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RESEARCH ARTICLE

# Movement ecology of wolves across an industrial landscape supporting threatened populations of woodland caribou

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**Abstract** Woodland caribou (*Rangifer tarandus caribou*) are a species of increasing conservation concern across North America. Throughout much of boreal Canada, human developments, including forestry and energy development, are now accepted causes of the decline in the number and distribution of caribou. One of the hypothesised mechanisms for the decline is altered predator–prey dynamics. We quantified the impacts of a variety of industrial activities on gray wolf (*Canis lupus*) and caribou interactions at a regional scale. We used animal locations collected with global positioning system collars and field data to examine how a range of industrial developments influenced the movements of wolves. We quantified the speed of wolf movements and the tortuosity of movement paths at two spatiotemporal scales across forested boreal and mountainous environments occupied by woodland caribou. Habitat and disturbance features better explained wolf movements during the weekly scale. In general, linear movements increased during winter, which paralleled past studies that suggested linear travel by wolves was associated with deep snow and the increased maintenance and patrol of territories. Wolves decreased movement rates but not sinuosity within close proximity to disturbance features, thus implying behaviours near such features were more closely associated with prey searching and hunting. Alternatively, wolves increased movement rates and linear travel through areas with high densities of linear and non-linear industrial features; this response suggested that wolves avoided spending time in high-risk areas associated with human activities. Results of this study further our understanding of wolf distribution and behaviour in habitats supporting populations of caribou within a matrix of industrial developments.

**Keywords** Anthropogenic disturbances · British Columbia · Linear features · Movement paths · Resource selection functions

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## Introduction

Throughout Canada, the increasing rate of industrial development provides economic opportunities, but also habitat change and fragmentation, altered community dynamics, and ultimately, a reduction in biodiversity (Schneider et al. 2003; Festa-Bianchet et al. 2011; Naugle 2011). Since the early 1990s, the South Peace region of northeastern British Columbia (BC) has undergone dramatic land-use changes associated with increasing levels of commercial forestry and energy development (Nitschke 2008). As with much of boreal Canada, woodland caribou (*Rangifer tarandus caribou*) are now of considerable conservation concern across the South Peace region (Festa-Bianchet et al. 2011; Williamson-Ehlers et al. 2012). These caribou were recently classified as Central Mountain caribou (Designatable Unit 8) and are behaviorally distinct, generally secluded by topography and genetically dissimilar from neighboring populations (Weckworth et al. 2001; McDevitt et al. 2009; COSEWIC 2011; Williamson-Ehlers 2012). These populations are exposed to a variety of industrial activities and are listed as threatened under the federal Species at Risk Act (SARA; Festa-Bianchet et al. 2011).

Activities related to industrial development serve as a catalyst for creating efficient travel corridors for gray wolves (*Canis lupus*), a primary predator of caribou in the boreal forest. Roads, seismic lines, pipelines, and other linear features (e.g., power lines) can provide greater mobility for wolves as well as access to habitats that would otherwise be isolated by topography or snow (Thurber et al. 1994; Paquet and Callaghan 1996; Latham et al. 2011). Following human developments, early seral forests become more abundant and support regenerating habitats that favour higher densities of primary prey species, such as moose (*Alces alces*), elk (*Cervus elaphus*), and deer (*Odocoileus* spp; Fuller and Keith 1981; Rempel et al. 1997; Schaefer 2003; Nitschke 2008). This change in landscape composition increases the distribution and abundance of wolves and the likelihood of interactions with caribou (James et al. 2004; Johnson et al. 2004; Wittmer et al. 2007; DeCesare et al. 2010).

Movement parameters describing animal paths can provide an index of animal behaviour relative to variation in resource availability (e.g., Ferguson et al. 1998; Johnson et al. 2002; Nams and Bourgeois 2004; Whittington et al. 2005). Past research has suggested wolves move more efficiently through habitats within close proximity to linear features with low human use (Mech 1970; Thurber et al. 1994; James and Stuart-Smith 2000; Rinaldi 2010; Latham et al. 2011; McKenzie et al. 2013). Thus, studying movements can increase our understanding of how wolves hunt for prey when using landscapes altered by human developments. Whittington et al. (2005), for example, recorded movement paths of wolves through snow and found that wolves avoided areas with high densities of trails and roads, but selected areas near linear features that were used infrequently by people. McCutchen (2007) used computer simulations of wolf movement to determine how linear corridors may contribute to predation on woodland caribou. Although results from McCutchen's (2007) study need to be assessed empirically, she found that predation was most influenced by an increase in the total number of wolves on the landscape, as opposed to wolf movement facilitated by linear corridors (McCutchen 2007).

We quantified variation in seasonal wolf movement as the rate of movement and sinuosity of paths and used those measures as an index of wolf behaviour. Movement patterns that have high tortuosity and short step lengths are generally indicative of areas where animals spend a lot of time foraging or hunting for prey (Wiens et al. 1995). Likewise, if animals are moving through an area, movements become more linear (i.e., minimal tortuosity and longer step lengths; Crist et al. 1992). If wolves in the South Peace region behave similarly to other populations across North America, we expected wolves to travel at increased rates and in a more linear direction in alpine habitats where fewer vegetative barriers, changes in topography, and increased snow hardness reduce the energetic costs of movement. Time spent by wolves searching and hunting throughout non-conifer habitats would increase (i.e., decreased movement rates) due to the availability of browse preferred by moose, elk and deer and in seasonal areas supporting populations of caribou. We expected non-linear features with low human use would aid behaviours of hunting and prey searching and linear features would facilitate linear travel across pack territories. Finally, we expected short-term (daily; fine-scale use) movements by wolves would indicate behaviours associated with hunting and searching. Alternatively, weekly movements (course-scale use), which facilitate patrol and defense of territories, would result in greater use of caribou habitat as wolves had increased opportunities to use features in mountainous and boreal habitats (e.g., alpine, established game trails) during

