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Faster and farther: Wolf movement on linear features and implications for hunting behaviour

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Running Title: Wolf movement on linear features

Summary

1. Predation by *Canis lupus* grey wolves has been identified as an important cause of *Rangifer tarandus caribou* boreal woodland caribou mortality and it has been hypothesized that wolf use of human-created linear features such as seismic lines, pipelines and roads increases movement, resulting in higher kill rates.

2. We tested if wolves select linear features and if movement rates increased while travelling on linear features in north-eastern Alberta and north-western Saskatchewan using 5-minute GPS (Global Positioning System) locations from twenty-two wolves in six packs.

3. Wolves selected all but two linear feature classes, with the magnitude of selection depending on feature class and season. Wolves travelled two to three times faster on linear features compared to the natural forest. Increased average daily travelling speed while on linear features and increased proportion of steps spent travelling on linear features increased net daily movement rates, suggesting that wolf use of linear features can increase their search rate.

4. *Synthesis and applications*. Our findings that wolves move faster and farther on human-created linear features can inform mitigation strategies intended to decrease predation on woodland caribou, a threatened species. Of the features that can realistically be restored, mitigation strategies, such as silviculture and linear deactivation (i.e. tree-felling and fencing) should prioritize conventional seismic lines (i.e. cleared lines used for traditional oil and gas exploration) and pipelines, as they were selected by wolves and increased travelling speed, before low-impact seismic lines.

Key-words: *Canis lupus*, functional response, kill rates, linear features, movement, oil and gas, *Rangifer tarandus*, predation, search rate, selection

Introduction

The proportion of prey consumed by predators, or the predation rate, is an important predictor of consumer-resource interactions (Vucetich *et al.* 2011). The predation rate is a product of the predator's functional and numerical response (Solomon 1949; Holling 1959a). The functional response can be interpreted as a predator's foraging efficiency, and reflects the interplay between the handling time of prey and the instantaneous search rate (Holling 1959b). The instantaneous search rate comprises the distance the predator travels per unit time, the buffer where they can detect prey and the proportion of encounters that result in a kill (Fryxell *et al.* 2007). It has been hypothesized that the instantaneous search rate can be increased by human alteration of the landscape (Wittmer *et al.* 2007; Apps *et al.* 2013), which can, in turn, affect the stability of predator-prey systems (Wittmer *et al.* 2007).

Altered predator-prey dynamics due to human-induced landscape change is thought to contribute to the decline of boreal woodland caribou (McLoughlin *et al.* 2003; Hervieux *et al.* 2013), which are provincially and federally listed as threatened (COSEWIC 2002). 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 energy exploration have been linked to increased predation on woodland caribou caused by greater spatial overlap with predators, higher wolf populations and changes to wolf hunting efficiency (Latham *et al.* 2011b; Hervieux *et al.* 2013). Wolves are hypothesized to use human-created linear features such as seismic lines and roads to increase movement and distance travelled, leading to increased instantaneous search rate (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), thereby increasing kill rate until predators are saturated by handling time (Holling 1959b). If wolf use of linear features increases search rates and thereby kill rates, and if these features are selected, these features have the potential to substantially influence caribou populations. Increased encounters with caribou, assuming caribou do not adequately avoid linear features to spatially separate from predators, and increased encounters with, and kills of, primary prey leading to higher predator populations, are expected to increase caribou predation.

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), but direct comparisons between movements on linear features and in forest are rare (but see Musiani, Okarma & Jędrzejewski 1998; McKenzie *et al.* 2012; DeCesare 2012). Previous studies on wolf movement related to linear features have not explicitly tested whether increased movement rates translated into greater daily travel distances (Latham *et al.* 2011a; McPhee, Webb & Merrill 2012; DeCesare 2012). The disc equation assumes predators have two basic behaviours; handling prey and hunting for prey (Holling 1959b). However, increased movement rates may not increase kill rates if wolves use the time they would otherwise be moving for other behaviours, such as resting or socialization.

Our objective was to determine if wolves select various linear features, and if wolf movement rate, as measured by travelling speed and overall daily distance moved, is higher on linear features compared to the forest; thereby testing if wolf search rate can be influenced by linear features. This study focuses on linear features and wolf movement behaviour, but does not concurrently monitor the direct link between linear features and caribou kill rates. Specifically, we ask (i) do wolves select linear features (ii) do wolves travel faster on linear features and (iii) is increased use of linear features related to increase daily movements?

