Evaluating the influence of anthropogenic landscape change on wolf distribution: implications for woodland caribou

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Abstract. Across much of the range of woodland caribou (Rangifer tarandus caribou), predator–prey dynamics have changed as a result of large-scale industrial development. Land clearing and associated early-successional forests have resulted in a greater density and distribution of moose (Alces alces), deer (Odocoileus spp.), and their associated predators. This process of apparent competition has resulted in increased predation on woodland caribou. We employed a combination of field and statistical methods to better understand the distribution and interactions of wolves (Canis lupus) and caribou across a region with high levels of industrial development. We used count models to investigate the frequency of wolf occurrence relative to landcover types, disturbance features, and caribou habitat. As predicted, the co-occurrence between caribou and wolves was rare. Similarly, the remains of caribou were identified at a small proportion of the sites where wolves killed large prey. Caribou occurred at low densities across the study area, and thus, wolves likely pursued other more abundant deer species. Encounters between wolves and caribou habitat was most likely to occur in the low-elevation boreal forest and areas closer to and with higher densities of forestry cutblocks. Our results highlight the importance of understanding the spatial dynamics of multi-species interactions when developing recovery strategies for threatened and endangered species.

Key words: apparent competition; Canis lupus; cumulative impacts; habitat; industrial development; Rangifer tarandus; resource selection.

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INTRODUCTION

The distribution of organisms is a fundamental concept for not only ecology, but also conservation. However, the dynamics of distribution, and the implications for conservation planning, are made more complex by multi-species interactions. When considering the spatial relationship between predators and their prey, predators orient themselves to areas where there are greater densities of prey, whereas prey avoids areas with increased predation risk while attempting to meet nutritional requirements (Lima and Dill 1990). Human activities and developments can influence that relationship. Loss of contiguous habitat, disturbance and displacement, and the generation of linear corridors can alter the density and distribution of both species. For example, human developments can change the quantity and quality of vegetation and force prey to concentrate in space facilitating predation (Schlapefer et al. 2002). Altered predator–prey
Changing patterns of land use over the past 100 years have altered the interactions among wolves (*Canis lupus*), woodland caribou (*Rangifer tarandus caribou*), and other prey species. Wolves are the primary predator of caribou across much of their range (Bergerud and Elliot 1986, Seip 1992, Festa-Bianchet et al. 2011). However, the rate of predation for caribou has likely increased following landscape change (Santomauro et al. 2012). Forestry, oil and gas exploration and development, and other types of industrial activity create early-successional plant types that favor higher densities of moose (*Alces alces*) and deer (*Odocoileus* spp.). This alteration in the distribution of plant communities, and associated herbivores, across large regions facilitates more abundant wolf populations and increasing opportunities to use caribou as an alternative prey species (James et al. 2004, Wittmer et al. 2007, Serrouya et al. 2011, Latham et al. 2013). This evolving predator–prey relationship is referred to as apparent competition (DeCesare et al. 2010). Moose and deer do not directly compete with caribou for forage or space, but increases in the distribution or density of these ungulates results in a greater number of wolves and an increase in mortality for caribou. Contributing to this dynamic, large-scale human development can result in a variety of linear features that occur as narrow paths of early-successional vegetation communities. These features can increase the distribution of ungulates, such as moose, as well as the vagility of wolves that must search for prey on a relatively unpredictable landscape. Although linear features can increase the rate of movement of wolves and decrease the spatial separation with caribou, it is the numerical response of wolves to an increasing ungulate prey base that is the primary cause of decreasing populations of caribou (McCutch en 2007, Latham et al. 2011a).

Woodland caribou are declining rapidly across much of their boreal and montane range (Hervieux et al. 2013, Johnson et al. 2015). The proximate cause is thought to be predation facilitated by landscape change (Serrouya et al. 2011, Peters et al. 2013). Wolves have the ability to adapt to spatial and temporal variation in resources, including the selection or avoidance of human activities and associated industrial features (Mladenoff et al. 1999). Despite theoretical guidance and research linking wolf occurrence with human presence, there is still a need to better understand the behavior and distribution of wolves in areas where cumulative anthropogenic disturbances might influence predator–prey dynamics (Nitschke 2008, Houle et al. 2010). In particular, past studies have considered wolf interactions with only a few disturbance types, often linear features such as roads and seismic lines, not the cumulative effects of multiple industrial activities that occur at the scale of the feature and the landscape (Lesmerises et al. 2012, Ehlers et al. 2014).