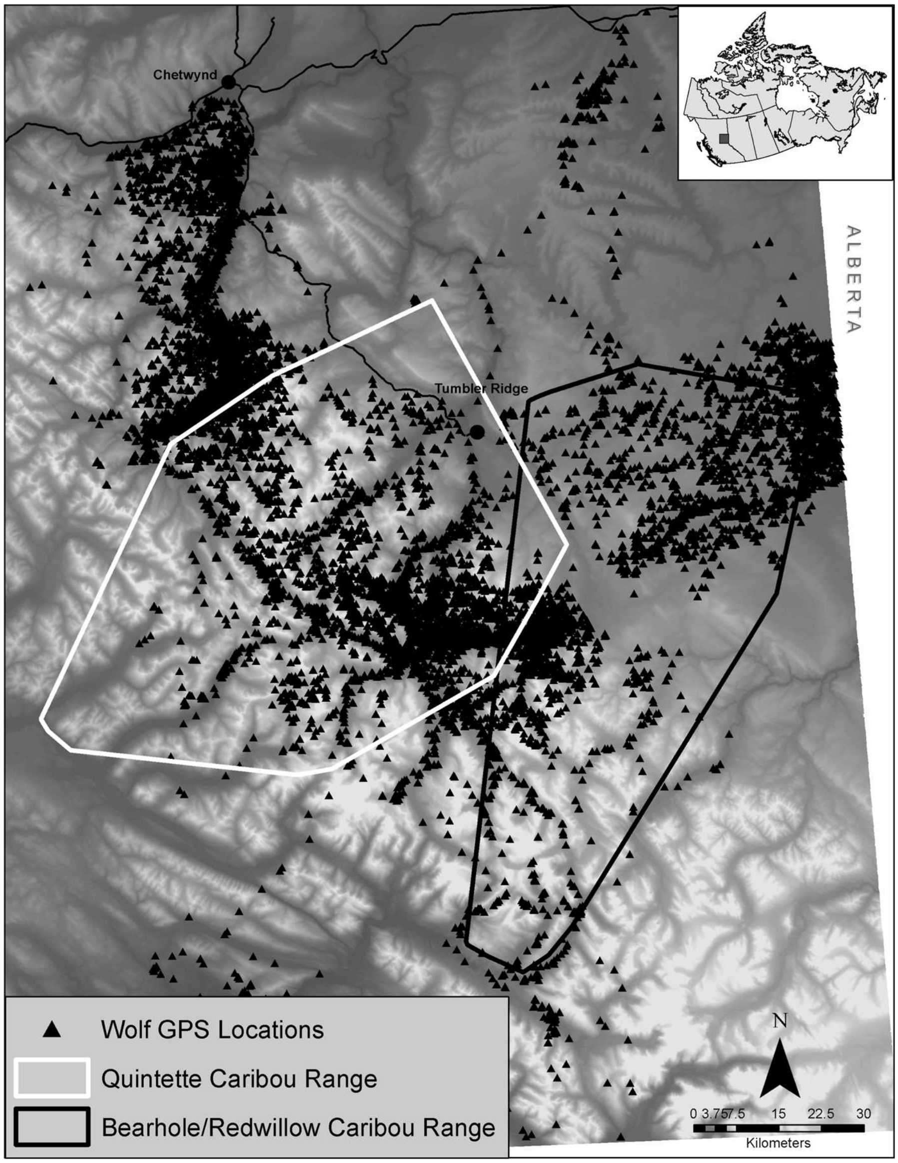



**Fig. 1** Locations from GPS collared gray wolves (*symbols*) and 95 % minimum convex polygons for woodland caribou across the South Peace region of British Columbia, Canada. Data include all locations collected from wolves ($n = 16$) in five packs between December 2007 and March 2010. Caribou were monitored between April 2003 and August 2009 and represent the Bearhole–Redwillow ($n = 5$) and Quintette ($n = 22$) herds

these large-scale movements (Supplement A summarizes predicted indices of movement behaviour for wolves).

There is considerable past research focused on the distribution and behaviour of wolves. However, researchers have not yet fully considered the variation in movement behaviour across multiple temporal scales in direct relation to populations of caribou (but see Latham et al. 2011 and Whittington et al. 2011). From a conservation perspective, studying movement parameters at both fine and coarse spatiotemporal scales can increase our knowledge of factors that may influence seasonal predation rates on caribou and how the movements of wolves are influenced by human-caused changes on the landscape. Furthermore, understanding the relationship between carnivore movements and landscape composition may have applications to other predator–prey systems influenced by human developments (Kinley and Apps 2001; Robinson et al. 2002; Cooley et al. 2008).

## Methods

### Study area and animal telemetry

The South Peace study area is approximately 12,000 km$^2$ and is located on the eastern slopes of the Rocky Mountains (54°07′ to 55°47′ N and 120°00′ to 122°13′ W) in northeastern British Columbia, Canada (Fig. 1).

Topography across the study area ranges from rugged mountains in the north and west to boreal forests in the south and east; elevation ranges from 385 to 3,058 m above sea level. Four Biogeoclimatic Ecosystem Classification zones characterize this region: Alpine Tundra (AT), Engelmann Spruce—Subalpine Fir (ESSF), and Sub-Boreal Spruce (SBS) dominate the mountainous regions, whereas SBS and Boreal White and Black Spruce (BWBS) become most prominent across the low-elevation boreal forests (Meidinger and Pojar 1991). Large-scale commercial forestry, natural gas, oil, mineral, and most recently, wind developments exist throughout the region (Sopuck 1985; Nitschke 2008). The cumulative effects resulting from these industrial developments have produced forested landscapes that are progressively younger and increasingly fragmented.

Between 2008 and 2010, 16 wolves from five packs were captured and fitted with global positioning system (GPS) collars (Lotek Inc., Newmarket, ON, Canada, model GPS 4400S). Collars were programmed to collect a location every 3 h ($n = 14$; two collars were programmed for high-frequency intervals and collected locations every 20 min) and were remotely downloaded from a fixed-wing aircraft approximately bimonthly. Data were examined for erroneous locations using the number of satellites required to obtain locations (2D or 3D) and visual inspection. We also collected GPS location data from caribou located in the Quintette (Q) and Bearhole–Redwillow (BHRW) herds (Fig. 1). The Quintette herd is found at higher elevations to the west of the boreal forest and winters primarily on windswept ridgelines in the alpine, whereas the BHRW herd remains in the low-elevation boreal forests during winter.