Materials and methods

STUDY SITE

Our study took place in northeastern Alberta and northwestern Saskatchewan (Fig. 1). The 18 000-km^2 study area contains boreal forest with a mosaic of peatlands, uplands, marshes and swamps, including black spruce bogs and black spruce-tamarack fens (Latham *et al.* 2011a). The topography is flat with an elevation of approximately 550 m, with various small lakes and rivers. The main prey species for wolves are moose *Alces alces* and white-tailed deer *Odocoileus virginianus*, however, woodland caribou, beaver *Castor canadensis* and snowshoe hare *Lepus americanus* 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. A large component of the linear feature footprint is conventional seismic lines; straight, 10 m wide, cleared lines used for traditional oil and gas exploration. Recent technology has led to the reduction of seismic line widths to approximately 5 m wide. With the implementation of Steam Assisted Gravity Drainage extraction techniques, narrower low-impact seismic lines have become more common. Other linear features, such as pipelines, trails (i.e All-Terrain Vehicle or small truck trails), roads, transmission lines, and railways are used to extract oil and gas, gain access to facilities, provide power to these facilities, and for transportation. Linear feature density ranges between 0.52 to 15.89 km km^{-2}.The mean availability of linear features within individual wolf home ranges was approximately 9% of the landscape, with each linear feature class separately covering less than 5% (Table 1).

WOLF CAPTURE AND COLLARING

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). Twenty-two Iridium GPS collars (Lotek Wireless, Aurora, Ontario, Canada) were deployed on wolves in six packs, with the area of inference defined by wolf territories (Fig. 1). Collars were programmed to provide locations on a cycle of 5 minutes for two days, and then hourly for four days from April 15 to July 15 (summer) of 2013 and 2014. In addition, collars provided 5-minute locations everyday from January 1 to March 31 (winter) of 2014.

LINEAR FEATURES

Linear features were visually classified at a 1:15 000 scale using 2012 SPOT imagery (2-m resolution) and Valtus Views (0.5-m resolution). Linear features were classified as conventional seismic lines, low-impact seismic lines, trails, roads, pipelines, transmission lines and railway (Table 1, Appendix S1). We converted linear features into polygons using a buffer based on each class's average width (Table 1). We measured three linear features of each class to the nearest 2.5 m (cell size of SPOT imagery) within each wolf pack's 100 % minimum convex polygon (MCP) and applied a buffer of the average width (rounded to the nearest 2.5-m) to each linear feature, on both sides.. MCPs were calculated using only 5-minute GPS locations using ArcGIS 10.1 (ESRI, 2013). Buffering both sides of the linear feature accounted for errors in the digitization process, such as lines being drawn on the edge of the linear feature instead of in the middle. Previous methods to assign GPS locations to linear features have included an additional term to encompass error in animal GPS locations (McKenzie *et al.* 2009). However, by not doing so we decreased the chance that wolf locations in the forest edge were misclassified as being on linear features.

DO WOLVES SELECT LINEAR FEATURES?

We evaluated the relationship between linear feature class and wolf selection by comparing 5-minute GPS locations to random locations. We define selection as features used more than their availability on the landscape, and avoidance as used less than their availability. Because we were interested in fine-scale movement, and linear features (i.e. low-impact seismic lines) were patchy within the study area, we constrained the characterisation of availability for each used location (Boyce *et al.* 2003). We compared each used location to 10 available locations within a radius of the 90th percentile maximum step length; 0.274 km (the 90th percentile distance between two consecutive locations). Each location was classified as in the forest or within the buffer of a linear feature class. If the location fell where multiple linear feature classes overlapped, the location was classified as the widest feature class.

We included landcover as a covariate to account for selection differences among landcover types. Each location was assigned a landcover category (deciduous, coniferous, mixedwood, wetland and other) based on Alberta Vegetation Inventory (AVI) and Saskatchewan Forest Inventory (SFI) and ecosite characteristics (Beckingham & Archibald 1996). Locations within linear feature buffers were assigned the adjacent landcover. The landcover of large-scale human-modified areas (for example a ranch or oil and gas facilities) was classified as other and were rare. Unknown landcover classifications were excluded from analyses.

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 forest, and if the magnitude of selection differed among each linear feature class. Coniferous forest and forest (off linear features) were set as the reference categories (Boyce *et al.* 2003). The interaction among linear feature class and landcover class was of interest; however models with interactions failed to converge. Selection coefficients were averaged across individuals and 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). Summer and winter seasons were analysed separately.

DO WOLVES TRAVEL FASTER ON LINEAR FEATURES?

