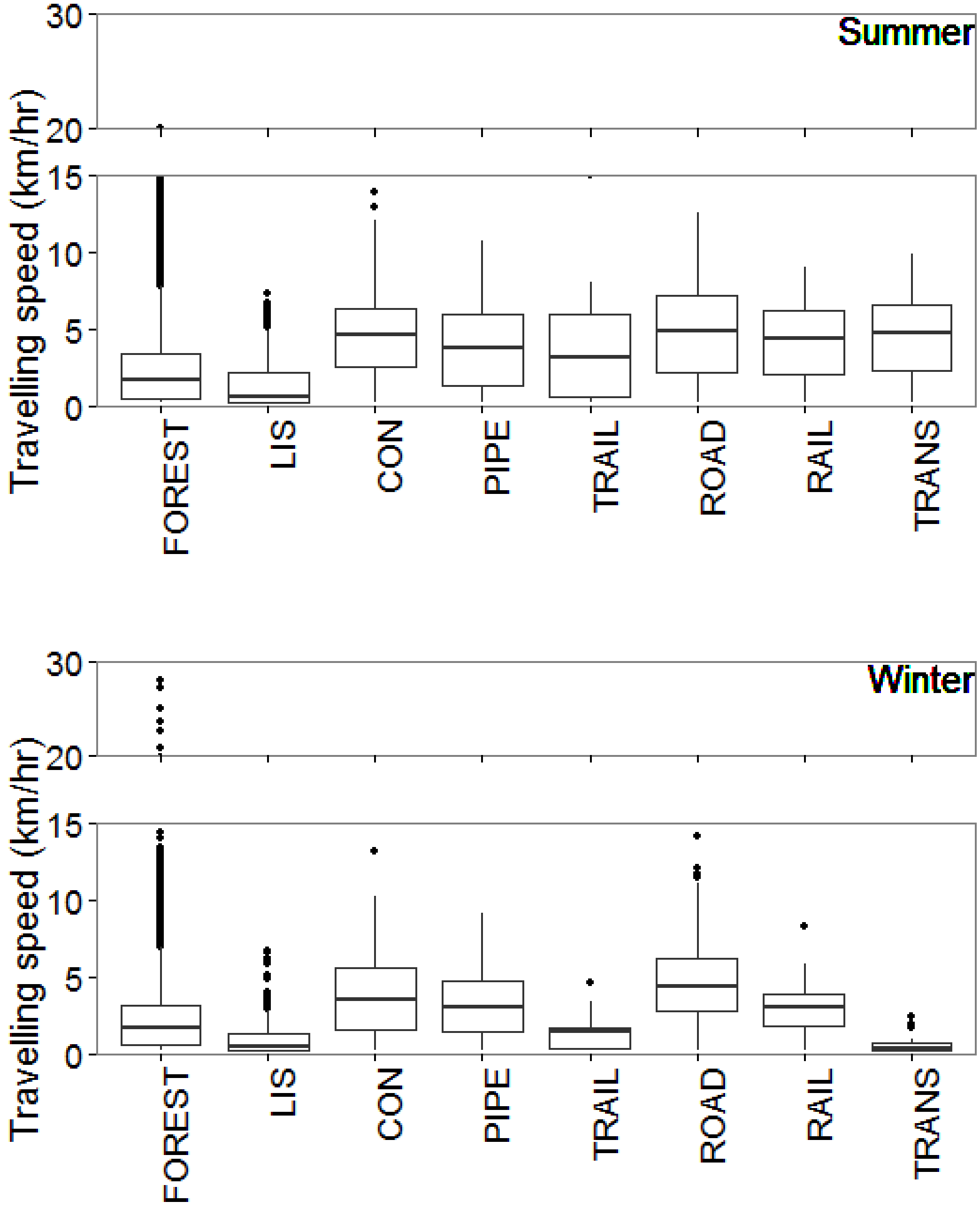

Figure 4: Median wolf travelling speed (km/hr) during 5 minute time travelling steps as a function of linear feature class, with undisturbed forest included for contrast, in summer and winter. Data from 20 wolves from 6 packs in summer and 13 wolves from 6 packs in winter were included. The upper and lower bounds of the boxplots correspond to the 1st and 3rd quartiles of the median, i.e. the 25th and 75th percentiles. Whiskers extend to the highest value within the inter-quartile range (distance between the 1st and 3rd quartiles) multiplied by 1.5. Data displayed

as points outside of the boxplot correspond to outliers identified by a Tukey test. FOREST = undisturbed forest, CON = conventional seismic lines, LIS = Low impact Seismic, PIPE = pipeline, RAIL = railway, ROAD = Roads, TRAIL = trails, TRANS = transmission lines.