### Defining seasons

We used past research to develop two biological seasons to quantify the movement of wolves: non-winter (April 16–October 14) and winter (October 15–April 15). Non-winter months included the time when wolves were responsible for the rearing and raising of pups and centralize around dens, rendezvous or homesites (Mech 1970; Ballard et al. 1991). By mid-October, pups were approximately 6 months old and had grown large enough to travel with the nomadic pack (Packard 2003). Winter extended through the breeding season until the wolves began localizing around den sites between March and May (Mech and Boitani 2003).

### Movement paths, rates, and sinuosity

We used consecutive GPS collar locations to generate daily and weekly movement paths for collared wolves. These paths allowed us to compare the relationship between movement rate or sinuosity and land cover, industrial developments and caribou habitat. Paths generated from 24-h intervals allowed us to identify fine-scale behaviours and provided results that were comparable to past studies of wolf movement (Fritts and Mech 1981; Jędrzejewski et al. 2001; Walton et al. 2001; Whittington et al. 2005). Wolves patrol territories in cyclic patterns approximately every week (Jędrzejewski et al. 2001); therefore, we analysed patterns over a longer 7-day period to capture movement across larger portions of pack territories.

We assumed a straight-line distance between consecutive GPS locations when inferring movement paths and used Julian dates from the GPS collars to define the temporal extent of each path segment. Movement paths were incomplete and discarded from analyses if the number of acquired locations was ≤50 % of the total number of expected GPS fixes for each temporally constrained interval (24-h or 7-day period). We calculated movement rate as the total distance travelled (km) by individual wolves for each daily (distance/day) and weekly (distance/week) interval. Sinuosity of each path was calculated as the total distance of all line segments divided by the net displacement (i.e., the straight line distance between the start and end locations of each path). We explored a number of metrics for representing the sinuosity of movement paths. Alternatives that we considered included the fractal D and deviations from a correlated random walk (i.e., $CRW_{Diff}$). However, both of those metrics have limiting assumptions (Kareiva and Shigesada 1983; Turchin 1998). As this study was

**Table 1** Variables used to model movement of gray wolves across the South Peace region of British Columbia, Canada

| Variable | Description |
|---|---|
| Alpine | High elevation with few or no trees with primary cover being rock, snow, herbs, shrubs, bryoids and terrestrial lichens |
| Conifer | Conifer trees including tamarack (*Larix laricina*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), whitebark pine (*P. albicaulis*), and spruce (*Picea* spp.) |
| Deciduous (Decid) | Deciduous trees including aspen (*Populus tremuloides*), cottonwood (*P. balsamifera*), birch (*Betula papyrifera*) |
| Mixed-other | Upland areas dominated by talus, rock, snow, tailing ponds, herbs, bryoids and shrubs as well as conifer stands dominated by Douglas-fir (*Pseudotsuga menziesii*) |
| Water | Distance (km) to nearest water features (lake, river) |
| BHRW | Resource Selection Function values representing habitat selected by caribou of the Bearhole–Redwillow herd |
| Quintette (Q) | Resource Selection Function values representing habitat selected by caribou of the Quintette herd |
| Road | Distance (km) to nearest road |
| SeisPipln | Distance (km) to nearest seismic line or pipeline |
| Cutblock (Ctblks) | Distance (km) to nearest forestry cutblock |
| Mine | Distance (km) to nearest coal mine footprint |
| Oil and gas (OG) | Distance (km) to nearest oil and gas well pad or facility $\geq 1$ |
| LF dens | Density ($km/km^2$) of linear features including roads, seismic lines, and pipelines |
| NLF dens | Density ($ha/km^2$) of non-linear polygonal features including cutblocks, mine, oil, and gas facilities |

focused on the conservation ecology of woodland caribou and wolves, not the theoretical construct of animal movement, we decided to adopt the more simple metric (i.e., sinuosity is the total distance of all line segments divided by the net displacement).

We used polygonal buffers around each movement path to quantify the characteristics of the landscape traversed by collared wolves. For that calculation, we grouped high-frequency, 20-min locations into 24-h intervals and calculated the 100 % MCP around each temporally constrained group of locations to represent the average (i.e., median) area ($km^2$) used by each of the collared wolves; this value, representing the average area of use by wolves, became the radius (km) for the movement buffers applied to each daily and weekly movement path.

## Resource and human disturbance variables

We drew from past research on wildlife–human development interactions to identify five classes of variables (Table 1) that we hypothesized would influence movement behaviours of wolves (forest cover, distance to water, relative value of caribou habitat, and distance to and density of disturbance features).

Forest cover was estimated using the provincial Vegetation Resource Inventory (VRI; BC Ministry of Forests and Range 2007a, b). We consolidated the vegetation types into four classes: alpine, conifer, deciduous, and mixed-other forests. Each class of forest cover was converted to a binary layer so the average (%) could be extracted for each movement polygon. We also tested the importance of water (proximity) as a predictor of wolf movement; water features included lakes, rivers, streams, and reservoirs. We used Resource Selection Functions to model the seasonal distribution of habitat selection for the Bearhole–Redwillow and Quintette caribou herds (see Williamson-Ehlers 2012; Supplement C summarizes the resource selection function analysis for woodland caribou). The average RSF value was extracted each season for the buffered area around each wolf movement path. Non-winter represented the median value for caribou habitat modeled during the spring, calving and summer-fall, whereas winter was used in its original context.

We used databases from government and industry to identify the location of disturbance features across the South Peace region (BC Land and Resource Data Warehouse 2007; Oil and Gas Commission of BC 2009, West Fraser Timber Company Ltd., Western Coal, Inc., Peace River Coal Ltd.). We used a moving window size of 1.56 ha (as determined using AIC sensitivity analysis; Williamson-Ehlers 2012) to calculate the density of industrial features (total area of features/unit area; $ha/km^2$). We combined polygonal data for forestry (cutblocks) and mine/oil/gas sites to create a variable representing the density of non-linear features ($ha/km^2$). Variables for distance (km) and density were modeled as linear and 2-term quadratic functions (e.g., distance to road + distance to road$^2$). We used a zonal raster analysis to extract the average distance and disturbance values for each movement path. We used Hawth's Tools and GME (Spatial Ecology LLC 2009) in ArcGIS 9.3 (2009; ESRI, Redlands, CA) to create daily and weekly movement paths for wolves, as well as to attribute habitat, caribou RSF and disturbance values for each buffered movement path.