To determine if wolves travelled faster on linear features, we connected successive GPS locations for each individual using ArcGIS 10.1 (ESRI, 2013) and calculated travelling speed (the distance between two successive GPS locations divided by the time between locations, converted to km hr^{-1}). We limited travelling speed analyses to steps between 5-minute locations to maintain consistent sampling frequency. The natural logarithm of travelling speed revealed a bimodal distribution suggesting two types of movement (Fig. 2); slow and fast. We calculated a breakpoint of 0.21 km hr^{-1} using the segmented package in R (Muggeo 2014). We assumed that short step lengths (< 0.21 km hr^{-1}) corresponded to resting and feeding while longer step lengths ($\geq$ 0.21 km hr^{-1}) corresponded to travelling movements, hereafter termed 'travelling steps'. Because we were interested in how linear features affect the latter, step length analyses were restricted to travelling steps only. We 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 step was completely contained within a linear feature's buffer.

We 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 (Bates *et al.* 2014).We transformed travelling speed using the natural logarithm to better meet normality assumptions, with forest as the reference category. We approximated *P* values using the lmerTest package with a Satterthwaite approximation (Kuznetsova, Brockhoff & Bojesen 2014). Summer and winter seasons were analysed separately.

DOES 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, we evaluated whether overall daily wolf movements (i.e. net movement regardless of whether steps were classified as resting/feeding or travelling) increased as 1) travelling speed on linear features increased and 2) time spent travelling on linear features increased.

We 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. We calculated the total distance wolves moved, regardless of movement type, for each day. Days were defined as 24-hour periods from the time collars began transmitting 5-minute GPS locations. Only days with a minimum of 200 steps were used. We calculated the average travelling speed while on linear features, regardless of feature type, using travelling steps only. We then 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. The proportion of travelling steps on linear features was calculated as the number of travelling steps on a linear feature divided by the total number of steps taken in that day, regardless of movement type (i.e. short and long) and location. We assessed these relationships using two separate generalized mixed-effects models as described above for travelling speeds as a function of linear feature class.

A CASE FOR THE INDEPENDENCE OF WOLVES

Obtaining population-level inferences from multiple individuals is commonly attempted using one of two analytical methods; mixed-effects models or modelling individuals and averaging coefficients across individuals (Boyce 2006; Webb, Hebblewhite & Merrill 2008; Sawyer, Kauffman & Nielson 2009; Northrup *et al.* 2012; Squires *et al.* 2013). For selection analyses we opted to obtain population-level inferences by modelling individuals separately and then averaging estimates across individuals (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 (Latham et al. 2011a; McKenzie et al. 2012; DeCesare 2012). However, we found little evidence that, for our analyses, individuals within a pack were not independent and therefore included all individuals, regardless of pack (Appendix S2).

Results

We obtained 145 888 GPS locations, resulting in 49 239 5-minute travelling steps, from 20 wolves in six packs during the summers of 2013 and 2014 (Appendix S3). We also obtained 79 633 locations from 11 wolves and 21 826 travelling steps from 13 wolves in six packs in winter of 2014 (Appendix S3). Data from two wolves in winter were withheld from selection analyses due to failure to converge. We also identified 451 and 274 wolf days in summer and winter with over 200 GPS locations. Average wolf travelling speed varied greatly on linear features (0.22 - 15.02 km hr^{-1}), as did total distance moved per day (0.96 - 70.4 km) and the proportion of travelling steps on linear features per day (0.00 - 0.15).

DO WOLVES SELECT LINEAR FEATURES?

The relative abundance of linear feature classes varied on the landscape, with conventional seismic lines being the most common (Fig. 3). Wolves, on average, selected each linear feature class more than the forest, with the exception of low-impact seismic lines in summer and trails in winter (Table 2). However, individual responses varied (Table 3).

In summer, the odds of wolves selecting conventional seismic lines, trails, pipelines, roads and transmission lines were approximately 2× higher than the forest. All 20 wolves were exposed to conventional seismic lines and trails; 15 individuals (75%) selected conventional seismic and 12 (60%) selected trails (Table 3). Most wolves were exposed to pipelines and roads, but only 53% and 61% selected those features, respectively (Table 3). While only six wolves were exposed to railways and transmission lines, 83% selected them (Table 3); the odds of wolves selecting railways were 6.3× higher than the forest. Low-impact seismic lines were present in few individual's home ranges and only 29% selected these features while 43% avoided them (Table 3).

In winter, the odds of wolves selecting roads, railways and transmission lines were 3, 4 and 8 × higher than the forest, respectively. Of the eight wolves exposed to roads in the winter, 75% selected them (Table 3). While only three wolves were exposed to railways, all selected them. Two of the three wolves exposed to transmission lines selected them. The odds of wolves selecting conventional seismic lines and pipelines were approximately 2× higher than the forest. Of the wolves that were exposed to conventional seismic lines, 82 % selected them, whereas only 67% of the wolves exposed to pipelines selected pipelines (Table 3). Wolves selected low-impact seismic lines more than the forest during winter; with the magnitude of selection 1.2× smaller than for other feature classes (Table 2). All four wolves exposed to low-impact seismic lines in winter selected them more than the forest.