Our objective was to better understand the resource selection strategies of wolves and resulting predation risk for woodland caribou across a landscape with high levels of industrial development. We predicted that wolves would select industrial features that facilitated movement and a higher likelihood of spatial interaction with deer and moose, the most abundant prey species in the study area. Given current observations of apparent competition between caribou and other ungulate species (Wittmer et al. 2005, Serrouya et al. 2011), and the low density of caribou in the study area, we further predicted relatively little overlap between wolf distribution and seasonal habitats used by caribou. As a corollary, we predicted that moose and deer would be the primary prey identified at the kill sites of wolves.

Detailed investigations of the habitat ecology of wolves and caribou serve as a foundation for increasing our knowledge of the spatial and temporal relationships of these two species with implications for the conservation of woodland caribou (Festa-Bianchet et al. 2011). Such insights may also apply to other species influenced by increasing human disturbances and apparent competition (DeCesare et al. 2010).

**Methods**

**Study area**

The South Peace study area is approximately 12,000 km² 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 eastern British Columbia (BC), 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. Four Biogeoclimatic Ecosystem Classification zones characterize this region: Boreal Altai Fescue Alpine (BAFA), Engelmann Spruce–Subalpine Fir (ESSF), and Sub-Boreal Spruce (SBS) dominate the mountainous regions, whereas SBS and Boreal White and Black Spruce (BWBS) are most prominent across

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**Fig. 1.** Locations of 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 four 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.
the low-elevation (~1300 m) boreal forests (Meidinger and Pojar 1991). Dominant tree species in the SBS and BWBS include hybrid white spruce (Picea engelmannii × glauca), black spruce (P. mariana), and tamarack (Larix laricina) on bog-type sites, and drier stands of lodgepole pine (Pinus contorta). The ESSF zone occurs at mid-elevations where dominant tree species include white spruce (P. glauca), subalpine fir (Abies lasiocarpa), and trembling aspen (Populus tremuloides). At the highest elevations (>2000 m), caribou are found across the BAFA ecosystem. Large-scale commercial forestry, natural gas, oil, mineral, and most recently, wind developments exist throughout the region (Nitschke 2008, Johnson et al. 2015). These industrial developments have produced forested landscapes that are progressively younger and increasingly fragmented.

Animal location data

Between March 2007 and March 2010, 16 wolves from four packs (Upper Sukunka, Onion Creek, Upper Murray, and Chain Lakes) were captured and fitted with a remotely downloadable GPS collar (Lotek, Newmarket, Ontario, Canada, model: GPS 4400S). All wolves were chemically restrained with Telazol prior to collar attachment. The drug was delivered in a 3-ml light-weight, disposable dart fired from a helicopter at the lowest effective velocity setting. GPS collars were equipped with VHF transmitters, as well as remote-release devices. Collars were programmed to take a location fix every 3 h (n = 14; two collars were programmed for high-frequency intervals and collected a location every 20 min) and were remotely downloaded from a fixed-wing aircraft approximately bimonthly during routine tracking flights. Location data were screened and examined for erroneous locations (see Williamson-Ehlers 2013 for further details of GPS collar fix and success rate). The collars in this study performed well, achieving an average fix success rate of 85.2% (SD = 7.2, range = 76–98%).

Defining seasons

We used past research to develop three biological seasons to model the response of wolves to their environment: non-winter (16 April–14 October), early winter (15 October–31 January), and late winter (1 February–15 April). Non-winter months include the time when wolves become responsible for the raising and rearing of pups and, therefore, centralize around dens or homesites (Mech 1970, Ballard et al. 1991). By mid-October, pups are approximately six months old and have grown large enough to travel with the nomadic pack as they transition toward the winter months (Packard 2003). In North America, breeding season occurs between late January and early April, depending on latitude; this marks the transition into late winter (Kreeger 2003). Late winter extends until the wolves begin localizing around a den site between the months of March and May (Fuller 1989). Drawing on variation in biology, snow conditions, and movement patterns, Jones et al. (2007) identified biological seasons for four herds of caribou found adjacent to, or within, the study area. We used this information to define four primary seasons for the study of resource selection by caribou: spring (1 April–14 May), calving (15 May–14 June), summer/fall (15 June–31 October), and winter (1 November–31 March).