## Statistical analysis of wolf movements

We used mixed effects generalized linear models to statistically relate movement rate and sinuosity to landscape variables recorded within the area of each 24-h or 7-day movement interval. We added a random effect to account for variance that may have occurred among individuals or packs. This approach does not rarify or thin the data, but statistically controls for temporally or spatially correlated samples. Furthermore, we used a robust variance estimator which produces a confidence interval that can accommodate mis-specified correlation structures that may be associated with autocorrelation (Rogers 1993). We conducted an AIC sensitivity analysis to determine if a random effect was required for individual wolf, pack, or wolf and pack (Gillies et al. 2006; Hebblewhite and Merrill 2008).

We used linear regression to model movement rate normalized using a square root transformation. Because of extremely non-normal sinuosity data and variation in the distribution of those data across animal and season, we transformed those measures into binary categories and applied logistic regression. We used the median value across each seasonal dataset to classify paths as high (1) or low (0) sinuosity. This reduced the information content of each path, but allowed us to statistically model the complex process of wolf movement.

We identified 19 ecologically plausible candidate models to determine the influence of habitat and disturbance variables on wolf movement (Table 2). We used tolerance scores (<0.2) and visual inspection of bivariate correlation matrices to assess multicollinearity; where collinearity occurred between disturbance variables, we preferentially removed non-linear to retain linear features. We used an information-theoretic approach to identify the most parsimonious fixed effects linear or logistic regression model for each season (Burnham and Anderson 2002).

**Table 2** Candidate models to examine movement of gray wolves monitored across the South Peace region of British Columbia, Canada

| Model group | Model name | Model variables |
|---|---|---|
| Habitat | Land cover | % Land cover (alpine, conifer, deciduous, mixed-spp) |
| | Caribou-water distance (Dist; CarWat) | Caribou RSF + water dist |
| | Landscape | % land cover + caribou RSF + water dist |
| Linear features (LF) | Road dist | Landscape + road dist |
| | LF (roads, seismic lines or pipelines) dist | Landscape + LF dist |
| | LF density (LF dens) | Landscape + LF dens |
| | LF total (LF CE) | Landscape + LF dist + LF dens |
| Cumulative effects (CE) | CE dist | Landscape + LF dist + non-linear feature (NLF) dist |
| | CE dens | Landscape + LF dens + NLF dens |
| | CE total (CE) | Landscape + LF dist + LF dens + NLF dist + NLF dens |

Each model (except land cover) was fit as either a linear or Gaussian (squared) term depending on best fit for each movement parameter and season

If competing models were present, we considered the model with the smallest $AIC_c$ difference ($\Delta$) to be the most parsimonious. We applied the random effect to the most parsimonious model and reran the analysis to generate model coefficients. We then used the coefficient of determination ($R^2$) to assess predictive fit for linear regression models. We randomly partitioned wolf movement paths into training (80 %) and testing (20 %) groups. Using the withheld (testing) data, we assessed if there was a relationship between the observed and predicted movement rates (prcounts.ado: Long and Freese 2006). As a second measure of model fit and prediction, we calculated the unstandardized residuals; perfect prediction occurred when the mean residuals for movement rate equaled zero, whereas positive values indicated under-prediction and negative values indicated over-prediction. We also evaluated fit for the top-ranked logistic regression

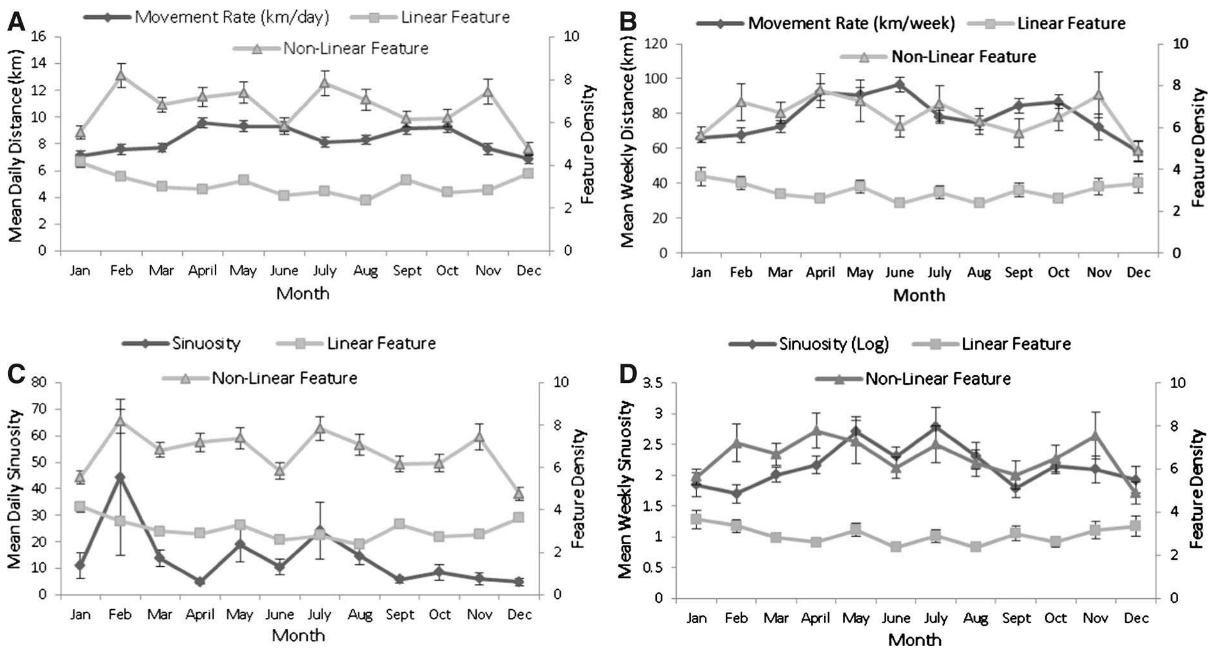



**Fig. 2** Mean (±SE) monthly movement rates (**a**, **b**) and sinuosity (**c**, **d**) for daily and weekly sampling periods in relation to densities of linear (km/km$^2$) and non-linear (ha/km$^2$) features across the South Peace region of British Columbia, Canada, 2008–2010

model of sinuosity by calculating the area under the receiver operating characteristic curve (AUC; Hosmer and Lemeshow 2000).