DO WOLVES TRAVEL FASTER ON LINEAR FEATURES?

The magnitude of effect of linear feature class on wolf travelling speed varied among linear feature classes (Fig. 4). 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 forest during summer (Table 4). Conversely, wolves travelled 31% slower (0.98 km hr^{-1}) on low-impact seismic lines than forest. In winter, wolves travelled 2× faster on conventional seismic lines, pipelines and railways compared to forest, and 3× faster on roads. Wolves travelling on low-impact seismic and transmission lines moved 53% (0.64 km hr^{-1}) and 48 % (0.70 km hr^{-1}) slower than in forests, respectively (Table 4).

DOES USE OF LINEAR FEATURES INCREASE DAILY MOVEMENTS?

As the average daily travelling speed on linear features increased, the total distance moved per wolf per day 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^{-1} increase in 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^{-1} on linear features in a day, the total distance they moved that day increased by 10 km or 14 km in summer and winter, respectively. Variation attributed to the mixed effects was minimal; with higher variation among individuals within the same pack ($SD_{summer} = 0.047$, $SD_{winter} = 0.003$) than among packs ($SD_{summer} < 0.001$, $SD_{winter} < 0.001$).

The total distance moved per wolf per day increased as the proportion of travelling steps on linear features increased in summer ($\beta = 10.903$, SE = 1.195, $P < 0.001$) and winter ($\beta = 12.650$, SE=1.621, $P < 0.001$; Fig. 6). The total distance moved per day increased by 11% (summer) and 13% (winter) with a 1% increase to the number of travelling steps on linear features; a 46% and 54% increase in daily distance moved for every hour wolves spent travelling on linear features. For example, if wolves travel 15.13 km in a day when they did not travel on linear features, the total distance moved increased by 6.9 km when using linear features for an hour in summer. There was higher variation among individuals within the same pack ($SD_{summer} = 0.083$, $SD_{winter} = 0.045$) than among packs ($SD_{summer} = 0.011$, $SD_{winter} < 0.001$).

Discussion

We provide strong empirical evidence that wolves selected linear features and movement rates were higher on linear features. While previous studies have shown that wolves select linear features, and these features influence wolf movement (James & Stuart-Smith 2000; Latham *et al.* 2011a; McKenzie *et al.* 2012), we showed that wolves travelled faster on linear features and their use increased daily distance moved.

Wolves selected nearly all linear feature classes more than the forest, 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 of linear features could be associated with physical structure or human disturbance. Wolves selected long, straight features (railways, conventional seismic and pipelines) but not narrow and sinuous features (low-impact seismic lines and trails); which may be less beneficial to wolf movement if they do not provide a direct path or hinder line-of-sight. Wolves selected features consistently cleared of obstruction (railways, transmission lines and roads). However, high human disturbance (i.e. on roads) may decrease attraction; suggesting a trade-off between facilitating movement and human avoidance (Thurber *et al.* 1994; Muhly *et al.* 2011; Ciuti *et al.* 2012). While the influence of human use on wolf behaviour and habitat selection has been studied (Hebblewhite *et al.* 2005; Hebblewhite & Merrill 2008), the interaction with each feature class remains unaddressed.

Wolves travelled faster while on linear features compared to the forest, suggesting linear features benefit movement (Latham *et al.* 2011a; McKenzie *et al.* 2012). In both seasons wolves travelled faster on roads, conventional seismic lines, pipelines and railways. Increases in wolf travelling speed on trails and transmission lines were small in summer, and speed did not increase in winter; suggesting these features provided less of a benefit to wolf movement. Wolves tended to select linear feature classes that they travelled faster on; in summer low-impact seismic lines were the only features not selected and were the only feature wolves travelled slower on. This suggests that wolves select linear features because they increase movement rates. However, wolves selected low-impact seismic lines and transmission lines in the winter despite decreased movement rates, suggesting a secondary mechanism for wolf selection of linear features. When evaluating the importance of various linear feature classes on wolf selection and movement, it is important to consider their abundance across the landscape. If wolf selection and movement was strongly influenced by a specific linear feature class, i.e. railways, broad-scale implications to prey populations may be limited if that feature class is rare. Conversely, common features, i.e. conventional seismic lines, may have a larger effect on wolf movement. Additionally, the influence of individual-traits such as age, sex and breeding status on wolf selection and movement on these features, which have been found to influence hunting success (Mech & Boitani 2003), remains unaddressed.