Resource selection of wolves: count models

To test our first hypothesis that the spatial distribution of wolves correlated with human developments, we used count models to relate the number of wolf locations, or counts, within a habitat selection unit (HSU), to covariates that represented environmental or industrial features. Where the data allowed (i.e., model convergence), we used a two-process model (i.e., zero-inflated; Nielsen et al. 2005) that first represented the presence/absence (binary) portion of the observed location data, the probability of occurrence of wolves within an HSU, and second, the count portion of the model that represented the relative frequency of use of an HSU by wolves (Sawyer et al. 2006). This approach allowed us to not only identify covariates that correlated with the use of an HSU, but also the intensity of use as measured by a greater number of counted wolf locations across a standard spatial area. We assumed that a greater number of counts indicated an increased value of some set of resources for wolves relative to hunting of some other seasonal life-history requirement (e.g., denning).

We used a likelihood ratio test to check for over-dispersion and to determine whether a
Poisson (PRM) or negative binomial (NBRM) distribution was most appropriate for the zero-inflated count models. Because data collected with GPS collars were correlated in space and time, we used the robust option in Stata (Release 10.0, StataCorp, College Station, Texas, USA), to adjust standard errors (SE) for an autocorrelated error structure.

To define a biologically meaningful spatial extent of the HSU, we calculated the average area occupied by wolves after killing and consuming what was assumed to be a large prey item (e.g., moose, caribou, deer). The HSU was premised on a dominant behavior, hunting and killing of prey, and was less arbitrary than past applications of this method (e.g., Sawyer et al. 2006). Also, numerous past works have validated the clustering of wolf locations, and by extension occupancy, at kill sites (e.g., Lake et al. 2013).

During three summers (2008–2010), we investigated wolf kill sites identified from clusters of GPS collar locations distributed throughout each pack territory. Each cluster represented a grouping of GPS collar locations defined as two or more consecutive locations within 200 m of one another. To minimize search effort of non-kill sites (e.g., bed sites), we investigated clusters containing ≥ four location fixes (four fixes = 12 h of time) only. The area of use (AOU; ha) by collared wolves at each identified kill site was calculated as the minimum convex polygon (100% MCPs) of locations that occurred within a one-week time period surrounding the location and assumed date of kill (Fig. 2). For each pack territory, the area of a HSU was calculated as the mean of all AOsUs for collared wolves of that pack. Each HSU served as a datum, defining the number of locations recorded for GPS-collared wolves and resource attributes that might explain the variation in wolf locations among HSUs.

Habitat and human disturbance variables

Drawing from past research on wildlife development interactions and observations of the study area, we identified a number of variables that in combination served as hypotheses for explaining the responses of wolves to the environment (Table 1). Seasonal count models contained combinations of variables representing vegetation cover type (categorical), seral stage of forest (categorical), value of caribou habitat, distance to nearest water source, and distance to and density of disturbance features. We used a systematic grid of locations to sample the habitat and human disturbance variables within each HSU (Fig. 3). Continuous variables were calculated as the median value within an HSU, for example, the median distance of the sample locations to the nearest linear feature and the median RSF score for caribou within the HSU. Categorical variables were modeled with deviation coding (Menard 2002).

Vegetation cover type.—Forest type and seral stage were estimated using the provincial Vegetation Resource Inventory (VRI; British Columbia Ministry of Forests and Range 2007). We consolidated categories of forest from the VRI into 11 new classes, based on the leading commercial or brush species (Table 1). We categorized seral stage into five age classes based on regimes of fire disturbance for dominant species in each BEC zone (Meidinger and Pojar 1991). Across the study area, VRI data were incomplete for a portion of alpine-type habitats. Therefore, we classified age in those “no age data” habitats as late-successional forests (i.e., old).