## Results

We used 25,254 GPS locations collected from wolves to develop 3,749 daily and 493 weekly movement paths. Greater than 75 % of all daily movement paths contained ≥6 wolf locations out of a maximum of 8 (non-winter = 75.1 %; winter = 92.1 %). Likewise, ≥84 % of all weekly paths contained ≥41 locations out of a maximum of 64 (non-winter = 84.9 %; winter = 97.4 %). Two wolves of the Chain Lakes pack provided an additional 8,493 high-frequency locations ($n = 168$ daily MCPs). The daily area used by these two wolves (median area) was 4.44 km$^2$; we used those data to identify the area of use (typical area an animal could use each day) around each daily and weekly movement path. In general, movement and sinuosity measures varied by season and scale of measurement (Fig. 2).

As predicted, movement rates of wolves were highest during the non-winter season. Wolves travelled the greatest distances during the non-winter season. However, seasonal variation in movement was greater than variation in the use or proximity to linear and non-linear features, suggesting that other factors also influenced the movement dynamics of wolves (Fig. 2).

For each season, the most parsimonious models for daily (non-winter $AIC_w = 1.00$, winter $AIC_w = 1.00$) and weekly (non-winter $AIC_w = 0.99$, winter $AIC_w = 1.00$) movement rates were also the most complex and contained variables for all cover types and human-caused disturbances (Supplement B summarizes the number of parameters ($k$), log-likelihoods (LL), AIC differences (ΔAIC), and $AIC_c$ weights ($AIC_w$) for daily and weekly movement rates and sinuosity of movements of gray wolves). Models with a random effect for pack performed best across all models for seasonal movement rate and sinuosity. One model (daily movement rate during the winter season) was an exception and performed better with a random effect for individual wolf. Greater than 34 % of the variation in movement rate was explained by the weekly (non-winter $R^2 = 0.343$, winter $R^2 = 0.501$) regression models. When modeling daily movement rates, ≤18 % of the overall variation was explained (non-winter $R^2 = 0.117$, winter $R^2 = 0.175$) by variables representing habitat and disturbance features.

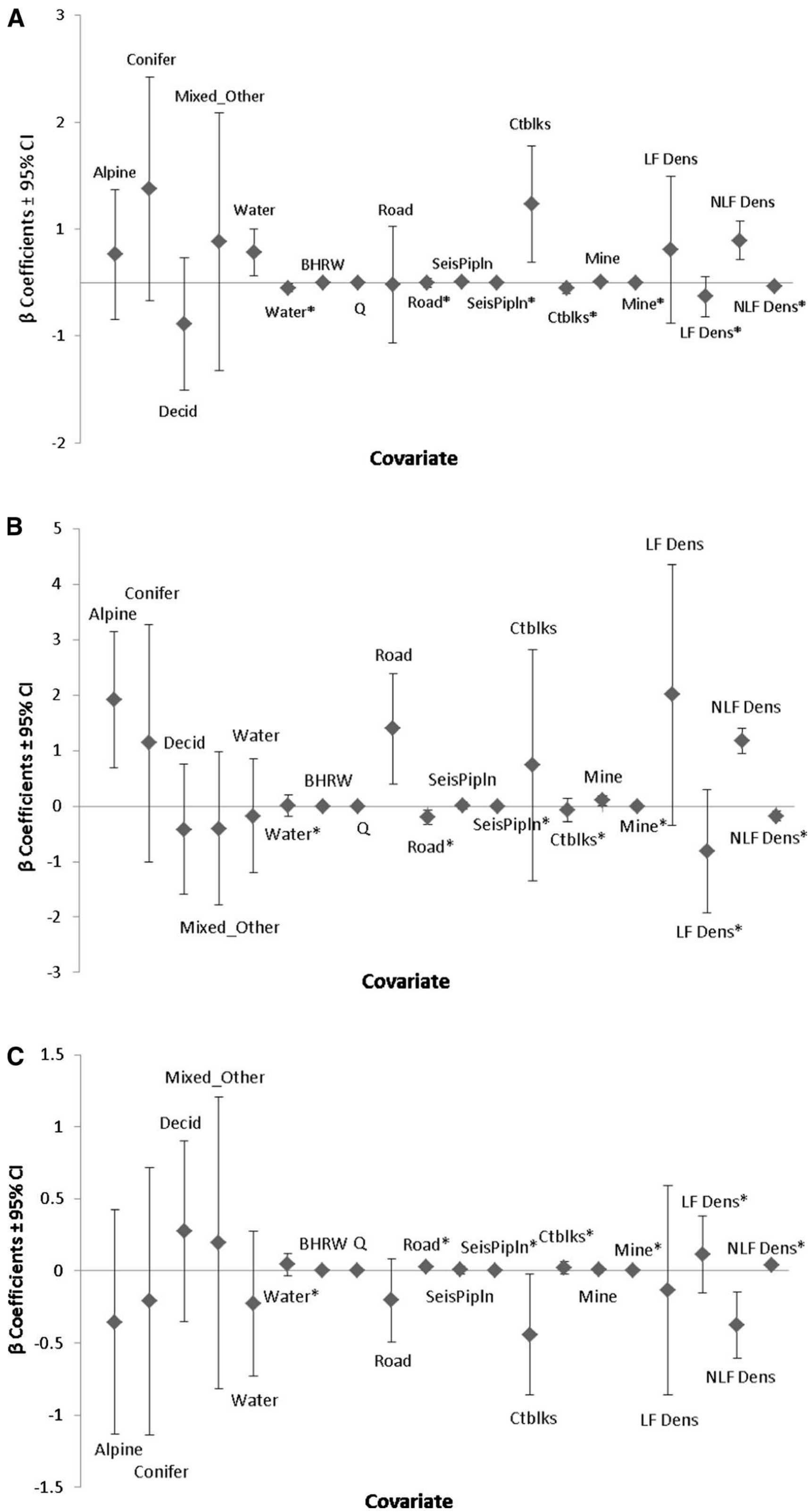
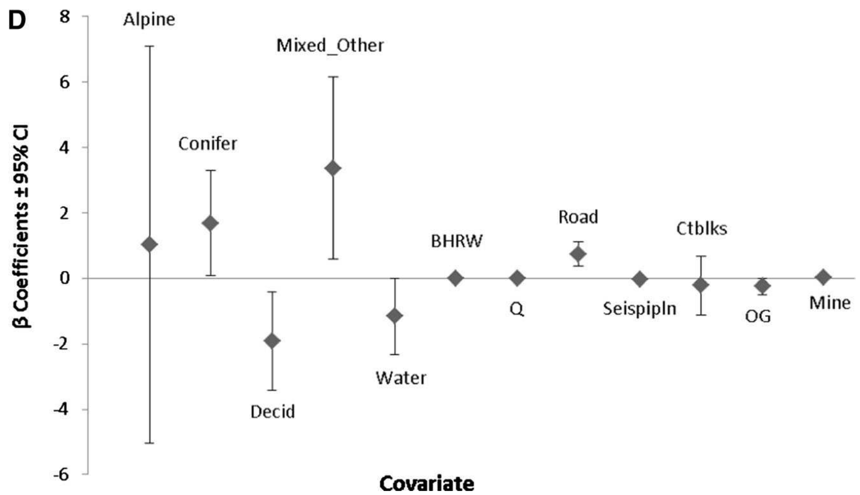