Increased wolf travelling speed on linear features was less pronounced in winter, and the relationship between selection and travelling speed was less apparent, supporting reduced effects of linear features on wolf movement in winter (Latham *et al.* 2011a). Resistance to movement caused by deep, non-compacted snow may reduce the benefits of linear features (Fuller 1991;

Huggard 1993; Metz *et al.* 2012) if snow is intercepted by forest canopies and thereby deeper on linear features. Seasonal differences in diet, prey distribution and movement behaviour may also change linear feature use. For example, facilitated movement via linear features may become more important in summer, when wolves consume smaller prey on average compared to winter (Latham *et al.* 2011b); the ratio of search time to handling time increases, placing a premium on speed to find prey. Alternatively, wolves may concentrate efforts on hunting or moving among high prey-availability habitats in an attempt to conserve energy in winter (Metz *et al.* 2012).

Increased travelling speeds on linear features and increased net daily movement when wolves use linear features suggests that linear features function to increase the instantaneous search rate. Given that the instantaneous search rate within the disc equation is comprised of distance travelled (Fryxell *et al.* 2007), a greater distance travelled will result in a higher search rate if the search buffer and attack success remain unchanged. All else being equal, an increase in the instantaneous search rate results in a higher kill rate, and consequently the predation rate is expected to increase (Messier & Crête 1985). This relationship has been suggested using simulations (McKenzie *et al.* 2012), and recent work shows wolf kill rates of moose was strongly related to wolf movement rates (Vander Vennen *et al.* 2016). However, the instantaneous search rate may increase without increasing kill rates if prey saturate the landscape (Holling 1959b). Alternatively, wolves may use linear features to facilitate movement during territory monitoring, scent marking, travelling to and from rendez-vous sites, among habitat patches, or den sites, without influencing hunting behaviours (Mech & Boitani 2003; Tsunoda *et al.* 2009; Giuggioli, Potts & Harris 2011). While movement rates increased when wolves used linear features, the time spent on these features was low; potentially limiting their effect on behaviours such as hunting. However, even spending a small proportion of their overall daily movements travelling on linear features substantially increased the distance travelled. While spatio-temporal GPS clusters could be used to measure kill rates (Webb, Hebblewhite & Merrill 2008), these measures are largely influenced by the probability of attendance at kills, which is in turn influenced by season and prey size (Metz *et al.* 2011). While these methods perform reasonably well with large prey in winter, kill rates in snow-free seasons (Palacios & Mech 2011; Metz *et al.* 2011; Vucetich *et al.* 2012) and of small prey such as caribou and neonates (Webb, Hebblewhite & Merrill 2008) may be underestimated. Therefore, without conducting kill site investigations it is not possible to directly investigate the relationship between linear features and kill rates, an important relationship that remains unaddressed.

Prey density and distribution may confound the effect of linear features on wolf movement. Increased search rates could be compounded in areas of high linear feature density if prey density is higher due to higher food availability (Serrouya *et al.* 2011) or if prey select linear features (Berger 2007; McKenzie *et al.* 2012). Alternatively, increased per capita kill rates from increased search rates may be less important if prey density is low, caused by increased mortalities (see Fahrig & Rytwinski 2009 for review) or prey avoidance of linear features (James & Stuart-Smith 2000; Dyer *et al.* 2001). Large-scale responses to linear feature density are unlikely given linear features make up a small proportion of the landscape. Because prey densities are a key component of per capita kill rates (Holling 1959b), it is crucial to determine how linear features affect both the density and distribution of prey species.

Understanding how predators (Dickson, Jenness & Beier 2005; Whittington, St. Clair & Mercer 2005; Northrup *et al.* 2012), prey (Yahner & Mahan 1997; Ciuti *et al.* 2012), their interactions (Davies-Mostert, Mills & Macdonald 2013) and biodiversity of various ecosystems (Fahrig 2003) is influenced by linear features is fundamental as human development continues (see reviews by Fahrig & Rytwinski 2009; Benítez-López, Alkemade & Verweij 2010; Taylor & Goldingay 2010). Many studies focus on the effect of roads on various species, however understanding differences between various anthropogenic corridors will become useful as corridors associated with resource extraction and recreational activities increase. Additionally, how the effect of linear features on predators differs among various behaviours (Abrahms *et al.* 2015) is becoming more important as we strive to understand the influence of these features on predator-prey dynamics.

CONCLUSIONS

Our results have implications for linear feature restoration to mitigate the effects of linear features on increased wolf movement. If managers aim to restore linear features to reduce wolf use and movement, for example by restoring vegetation using silviculture or obstructing features using tree-felling or biodegradable barriers, it is important to note that wolves do not respond to all linear features 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. Nonetheless, these features should be considered during the restoration process, as intensive restoration activities in proximity to permanent linear features may be sub-optimal. Of the features that can realistically be restored (trails, pipelines, conventional and low-impact seismic lines), our results suggest that conventional seismic lines and pipelines should be prioritized as they were selected by wolves and increased travelling speed in both seasons.