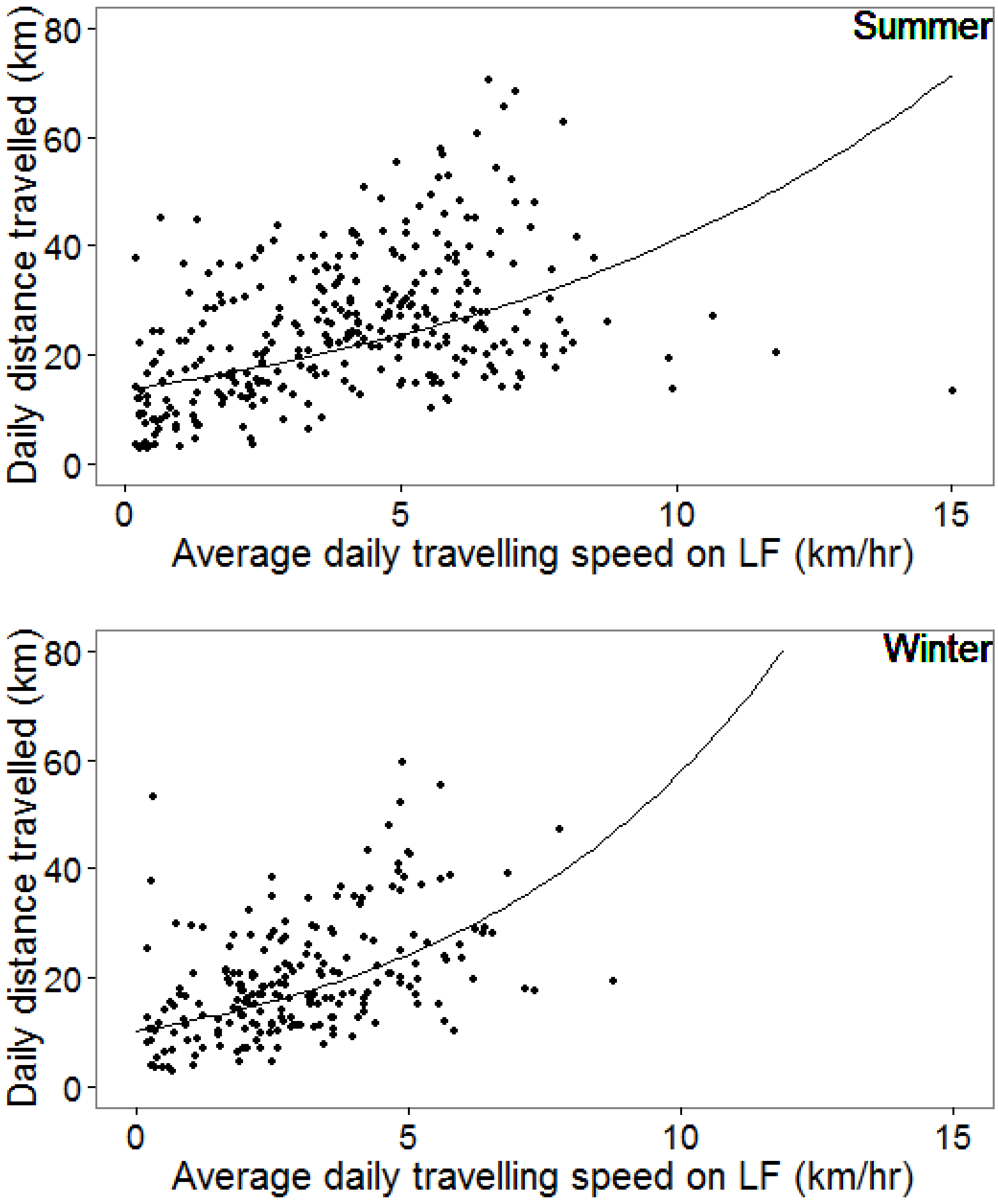

Figure 5: The relationship between total distance moved by wolves in a day (km) and the average daily travelling speed while on linear features (km/hr) from individual wolves in summer and winter. Data from 20 wolves from 6 packs in summer and 13 wolves from 6 packs in winter were included.