**Fig. 3** Coefficients for the parameters in the most parsimonious mixed-effects models for daily ($n = 1{,}599$) and weekly ($n = 212$) movement rates (**a**, **b**) and sinuosity (**c**, **d**) during the non-winter season for gray wolves in the South Peace region of British Columbia, Canada. An *asterisk* indicates a quadratic term. For example, wolves increase movement rates as NLF Dens increase to some point where movement rates then decrease; this is an example of a (+) NLF Dens followed by a (–) NLF Dens$^2$. Model variables are given in Table 1

**Fig. 3** continued




Similar to movement rate, the most parsimonious logistic regression models for sinuosity of daily movements were also the most complex in each candidate set (non-winter $AIC_w = 0.88$, winter $AIC_w = 1.00$; Supplement B). AUC scores indicated poor predictive performance for the best-ranked seasonal models for daily sinuosity (non-winter AUC = 0.55, winter AUC = 0.62). Results from the weekly sinuosity models indicated multiple candidate models had reasonable support compared to the top-ranked model. During the non-winter season, the most parsimonious model ($AIC_w = 0.35$) for weekly sinuosity included covariates for forest cover, distance to water, caribou habitat selection, and distance to linear features. The top model ($AIC_w = 0.27$) for weekly sinuosity during winter was similar to non-winter, but included covariates for linear feature density (in addition to distance) across the landscape. Model fit was generally poor for weekly sinuosity models during the non-winter season (AUC = 0.64), but improved during winter (AUC = 0.75).

Movements during non-winter

Daily movement rates for wolves decreased during the non-winter season as they traveled closer to water features and cutblocks (Fig. 3a).

However, the large confidence interval surrounding the coefficient for cutblocks suggested considerable variation in response by wolves. Higher daily and weekly movement rates were associated with intermediate densities of non-linear features (oil and gas well sites, facility stations, coal mines; Fig. 3a, b). Weekly movement rates decreased slightly near coal mines, but increased in alpine habitats (Fig. 3b). Roads were the only linear feature wolves responded to during the non-winter months; movement rates decreased as wolves travelled within close proximity to roads at the weekly scale (Fig. 3b).

During the non-winter season¸ movement paths became increasingly linear as wolves travelled near deciduous habitats and areas with moderate densities of non-linear features (Fig. 3c, d). In addition, the probability of linear movements increased slightly near roads and coal mines, whereas the probability of sinuous movements increased at the weekly scale near conifer forests, mixed-species forests and cutblocks (Fig. 3d). At the daily scale, the probability of sinuous movements by wolves increased slightly in low-elevation boreal habitats selected by the BHRW herd and high-elevation mountainous habitats selected by Quintette herd (Fig. 3c). Similarly, the probability of sinuous movement paths at the weekly scale increased slightly in habitats selected by the BHRW herd.

Movements during winter

Daily movement patterns of wolves during the winter season were influenced more by forest cover, caribou habitat selection, and disturbance features than during non-winter (Fig. 4).

Daily movement rates decreased in habitats dominated by conifer forests (Fig. 4a); weekly movement rates increased in mixed-species forests (Fig. 4b). Daily movement rates decreased as wolves approached water features and cutblocks (Fig. 4a). Although to a

**Fig. 4** Coefficients for the parameters in the most parsimonious mixed-effects models for daily ($n = 1,403$) and weekly ($n = 186$) movement rates (**a**, **b**) and sinuosity (**c**, **d**) during the winter season for gray wolves in the South Peace region of British Columbia, Canada. An *asterisk* indicates a quadratic term. For example, weekly movements become more sinuous (**d**) as wolves get closer to water up to a certain distance where linear movements then increase; this is an example of a (–) water followed by a (+) water$^2$. Model variables are given in Table 1