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Data accessibility

Attributed GPS location and path data are available from Dryad Digital Repository http://dx.doi.org/10.5061/dryad.s7r47 (Dickie *et al.* 2016).

References

Abrahms, B., Jordan, N.R., Golabek, K.A., McNutt, J.W., Wilson, A.M. & Brashares, J.S. (2015) Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads. *Animal Conservation*, 1 – 9.

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.

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.

Benítez-López, A., Alkemade, R. & Verweij, P.A. (2010) The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, **143**, 1307–1316.

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.S. (2006) Scale for resource selection functions. *Diversity and Distributions*, **12**, 269–276.

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

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.

Davies-Mostert, H.T., Mills, M.G.L. & Macdonald, D.W. (2013) Hard boundaries influence African wild dogs' diet and prey selection. *Journal of Applied Ecology*, **50**, 1358–1366.

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

Dickie M., Serrouya R., McNay S., Boutin S. (2016) Data from: Faster and farther: Wolf movement on linear features and implications for hunting behaviour. Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.s7r47

Dickson, B.G., Jenness, J.S. & Beier, P. (2005) Influence of vegetation, topography, and roads on cougar movement in Southern California. , **69**, 264–276.

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.

ESRI (Environmental Systems Resource Institute). (2013) ArcGIS: release 10.1 edition.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

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. (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.

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. & 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.

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

Chicago Press, Chicago.

Messier, F. & Crête, M. (1985) Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia*, **65**, 503–512.

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 behaviour: implications for estimating summer kill rate. *Plos One*, **6**, e17332.

Muggeo, V.M.R. (2014) Regression models with breakpoints/changepoints estimation. R package version 0.5-1.2. https://cran.r-project.org/web/packages/segmented/segmented.pdf

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.

Musiani, M., Okarma, H. & Jędrzejewski, W. (1998) Speed and actual distances travelled by radiocollared wolves in Białowieża Primeval Forest (Poland). *Acta Theriologica*, **43**, 409–416.

Northrup, J.M., Pitt, J., Muhly, T.B., Stenhouse, G.B., Musiani, M. & Boyce, M.S. (2012) Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. *Journal of Applied Ecology*, **49**, 1159–1167.

Palacios, V. & Mech, L.D. (2011) Problems with studying wolf predation on small prey in summer via global positioning system collars. *European Journal of Wildlife Research*, **57**, 149–156.

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.

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

Sawyer, H., Kauffman, M.J. & Nielson, R.M. (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, **73**, 1052–1061.

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.

Squires, J.R., DeCesare, N.J., Olson, L.E., Kolbe, J. a., Hebblewhite, M. & Parks, S. a. (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biological Conservation*, **157**, 187–195.

Taylor, B.D. & Goldingay, R.L. (2010) Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. *Wildlife Research*, **37**, 320.

Therneau, T. (2014) A Package for Survival Analysis in S. 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.

Vander Vennen, L., Paterson, B., Rodgers, A., Moffatt, S. & Fryxell, J. (2016) Diel movement patterns influence daily variation in wolf kill rates on moose. *Functional Ecology*.

Vucetich, J.A., Hebblewhite, M., Smith, D.W. & Peterson, R.O. (2011) Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. *The Journal of Animal Ecology*, **80**, 1236–1245.

Vucetich, J.A., Huntzinger, B.A., Peterson, R.O., Vucetich, L.M., Hammill, J.H. & Beyer Jr, D.E. (2012) Intra-seasonal variation in wolf *Canis lupus* kill rates. *Wildlife Biology*, **18**, 235–245.

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.

Wittmer, H.U., Mclellan, B.N., Serrouya, R. & Apps, C.D. (2007) Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology*, **76**, 568–579.

Yahner, R.H. & Mahan, C.G. (1997) Effects of logging roads on depredation of artificial ground nests in a forested landscape. *Wildlife Society Bulletin*, **25**, 158–162.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1: Linear feature classification

APPENDIX S2: Testing the independence of individual wolves within and among packs

Table S2.1: The effect of pack on wolf selection coefficients.

APPENDIX S3: Individual-traits of wolves used in selection and movement analyses

Table S3.1: Summary of the number of individual-traits of wolves used in selection and movement analyses.

Table 1. Average width (m), standard error and buffer distances (m) used to buffer linear either side of hand digitized linear features for each linear feature class. Linear features were measured to the nearest 2.5 m. The average availability of these features within wolf home ranges (separated by season) and their characteristics are included.