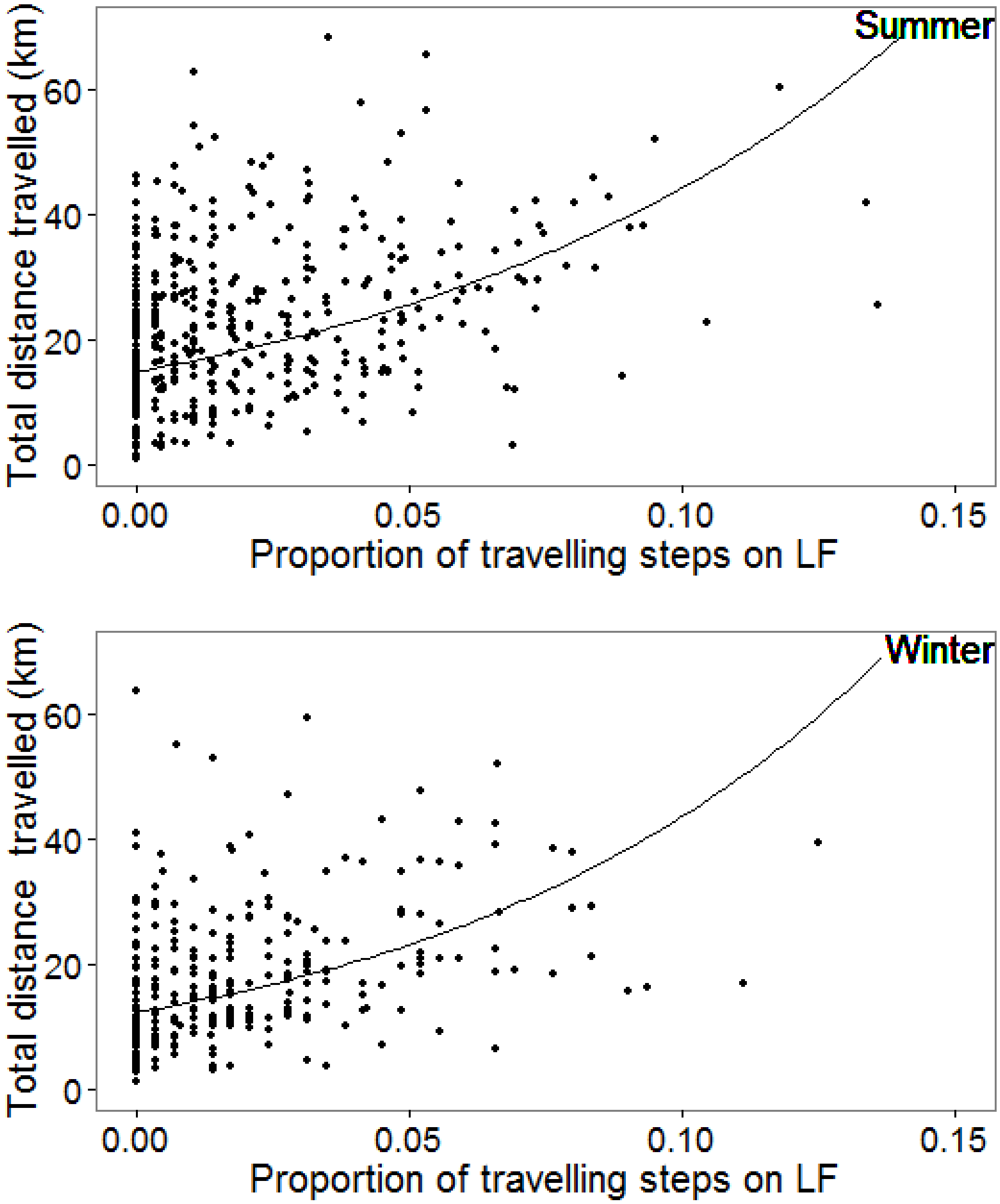

Figure 6: The relationship between total distance moved by wolves in a day (km) and the proportion of travelling steps on linear features (km/hr) from individual wolves in summer and winter. Data from 20 wolves from 6 packs in summer and 13 wolves from 6 packs in winter were included.