Disturbance features.—We used databases from government and industry to identify the location of roads and forestry cutblocks. We did not classify roads by use or status. During the period of monitoring, the Wolverine and Trend coal mines were fully operational and spatial data were acquired directly from their parent corporations (Western Coal and Peace River Coal). Lastly, we used the Oil and Gas Commission of BC’s public database to identify the spatial locations of seismic lines, pipelines, well sites, and other developed areas related to the exploration and development of petroleum reserves (i.e., natural gas) across the South Peace (Oil and Gas Commission of British Columbia 2009). We calculated the median distance (km) of each HSU to human disturbance features as well as the density of disturbance features (total area of features/unit area; linear features = km/km², non-linear features = ha/km²). The density of disturbance features represented a broader geographic effect, where wolves might not have responded to the adjacency (i.e., distance) of one feature, such as a road, but instead a larger collection of those features across some area (e.g., Houle et al. 2010).
The density of such features might be considered a cumulative impact of resource development. We used a standard moving-window algorithm to calculate the density of disturbance features (IDRISI V 15.0, Andes Edition).

Quantification of caribou habitat.—A total of 27 caribou within two herds (Bearhole/Redwillow [BHRW] \( n = 5 \), Quintette \( n = 22 \)) were captured between February 2003 and March 2009 by net-gunning from a helicopter. The majority of caribou were fitted with either Televilt (Televilt, TVP Positioning AB, Lindesberg, Sweden) or ATS (Advanced Telemetry System, Isanti, Minnesota, USA) GPS collars equipped with VHF transmitters and remote-release devices. 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.

We used paired (conditional) resource selection functions (RSFs) to quantify the relationships between GPS-collared caribou and a number of variables that were hypothesized to influence distribution (Table 1). Models were developed seasonally, based on the known life history of caribou in the study area: spring (1 April–14 May), calving (15 May–14 June), summer/fall (15 June–31 October), and winter (1 November–31 March). We used 12,297 GPS collar locations from the BHRW and 25,819 locations from the Quintette caribou herds to fit those models. Resource availability was constrained to the area that we assumed a caribou could transit during a fixed time interval. For this calculation, we centered a circular buffer, representing the 95th percentile movement distance for a period of 24 h, on the preceding collar location for each individual study animal (Johnson et al. 2005). Five comparison locations were then randomly selected from within this spatial and temporal buffer, defined as the availability radius.

We used GIS to apply RSF coefficients from the top-ranked models to the corresponding spatial data and produced maps representing the relative value of habitat, by season, across the range of the Quintette and BHRW caribou herds (Appendix S1). We used unstandardized RSF values to fit covariates for the wolf count models. As these maps represent only one hypothesized predictor of wolf distribution, we do not present the full set of methods or explore those particular

| Variables | Description |
|-----------|-------------|
| Alpine    | High elevation with few or no trees with primary cover being rock, snow, herbs, shrubs, bryoids, and terrestrial lichens |
| Black Spruce | Black spruce (*Picea mariana*) |
| No VRI    | No VRI data available |
| Other     | Specific to pack/herd and season; combination of variables listed with too few occurrences to model |
| Pine      | Lodgepole pine (*Pinus contorta*), whitebark pine (*P. albicaulis*) |
| Spruce    | Other spruce varieties: *Picea* spp., Engelmann (*P. engelmannii*), white (*P. glauca*), hybrid (*P. engelmannii x glauca*) |
| Tamarack  | Tamarack (*Larix laricina*) |
| Tree—Broadleaf | Other non-listed broadleaf trees: aspen (*Populus tremuloides*), cottonwood (*P. balsamifera*), and birch (*Betula papyrifera*) |
| Tree—Other | Other non-listed conifers, Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*) |
| No Age    | No data available to determine seral age of forest |
| Young–Growing (YG) | Forest age 0 ≤ 80 yr |
| Young–Growing–Mature (YGM) | Forest age 0 ≤ 120 yr |
| Young     | Forest age 0 ≤ 40 yr |
| Growing   | Forest age 41 ≤ 80 yr |
| Mature    | Forest age 81 ≤ 120 yr |
| Old       | Forest age ≥121 yr |
| Water     | Distance (km) to nearest water feature |
| RSF_BHRW  | Resource selection function values representing habitat selected by caribou of the Bearhole/Redwillow (BHRW) herd |
| RSF_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 combined |
| Cutblock (Ctblk) | Distance (km) to nearest forestry cutblock |
| Oil and Gas (OG) | Distance (km) to nearest non-linear natural gas well pad or facility pad ≥1 ha in size |
| Mine      | Distance (km) to nearest coal mine footprint |
| MOG_Dens  | Density of the area of oil and gas features as well as coal mines (ha/km²); moving window = 1.56 ha |
| FOR_Dens  | Density of the area of cutblocks <30 yr since harvest (ha/km²); moving window = 1.56 ha |
| LF_Dens   | Density of linear features, including roads, pipelines, and seismic lines (km/km²); moving window = 1.56 ha |
results; details of RSF modeling and mapping are presented in Williamson-Ehlers (2013) and were duplicated by Johnson et al. (2015).