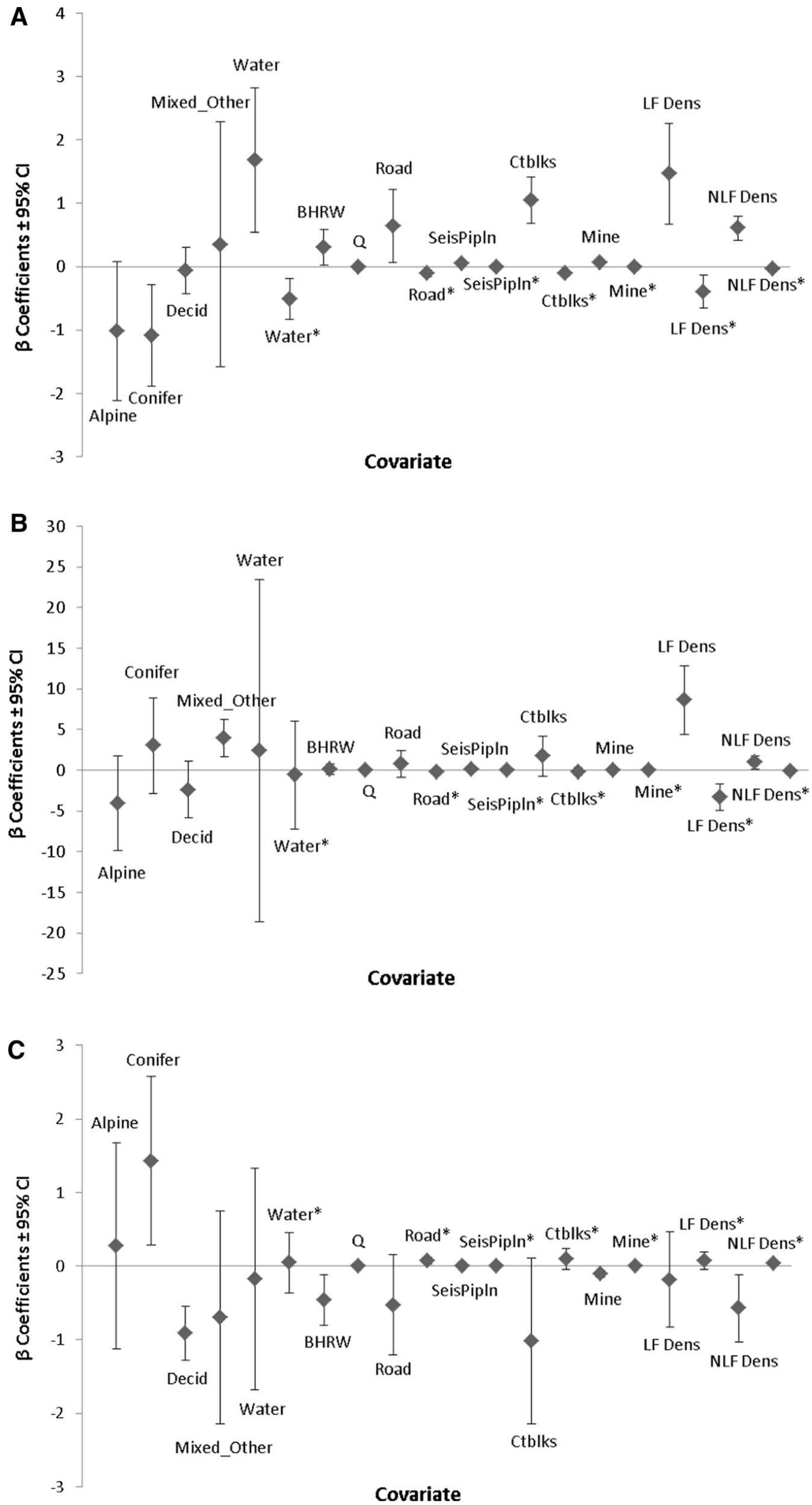
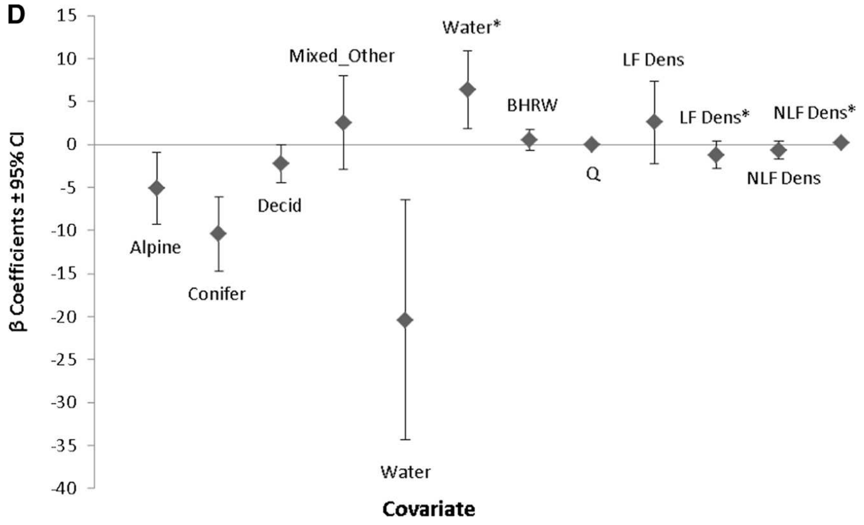


**Fig. 4** continued




lesser extent, daily movement rates of wolves also decreased near roads, seismic lines, pipelines, and mines during winter (Fig. 4a). However, as densities of linear and non-linear disturbance features increased across the landscape, wolves increased both daily and weekly movement rates (Fig. 4a, b). Daily movement rates also increased when wolves occupied low-elevation habitats selected by BHRW caribou (Fig. 4a).

The probability of sinuous movement paths decreased in areas dominated by deciduous forest (Fig. 4c, d). Conifer forests facilitated an increase in the probability of sinuous movements at the daily scale. Wolves demonstrated an increased probability of linear travel in alpine habitats at the weekly scale only. During winter, the probability of sinuous movements increased slightly in high-elevation habitats selected by Quintette caribou (Fig. 4). Wolves demonstrated an increased probability of daily linear travel where the density of non-linear features increased and in low-elevation habitats selected by BHRW caribou (Fig. 4c). As wolves traveled close to coal mines, we observed a slight relative increase in the probability of sinuous movements (Fig. 4c).