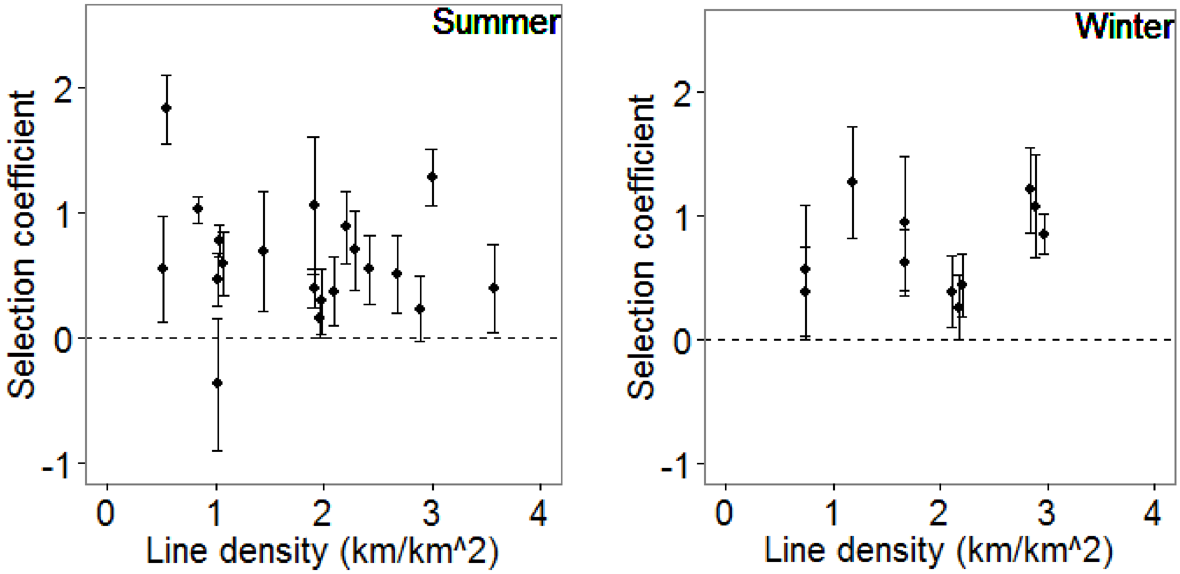

Figure 7: The magnitude of wolf selection of linear features, averaged across linear feature classes, as a function of the average linear feature density (km/km^2) in each wolf's home range (km/km^2) in summer and winter. Wolf selection coefficients of linear features were derived from individual conditional logistic regression controlling for landcover. Low-impact seismic lines were not included in linear feature density to maintain consistency with other reports of linear feature density in northern Alberta. Error bars represent 95% confidence intervals. Data from 20 wolves from 6 packs in summer and 11 wolves from 6 packs in winter were included. A horizontal dotted line represents no selection or avoidance.

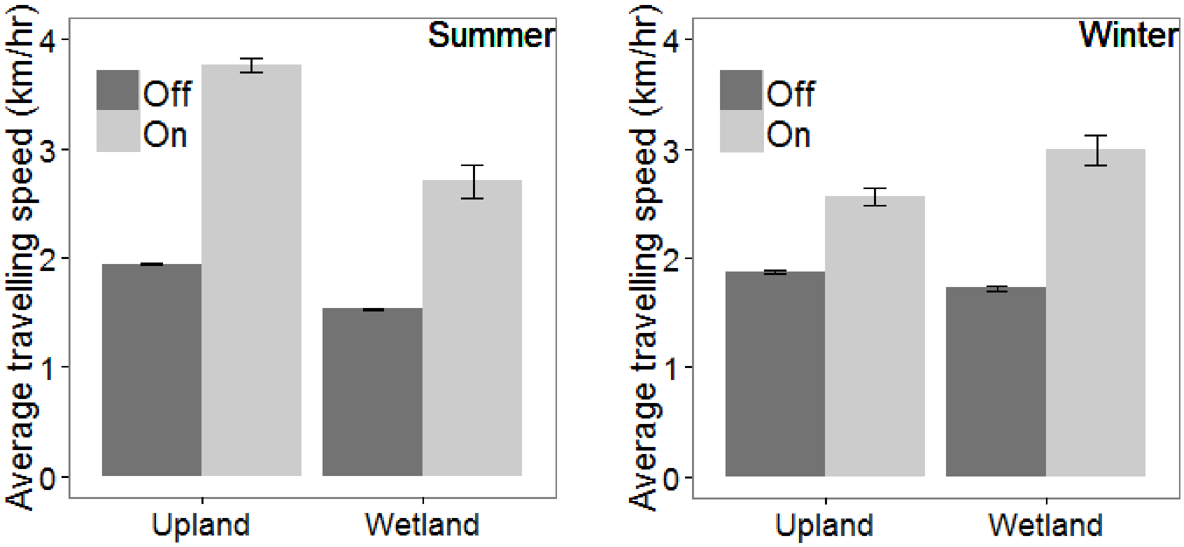

Figure 8: Average travelling speed (km/hr) of wolves on and off linear features in upland and wetland habitats in summer and winter. Error bars represent 95% confidence intervals. Only travelling steps connecting successive 5-minute GPS locations were included. Steps were classified as on a linear feature if the step was completely contained within the buffer of a linear feature derived from imagery. Steps were classified as upland or wetland only if the entire step traversed the given landcover type. Data from 20 wolves from 6 packs in summer and 13 wolves from 6 packs in winter were included.