**Model selection and validation**

We used Akaike’s information criterion for small sample sizes ($\text{AIC}_c$) and Akaike weights ($\text{AIC}_w$) to identify the most parsimonious model from a suite of ecologically plausible candidate models (Anderson et al. 2000). One of our objectives was to understand the cumulative impact of industrial development relative to the distribution of wolves. This was represented by statistical models that contained the full set of

![Grid of habitat selection units (HSUs) developed from the average AOU for collared members of the Chain Lakes wolf pack in the South Peace region of British Columbia, Canada. Size of the HSU cell was determined as the average wolf(s) AOU affiliated with kill sites identified throughout the territory.](image-url)
disturbance features (i.e., forest harvest, linear features, oil, gas, and mine features; Table 2). We reported coefficients (β) from the most parsimonious model and used 95% confidence intervals to illustrate the precision of each covariate. For covariates that fell close to or overlapped 0, selection or avoidance of habitat or disturbance features could not be determined. We used tolerance scores to assess collinearity among variables (Menard 2002). Where tolerance scores were less than the threshold value of 0.2, we used bivariate correlation to remove one of the variables from an individual model.

We randomly partitioned wolf locations into training (80%) and testing (20%) groups. Using the withheld data, we determined whether there was a relationship between the observed probabilities of counts and the predicted probabilities of counts (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 a count class equaled zero, whereas positive values indicated under-prediction and negative values indicated over-prediction.

**Results**

Seventy-three kill sites (Upper Sukunka \(n = 20\); Upper Murray \(n = 15\); Onion Creek \(n = 17\); and Chain Lakes \(n = 21\)) served as the foundation for determining the AOU and size of the HSU for each wolf pack. Habitat selection units ranged in size from 6.6 ha for the Upper Sukunka pack to 91.0 ha for the Chain Lakes pack (Fig. 4). Caribou were rarely identified as prey at the kill sites that we investigated (\(n = 1\); Fig. 5). The most frequently occurring prey item was moose (\(n = 43\)), followed by deer (\(n = 14\)) and unknown species (\(n = 9\)).

We used 24,075 GPS collar locations for the Upper Sukunka (\(n = 6783\)), Upper Murray (\(n = 6478\)), Onion Creek (\(n = 4624\)), and Chain Lakes (\(n = 6190\)) wolf packs to generate negative

| Grouping category | Model name | Variables |
|-------------------|------------|-----------|
| Habitat           | Cover      | Forest Cover (Categorical) |
| Age               | Forest Age | Forest Age (Categorical) |
| Water             | Water      | Distance to Water |
| Caribou           | Caribou    | Caribou RSF Habitat Value |
| Landscape         | Landscape  | Forest cover + Forest age + Distance to Water + Caribou RSF Value |
| Linear Feature Distance | Landscape + LF Dist | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Distance to Linear Feature |
| Linear Feature Distance and Density | Landscape + LF Dist + LF Dens | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Distance to Linear Feature + Linear Feature Density |
| Cutblock Distance | Landscape + Cutblock Dist | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Distance to Road + Distance to Cutblock |
| Cutblock Distance and Density | Landscape + Cutblock Dist + Cutblock Dens | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Distance to Road + Distance to Cutblock + Road Density + Cutblock Density |
| Mine/Oil/Gas Distance | Landscape + MOG Dist | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Distance to Mine/Oil/Gas Feature |
| Mine/Oil/Gas Distance and Density | Landscape + MOG Dist + MOG Dens | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Distance to Mine/Oil/Gas Feature + Mine/Oil/Gas Density |
| Cumulative Effects Distance | Landscape + CE Dist | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Linear Feature Distance + Forestry Distance + Mine/Oil/Gas Distance |
| Cumulative Effects Distance and Density | Landscape + CE Dist + CE Dens | Forest Cover + Forest age + Distance to Water + Caribou RSF Value + Linear Feature Distance + Forestry Distance + Mine/Oil/Gas Distance + Linear Feature Density + Forestry Density + Mine/Oil/Gas Density |