## Discussion

We used two parameters as an index of movement behaviour of gray wolves across mountainous and forested boreal environments occupied by woodland caribou. Our results indicated that cumulative effects from industrial disturbances, parameterised as densities of linear and non-linear features, influenced movement behaviour of wolves in both environments. Past studies of wolf movement did not quantify compounding effects from multiple sources of human disturbances (e.g., forestry and oil/gas extraction), determine how those behaviours change across spatiotemporal scales, or examine how wolves move across areas supporting populations of caribou (but see Kuzyk et al. 2004; Neufeld 2006; Houle et al. 2010; Latham et al. 2011).

### Scale

At the weekly scale, our results indicated that movements were generally greater for wolves across the South Peace region during non-winter than winter months. If wolf packs across the study area successfully reproduced throughout the duration of this study, increased movement rates (up to 2 km/h) could result from rapid travel back to dens or homesites after feeding bouts (Mech 1994). However, as responsibilities associated with pup care are dependent on an individual's pack status, behavioural interpretation remains challenging without investigating the direct ecological determinants of path characteristics (e.g., behaviour, activity type, or association with a den or homesite).

### Habitat features

Unlike conifer and mixed-species forests, deciduous habitats facilitated linear movements during both seasons. Moose, deer, and wolves were more common in harvested forests where the regrowth of deciduous species provides abundant forage for ungulates (Laurian et al. 2008; Hebblewhite et al. 2009). Linear travel by wolves through deciduous forests during winter might suggest ungulates seasonally shift habitat use, that wolves remain unpredictable to prey by altering seasonal movement patterns, or a response to components of the landscape that we did not assess (e.g., snow depth; Jędrzejewski et al. 2001; Mech and Boitani 2003; Whittington et al. 2011). Furthermore, sinuous movements associated with hunting in some habitats may become detectable only at finer observational scales, and the addition of a spatio-temporal cluster analysis in future studies could aid in refining our understanding of each behaviour (e.g., hunting, bed sites, predation sites, territory maintenance; Knopff et al. 2009; Morales et al. 2010). Throughout the year, wolves traveled more slowly near water, but this response was statistically significant for daily models only. Lowland or riparian habitats provide wolves with increased opportunities to hunt moose, deer, and beaver (*Castor canadensis*) and are also important in the selection of natal dens and homesites (Mech 1970; Packard 2003; Latham 2009). As important as lakes, rivers, or creeks may be for increasing travel efficiency and territory maintenance (Peterson 1977), we were unable to detect direct travel on these features in winter.

## Industrial disturbance

Industrial disturbances influenced the movement behaviour of wolves at both spatiotemporal scales throughout the year. During non-winter months, wolves decreased weekly travel rates and the probability of sinuous movement near roads. Levels of human activity dropped during this period, allowing low-risk opportunities for wolves to travel along road corridors for short intervals of time. Close proximity of wolves to roads may have been associated with searching and hunting for prey; moose select habitats near roads not only to forage on abundant vegetation and mineral deposits, but also to travel across seasonal ranges (Child et al. 1991; Rea 2003; Laurian et al. 2008). If roads were used by wolves to simply increase travel efficiency during winter, we would expect an increase in movement rates and linear travel. Our data did not support this hypothesis as increased linear movements were observed only at larger spatial scales during non-winter, when human activity related to industrial activities was less.

Linear features had the greatest influence on wolf movements at the daily scale during winter. Daily movement rates decreased near seismic lines and pipelines (in addition to roads) until those features became more abundant across the landscape. Furthermore, the cumulative densities of roads, seismic lines and pipelines did not result in more linear travel for wolves at either the daily or weekly scale. Slower movements and sinuous travel during winter suggested that these corridors were more important for hunting than increased travel efficiency.

Contrary to movements near individual features, wolves travelled more rapidly through habitats with intermediate densities of linear features. Hence, there may be a large-scale landscape effect in which wolves can exploit individual features within their range for hunting, but increasing densities of features, and associated human disturbance, result in the avoidance of such areas. Similar avoidance responses were noted for wolves studied in other jurisdictions (James 2000; Whittington et al. 2005; Hebblewhite and Merrill 2008; Houle et al. 2010; Lesmerisis et al. 2013).

Non-linear industrial features affected the movements of wolves more consistently than linear features. Movement rates decreased each season near forestry cutblocks and coal mines, but increased at both scales once the density of features increased. The initial phases of exploration or construction associated with forest harvesting and oil and natural gas extraction result in high levels of disturbance to wildlife (Bradshaw et al. 1997). Across the study area, human activities at oil and gas facilities peaked between September and December; increased rates and linear movements by wolves near these facilities during winter suggested a negative response to human activity (Houle et al. 2010; Energy and Resources Conservation Board 2011). For this study, we did not classify the age of disturbance features, or the level of human activity associated with each disturbance type. Such data could contribute to our understanding of the movement behaviours of wolves relative to prey availability and wolf tolerance for humans.

## Caribou habitat

The habitats we identified as selected by caribou did not influence the movement rates of collared wolves during the non-winter season. Differential habitat use by caribou and wolves at the patch scale further suggest some level of spatial separation between BHRW caribou and wolves in the boreal forest (James et al. 2004). However, even an opportunistic kill by wolves could hasten the decline of the BHRW herd that was estimated at 24 individuals in 2013 (Seip and Jones 2013).

Due to the complexity of cumulative effects from activities associated with resource exploration and extraction, we were unable to detect obvious correlations between wolf movement and increased predation risk for caribou. However, patterns of wolf movement (i.e., increased probabilities of sinuous movement and decreased movement rates) indicated caribou are most vulnerable to predation when in close proximity to disturbance features. As the density of these features continues to increase across the landscape, caribou will find it more challenging to find refuge from wolves.

Recorded movements of collared gray wolves suggested seasonal behaviour was driven by a combination of life cycle stage, environmental factors, prey availability, and human disturbances (Peters and Mech 1975; Bibikov et al. 1985; Jędrzejewski et al. 2001). These results further confirm the utility of fine-scale movement data for developing a better understanding of the interactions between landscape dynamics and animal behaviour. Our results provided novel insights regarding responses of wolves to landscape heterogeneity, but only across a small range of behavioural scales and with limited inference to the mechanisms influencing movement.

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