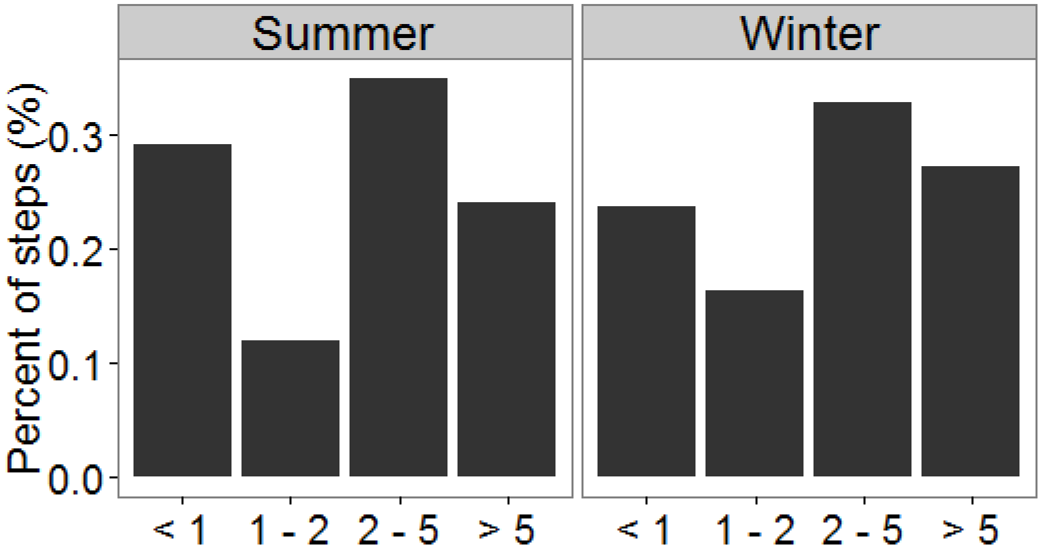

Figure 9: The percent of wolf travelling steps (%) in each vegetation height category in summer and winter. The linear weighted mean vegetation height was calculated for each travelling step connecting 5-minute GPS locations, and assigned a height category. Vegetation height categories were < 1 m (cleared linear features), 1 - 2 m (linear features with minimal revegetation), 2 - 5 m (linear features with moderate revegetation) and >5 m (linear features with high revegetation). Data from 12 wolves from 4 packs in summer and 4 wolves from 3 packs in winter were included.

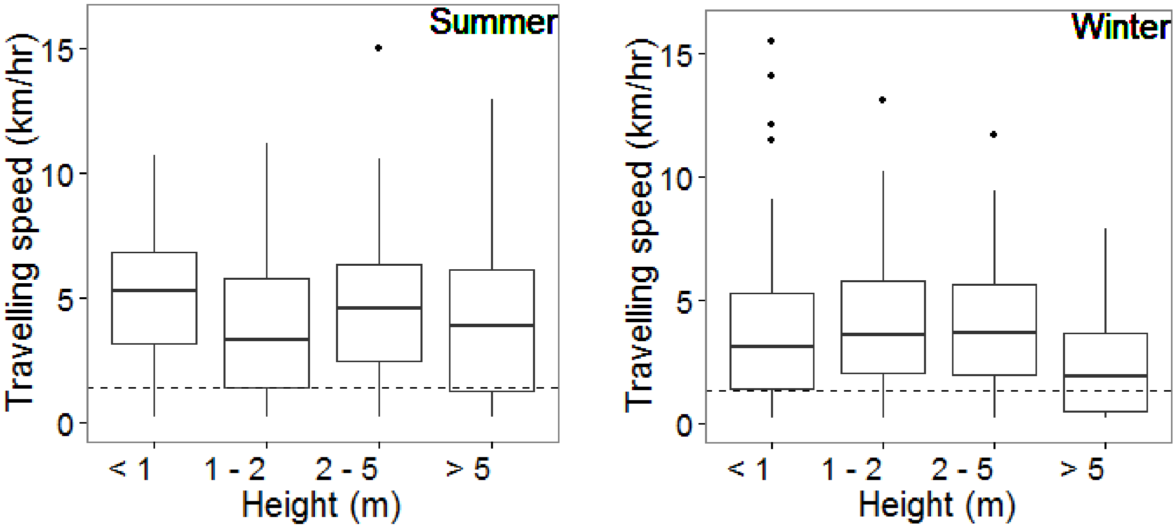

Figure 10: Median travelling speed (km/hr) of wolves travelling on linear features as a function of vegetation height (m) categories in summer and winter. A horizontal dotted line represents the average travelling speed of wolves in non-linear features forest, obtained from the intercept of Table 4. Data from 12 wolves from 4 packs in summer and 4 wolves from 3 packs in winter were included. The upper and lower bounds of the boxplots correspond to the 1st and 3rd quartiles of the median, i.e. the 25th and 75th percentiles. Whiskers extend to the highest value within the inter-quartile range (distance between the 1st and 3rd quartiles) multiplied by 1.5. Data displayed as points outside of the boxplot correspond to outliers identified by a Tukey test.