Class	Width (m)	SE	Buffer (m)	Availability (%) Summer	Availability (%) Winter	Characteristics
Low-impact Seismic	7	1	7.5	3.2	7.1	Sinuous, in a grid
Conventional Seismic	10	0.54	10	2.4	2.4	Long, straight
Trail	12	0.7	12.5	0.4	0.2	No visible road surface, need not be long, straight, or in a grid
Pipeline	20	2.94	20	1.2	1.5	Based on supplementary data from Government of Alberta
Road	30	6.87	30	1.0	0.5	Visible road surface, > 50 m long, included winter roads, gravel roads and highways
Railway	30	4.65	30	0.2	0.1	Visible railway tracks
Transmission Line	37	6.43	37.5	0.3	0.1	Based on supplementary data from Government of Alberta

Table 2. Wolf selection coefficients and 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. 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. 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 3. 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 (N) are shown for reference. Avoidance or selection was defined as confidence intervals that did not overlap zero.

Feature Class	**Summer**				**Winter**			
	Select (%)	**Neutral (%)**	**Avoid (%)**	**Total (N)**	**Select (%)**	**Neutral (%)**	**Avoid (%)**	**Total (N)**
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 2. The effect of linear feature class on wolf travelling speed (km hr^{-1}) compared to the 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***	**Estimate**	**SE**	***P***
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

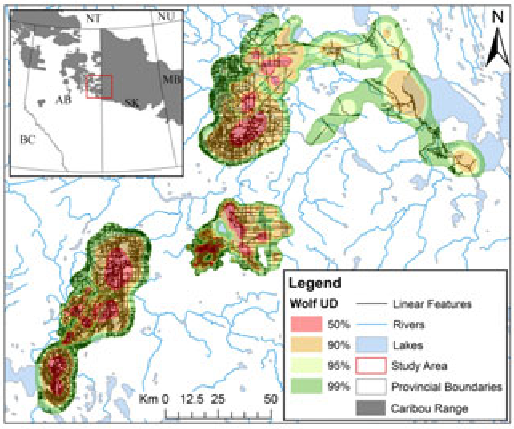

Fig. 1 Wolf utilization distributions (50%, 90%, 95% and 99%) with anthropogenic linear features in northeastern Alberta and northwestern Saskatchewan (n = 22 wolves in 6 packs). For reference, an outline of the general study area and provincial boundaries are included. The continuous range map of boreal woodland caribou is included, and reflects knowledge differences between provinces.

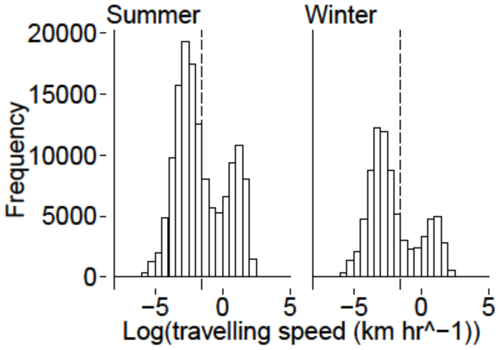

Fig. 2 Histogram of wolf log travelling speed (km hr^{-1}) in summer and winter using a 5-minute fix rate (n = 20 wolves from 6 packs in summer and 13 wolves from 6 packs in winter). A dotted vertical line represents the calculated breakpoint of 0.21 km hr^{-1}, corresponding to approximately -1.58.

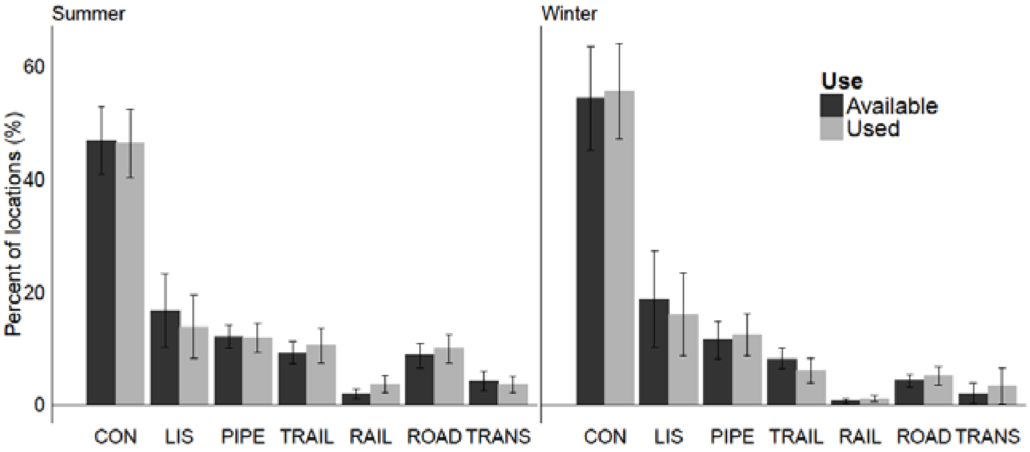

Fig. 3 The average percent of used wolf and available locations, restricted to linear features in the summer (n = 20 wolves from 6 packs) and winter (n = 13 wolves from 6 packs). The proportion of used and available locations, when on linear features, in each class was calculated for each wolf, and then 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.