*Note: Covariates for distance (km) and density (km/1000 km²) were modeled as either a linear or Gaussian (squared) relationship depending on best fit for each season (see Methods and Results).*
binomial count models. We were unable to maximize the log-likelihood values for five seasonal models using the preferred zero-inflated model. Tolerance scores for continuous variables were low for some packs and variables. With a primary focus on linear features, we excluded cutblocks and polygonal features associated with the oil and natural gas industry (e.g., well sites) from candidate models for the Upper Sukunka and Chain Lakes packs. For the Onion Creek pack, distance to mine was highly correlated with distance to natural gas features; we retained the distance to mine variable as the landscape occupied by the Onion Creek pack was less influenced by features associated with natural gas development.

The most parsimonious seasonal models for most packs were also the most complex in each candidate set and contained covariates representing vegetation cover, caribou habitat, and anthropogenic disturbance. With the exception of the Upper Sukunka pack during late winter and the Upper Murray pack during early winter, there was little model selection uncertainty (Table 3). In all cases, the distribution of wolves was influenced by the distance or density of mines as well as natural gas features. The predictive ability of seasonal count models was generally good for HSUs across the study area (Fig. 6). Inspection of residuals indicated that the model’s ability to predict the frequency of wolf locations across the landscape was relatively poor when the counts were small, but improved as the number of wolf locations within HSUs increased.

**Seasonal occurrence of wolves**

**Non-winter.**—Three packs with territories in the mountainous regions of the study area (Upper Sukunka, Upper Murray, and Onion Creek) showed higher frequencies of locations in HSUs containing upland or spruce habitats (Table 4; Appendix S2: Table S1). Wolves in the Chain Lakes pack were commonly located in the lower-elevation boreal areas with aspen, cottonwood, and birch (count $\beta = 0.791, P < 0.001$). Upper Murray and Onion Creek wolves avoided higher-quality habitats for Quintette caribou during the non-winter months (count $\beta < -0.001, P < 0.005$; binary $\beta = -0.003, P = 0.004$). Only wolves from the Upper Murray pack frequented habitats selected by the BHRW caribou herd (count $\beta = 0.001, P < 0.001$; Table 4; Appendix S2: Table S2).

Wolves of the boreal Chain Lakes pack had a greater number of locations in HSUs with few roads (count $\beta = 0.265, P = 0.009$). These wolves occurred closer to forestry cutblocks, but the total number of locations was not strongly related to such features (binary $\beta = -0.965, P = 0.005$; count $\beta = 0.086, P = 0.364$; Table 4). Similarly, wolves in the Onion Creek and Upper Sukunka packs were less frequently located near seismic lines and pipelines (count $\beta = 0.437, P < 0.001$; count $\beta = 0.089, P = 0.008$). In contrast, between mid-April and mid-October collared wolves from the...
Upper Sukunka pack demonstrated a non-linear response, using habitats near roads (count $\beta = -0.175, P = 0.001, \beta = 0.009, P = 0.002$ [quadratic]). Only the Upper Sukunka wolves frequented areas near natural gas facilities (count $\beta = -0.401, P < 0.001$) and the Upper Murray wolves near coal mines (count $\beta = -0.046, P < 0.001$).

**Early winter.**—Similar to non-winter, wolves in the Onion Creek pack occurred in HSUs where pine was the dominant species (count $\beta = 0.588, P = 0.049$) and wolves in the Upper Sukunka occurred in forest types dominated by mixed conifers (binary $\beta = 0.687, P = 0.032$; Table 5). Habitats dominated by broadleaf trees were avoided by wolves in the Upper Sukunka pack (binary $\beta = -1.561, P < 0.001$; count $\beta = -0.742, P = 0.013$), but were frequently used by members of the Chain Lakes pack that occurred in the boreal forest (count $\beta = 0.500, P = 0.001$).