REFERENCES

Apps, C.D., Mclellan, B.N., Kinley, T.A., Serrouya, R., Seip, D.R. & Wittmer, H.U. (2013) Spatial factors related to mortality and population decline of endangered mountain caribou. *The Journal of Wildlife Management*, **77**, 1409–1419.

Arditi, R. & Ginzburg, L.R. (1989) Coupling in predator-prey dynamics : Ratio-dependence. *Journal of Theoretical Biology*, **139**, 311–326.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-1.7. http://cran.r-project.org/web/packages/lme4/index.html

Beckingham, J.D. & Archibald, J.H. (1996) *Field Guide to Ecosites of Northern Alberta*. Natural Resources Canada, Canadian Forest Service, Northwest Region, Northern Forestry Centre, Edmonton, ALberta.

Berger, J. (2007) Fear, human shields and the redistribution of prey and predators in protected areas. *Biology letters*, **3**, 620–623.

Bergerud, A. & Elliot, J. (1986) Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology*, **64**, 1515–1529.

Bergerud, A., Jakimchuk, R. & Carruthers, D. (1984) The Buffalo of the North: Caribou (*Rangifer tarandus*) and Human Developments. *Arctic*, **37**, 7–22.

Boyce, M., Mao, E., Merrill, E., Fortin, D., Turner, M., Fryxell, J.M. & Turchin, P. (2003) Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, **10**, 421–431.

Canty, A. & Ripley, B. (2015) Bootstrap Functions (Originally by Angelo Canty for S). R package version 1.3-1.5. http://cran.r-project.org/web/packages/boot/boot.pdf

Chernick, M. (2007) *Bootstrap Methods: A Guide for Practitioners and Researchers*, Second Edi. John Wiley & Sons, Inc., Hoboken, New Jersey.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J. a & Boyce, M.S. (2012) Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PloS one*, **7**, e50611.

COSEWIC. (2002) *COSEWIC Assessment and Update Status Report on the Woodland Caribou, Rangifer Tarandus Caribou*. Ottawa, Ontario, Canada.

Dawe, K.L., Bayne, E.M. & Boutin, S. (2014) Influence of climate and human land use on the distribution of white-tailed deer (*Odocoileus virginianus*) in the western boreal forest. *Canadian Journal of Zoology*, **92**, 353–363.

DeCesare, N. (2012) Separating spatial search and efficiency rates as components of predation risk. *Proceedings of the Royal Society B: …*, **279**, 4626–4633.

Dyer, S.J., O'Neill, J.P., Wasel, S.M. & Boutin, S. (2001) Avoidance of industrial development by woodland caribou. *The Journal of Wildlife Management*, **65**, 531–542.

Environment Canada. (2011) Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada: 2011. p. 102 pp plus appendices. Ottawa, Ontario, Canada.

Environment Canada. (2012) *Recovery Strategy for Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada*. Ottawa.

ESRI (Environmental Systems Resource Institute). (2013) ArcGIS: release 10.1 edition. Environmental Systems Research Institute, Redlands, California, USA.

Fahrig, L. & Rytwinski, T. (2009) Effects of roads on animal abundance : an empirical review and synthesis. *Ecology and Society*, **14**, 21.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D. & Gunn, A. (2011) Conservation of caribou (*Rangifer tarandus*) in Canada : an uncertain future. *Canadian Journal of Zoology*, **89**, 419–434.

Fryxell, J.M., Mosser, A., Sinclair, A.R.E. & Packer, C. (2007) Group formation stabilizes predator-prey dynamics. *Nature*, **449**, 1041–1044.

Fuller, T.K. (1991) Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology*, **69**, 283–287.

Giuggioli, L., Potts, J.R. & Harris, S. (2011) Animal interactions and the emergence of territoriality. *PLoS Computational Biology*, **7**, e1002008.

Hayes, R., Baer, A., Wotschikowsky, U. & Harestad, A. (2000) Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology*, **78**, 49–59.

Hebblewhite, M. & Merrill, E.H. (2008) Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, **45**, 834–844.

Hebblewhite, M., White, C., Nietvelt, C., Mckenzie, J., Hurd, T., Fryxell, J.M., Bayley, S. & Paquet, P. (2005) Human activity mediates a trophic cascade caused by wolves. *Ecology*, **86**, 2135–2144.

Hervieux, D., Hebblewhite, M., DeCesare, N.J., Russell, M., Smith, K., Robertson, S. & Boutin, S. (2013) Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology*, **91**, 872–882.

Holling, C.S. (1959a) The components of predation as revealed by a study of small-mammall predation of the European Pine Sawfly. *The Canadian Entomologist*, **91**, 293–320.

Holling, C.S. (1959b) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **XCI**, 385–398.

Huggard, D. (1993) Effect of snow depth on predation and scavenging by gray wolves. *The Journal of Wildlife Management*, **57**, 382–388.