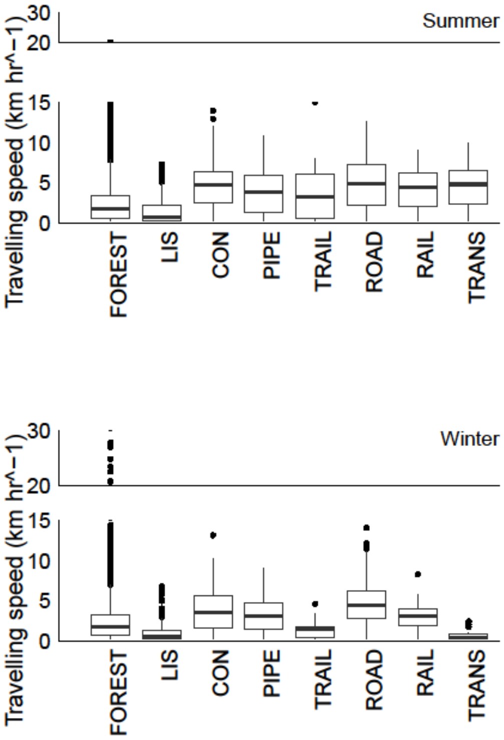

Fig. 4: Median wolf travelling speed (km hr^{-1}) as a function of linear feature class, with undisturbed forest included for contrast, in summer (n = 20 wolves from 6 packs) and winter (n = 13 wolves from 6 packs) during 5-minute time travelling steps. The upper and lower bounds of the boxplots correspond 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 multiplied by 1.5. Data 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.

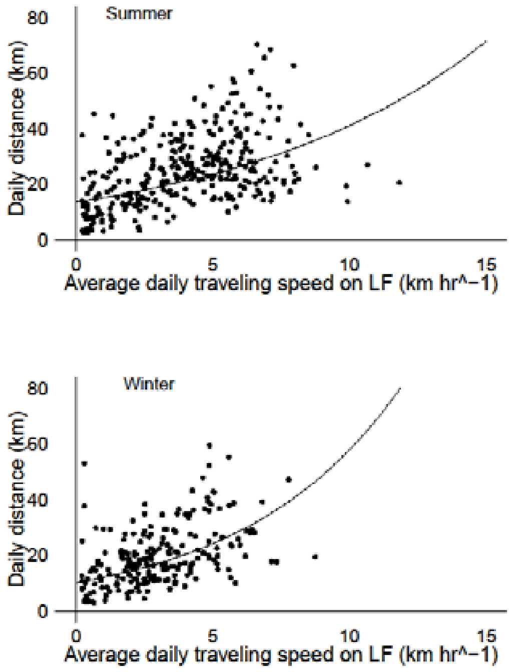

Fig. 4 The relationship between total distance moved by wolves in a day (km) and the average daily travelling speed while on linear features (km hr^{-1}) from individual wolves in summer (n= 20 wolves from 6 packs) and winter (n = 13 wolves from 6 packs).

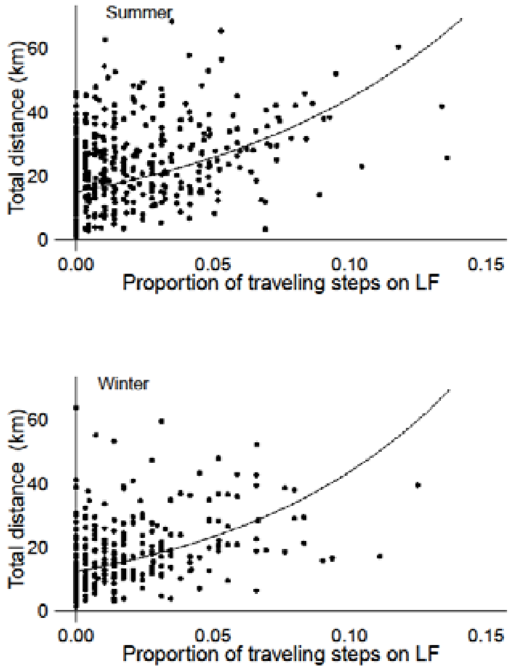

Fig. 5 The relationship between total distance moved by wolves in a day (km) and the proportion of travelling steps on linear features from individual wolves in summer (n = 20 wolves from 6 packs) and winter (n = 13 wolves from 6 packs).