James, A., Boutin, S., Hebert, D. & Rippin, A. (2004) Spatial separation of caribou from moose and its relation to predation by wolves. *The Journal of Wildlife Management*, **68**, 799–809.

James, A. & Stuart-Smith, A. (2000) Distribution of caribou and wolves in relation to linear corridors. *The Journal of Wildlife Management*, **64**, 154–159.

Kuznetsova, A., Brockhoff, P.B. & Bojesen, R.H. (2014) Tests in Linear Mixed Effects Models. R package version 2.0-20. http://cran.r-project.org/package=lmerTest

Latham, A., Latham, M., Boyce, M.S. & Boutin, S. (2011a) Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications*, **21**, 2854–2865.

Latham, A., Latham, M.C., McCutchen, N.A. & Boutin, S. (2011b) Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management*, **75**, 204–212.

Lee, P. & Boutin, S. (2006) Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. *Journal of Environmental Management*, **78**, 240–250.

McKenzie, H.W., Jerde, C.L., Visscher, D.R., Merrill, E.H. & Lewis, M. a. (2009) Inferring linear feature use in the presence of GPS measurement error. *Environmental and Ecological Statistics*, **16**, 531–546.

McKenzie, H., Merrill, E., Spiteri, R. & Lewis, M. (2012) How linear features alter predator movement and the functional response. *Interface Focus*, **2**, 205–216.

McLoughlin, P., Dzus, E., Wynes, B. & Boutin, S. (2003) Declines in populations of woodland caribou. *The Journal of Wildlife Management*, **67**, 755–761.

McPhee, H.M., Webb, N.F. & Merrill, E.H. (2012) Time-to-kill: measuring attack rates in a heterogenous landscape with multiple prey types. *Oikos*, **121**, 711–720.

Mech, L.D. (1970) *The Wolf: Ecology and Behaviour of an Endangered Species*. The Natural History Press, New York.

Mech, L. & Boitani, L. (2003) *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press, Chicago.

Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P. & Frair, J.L. (2010) Building a mechanistic understanding of predation with GPS-based movement data. *Philosophical Transactions of the Royal Society B*, **365**, 2279–2288.

Metz, M.C., Smith, D.W., Vucetich, J. a, Stahler, D.R. & Peterson, R.O. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *The Journal of Animal Ecology*, **81**, 553–563.

Metz, M., Vucetich, J., Smith, D., Stahler, D.R. & Peterson, R.O. (2011) Effect of sociality and season on gray wolf (Canis lupus) foraging behavior: implications for estimating summer kill rate. *Plos One*, **6**, e17332.

Muggeo, V.M.R. (2014) Regression models with breakpoints/changepoints estimation.

Muhly, T., Semeniuk, C., Massolo, A., Hickman, L. & Musiani, M. (2011) Human activity helps prey win the predator-prey space race. *PLoS One*, **6**, e17050.

Mysterud, A. & Ims, R. (1998) Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology*, **79**, 1435–1441.

Nelson, M. & Mech, L. (1986) Relationship between snow depth and gray wolf predation on white-tailed deer. *The Journal of Wildlife Management*, **50**, 471–474.

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D. & Courtois, R. (2012) Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, **76**, 189–199.

Rea, R. (2003) Modifying roadside vegetation management practices to reduce vehicular collisions with moose Alces alces. , **9**, 81–91.

Rettie, W. & Messier, F. (2000) Hierarchical habitat selection by woodland caribou: Its relationship to limiting factors. *Ecography*, **23**, 466–478.

Schneider, D. (2001) The rise of the concept of scale in ecology. *Bioscience*, **51**, 545–553.

Seip, D. (1992) Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology*, **70**, 1494–1503.

Serrouya, R., McLellan, B.N., Boutin, S., Seip, D.R. & Nielsen, S.E. (2011) Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology*, **48**, 935–942.

Solomon, M.. (1949) The Natural Control of Animal Populations. *Journal of Animal Ecology*, **18**, 1–35.

Therneau, T. (2014) Survival Analysis. R package version 2.37-7. http://cran.r-project.org/web/packages/survival/survival.pdf

Thurber, J.M., Peterson, R.O., Drummer, T.D. & Thomasma, S.A. (1994) Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin*, **22**, 61–68.

Tsunoda, H., Gula, R., Theuerkauf, J., Rouys, S., Radler, S., Pirga, B., Eggermann, J. & Brzezowska, B. (2009) How does parental role influence the activity and movements of breeding wolves? *Journal of Ethology*, **27**, 185–189.

Turner, M., Gardner, R. & O`Neill, R. (2001) *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer-Verlag, New York, New York, USA.

Webb, N.F., Hebblewhite, M. & Merrill, E.H. (2008) Statistical methods for identifying wolf kill sites using global positioning system locations. *The Journal of Wildlife Management*, **72**, 798–807.

Whittington, J., St. Clair, C.C. & Mercer, G. (2005) Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications*, **15**, 543–553.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J. & Musiani, M. (2011) Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *Journal of Applied Ecology*, **48**, 1535–1542.

Wu, J. (2004) Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology*, **19**, 125–138.

APPENDIX 1

I opted to obtain population level selection inferences by modelling individuals separately and then averaging estimates across individuals. However, there can be issues with modelling individuals separately when individuals are non-independent. I was concerned about the possibility that including multiple individual wolves within packs would affect my resource selection analyses due to non-independence among wolves. Therefore, I tested if packs had significantly different average selection estimates, and whether the variance among packs was higher than residual variance to help make the case that 2-4 individual wolves within a pack was not a big issue.

First, I tested the effect of pack on all selection estimates together, while controling for feature class using a 2-way ANOVA (Table A1). In summer, there was little variance explained by pack (SS = 6.991) and residual variability was higher (SS = 43.948). In addition, residual variance left unexplained by the model was higher than the pack by feature class interaction (SS = 28.591) This gives me confidence that differences among packs explained little variation in selection estimates, and instead residual variance left over from individual differences was high. In winter, again residual variance was higher than variance explained by pack (SS = 11.8485 and SS = 3.776, respetively). This again gave me confidence that individual variation was higher than pack variation. However, the variance explained by the interaction among pack and feature class (SS = 14.1197) was higher than the residual variance. I also tested whether packs had significantly different average selection estimates, and whether the variance among packs was higher than residual variance for each linear feature classes seperate (Table A1). This allowed me to directly test the differences for each feature class, however I was less trusting of these models becuse of the low number of individuals in each pack (ie replicates). Pack explained a significant amount of variation in wolf selection of linear features for only roads in summer (p = 0.022). However, variance partitioning was less clear because pack variation was larger than residual variation for roads in summer, as well as conventional seismic lines, pipelines, railways and roads in winter.

Table A 1: The effect of pack on wolf selection coefficients. 8 separate models are summarized; 1) a 2-way ANOVA in which all selection estimates were compared among packs, linear feature classes, and the interaction among them, 2) a 1-way ANOVA in which the selection estimates were compared among packs for low-impact seismic lines, 3) a 1-way ANOVA in which the selection estimates were compared among packs for conventional seismic lines, 4) a 1-way ANOVA in which the selection estimates were compared among packs for trails, 5) a 1-way ANOVA in which the selection estimates were compared among packs for pipelines, 6) a 1-way ANOVA in which the selection estimates were compared among packs for railways, 7) a 1-way ANOVA in which the selection estimates were compared among packs for roads and 8) a 1-way ANOVA in which the selection estimates were compared among packs for transmission lines. The degrees of freedom (df), sum of squares (SS), mean sum of squares (Mean S), F-statistic (F) and p-value (P) are provided for each variable in each season.

Model	Variable	Summer					Winter				
		df	SS	Mean S	F	P	df	SS	Mean S	F	P
Full	Pack	5	6.991	1.398	3.818	0.003	5	3.767	0.753	2.480	0.048
	Feature class	10	66.348	6.635	18.116	<0.001	10	22.112	2.211	7.278	<0.001
	Pack * Feature class	40	28.591	0.715	1.952	0.003	38	14.120	0.372	1.223	0.267
	Residual	120	43.948	0.366			39	11.849	0.304		
Low-impact seismic	Pack	3	1.782	0.594	0.681	0.620	2	0.011	0.005	0.179	0.858
	Residual	3	2.617	0.872			1	0.030	0.030		
Conventional seismic	Pack	5	0.605	0.121	0.406	0.837	5	1.482	0.296	1.701	0.287
	Residual	14	4.140	0.298			5	0.871	0.174		
Trail	Pack	5	1.972	0.395	1.189	0.363	5	3.692	0.738	0.692	0.652
	Residual	14	4.644	0.332			5	5.334	1.067		
Pipeline	Pack	5	3.261	0.652	1.712	0.201	5	1.240	0.248	2.369	0.254
	Residual	13	4.952	0.381			3	0.314	0.105		
Railway	Pack	1	0.253	0.253	0.420	0.552	1	0.455	0.455	12.040	0.179
	Residual	4	2.407	0.602			1	0.038	0.038		
Road	Pack	5	8.830	1.766	4.028	0.022	4	1.909	0.477	1.067	0.499
	Residual	12	5.262	0.439			3	1.342	0.447		
Transmission line	Pack	1	0.027	0.027	0.066	0.811	1	0.228	0.228	0.244	0.708
	Residual	4	1.670	0.418			1	0.936	0.936		