During early winter, wolves from the Upper Sukunka pack occupied HSUs containing cutblocks (binary $\beta = -1.919, P = 0.006$), coal mines (binary $\beta = -1.277, P < 0.001$), and natural gas features (binary $\beta = -1.277, P = 0.001$; count $\beta = -0.173, P = 0.002$). Conversely, boreal wolves of the Chain Lakes pack were uncommon in HSUs close to cutblocks (count $\beta = 0.179, P < 0.001$) or with a high density of linear features (count $\beta = -0.135, P < 0.001$; Table 5; Appendix S2: Table S3). The frequency of wolf locations was not related to habitats strongly selected by caribou. Only members of the Onion Creek pack occurred, but were not frequently located in HSUs containing high-value habitat for caribou in the BHRW herd (binary $\beta < 0.001, P = 0.017$; count $\beta < 0.001-0.175, P = 0.866$; Table 5).

**Late winter.**—Between February and mid-April, wolves in the Upper Sukunka pack used mountainous areas classified as upland and alpine (count $\beta = 0.911, P = 0.003$), as well as patches of broadleaf trees (count $\beta = 0.554, P = 0.025$). As in other seasons, wolves in the Upper Murray pack frequented forests dominated by lodgepole pine between 0 and 120 years of age (count $\beta = 1.308, P = 0.002$; Appendix S2: Table S5). Both Upper Murray and Chain Lakes wolves did occur, although not frequently, in late-successional forests (>120 yr) during late winter (binary $\beta = 0.804, P = 0.001$; binary $\beta = 0.726, P = 0.036$; Table 5).

Anthropogenic disturbances influenced the distribution of wolves across the study area throughout the late-winter months (Table 5). Wolves in the Upper Sukunka pack frequented HSUs near natural gas features (count $\beta = -0.414, P < 0.001$), and wolves in the Upper

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**Table 3.** Number of parameters ($k$), Akaike’s information criterion values ($\text{AIC}_k$), and $\text{AIC}_w$ weights ($\text{AIC}_w$) of the most parsimonious seasonal count models for wolves.

| Model/pack                        | Non-Winter          | Early Winter        | Late Winter         |
|-----------------------------------|---------------------|---------------------|---------------------|
|                                   | $k$ | $\text{AIC}_k$ | $\text{AIC}_w$ | $k$ | $\text{AIC}_k$ | $\text{AIC}_w$ | $k$ | $\text{AIC}_k$ | $\text{AIC}_w$ |
| Upper Sukunka ($n = 33,599$)      |     |               |                  |     |               |                  |     |               |                  |
| MOG Dist                          | 22  | 9636.6        | <0.01            | 23  | 5087.1        | <0.01            | 22  | 6116.9        | 0.45             |
| MOG Dist + MOG Dens†              | 23  | 9629.1        | <0.01            | 25  | 5084.8        | <0.01            | 23  | 6118.3        | 0.22             |
| CE Dist†                          | 19  | 9598.8        | 0.04             | 26  | 5073.1        | <0.01            | 23  | 6117.8        | 0.27             |
| CE Dist + CE Dens†                | 21  | 9592.2        | 0.96             | 32  | 5049.9        | 1                | 25  | 6120.6        | 0.07             |
| Upper Murray ($n = 35,499$)       |     |               |                  |     |               |                  |     |               |                  |
| MOG Dist                          | 16  | 11,027.1      | <0.01            | 15  | 4417.2        | <0.01            | 14  | 5816         | <0.01           |
| MOG Dist + MOG Dens               | 18  | 11,029.8      | <0.01            | 18  | 4357.2        | 0.72             | 15  | 5778.8        | <0.01           |
| CE Dist†                          | 20  | 11,026.9      | <0.01            | 15  | 4417.2        | <0.01            | 16  | 5789.3        | <0.01           |
| CE Dist + CE Dens†                | 27  | 10,987.9      | 1.00             | 17  | 4359.1        | 0.28             | 18  | 5683.6        | 1.00            |
| Onion Creek ($n = 10,493$)        |     |               |                  |     |               |                  |     |               |                  |
| CE Dist + CE Dens                 | 20  | 6722.1        | 1.00             | 25  | 3079.1        | 1.00             | 23  | 3675.6        | 1.00            |
| Chain Lakes ($n = 3389$)          |     |               |                  |     |               |                  |     |               |                  |
| CE Dist + CE Dens                 | 18  | 4014.2        | 1.00             | 22  | 7174.7        | 1.00             | 18  | 3252.2        | 1.00            |

Notes: Models were developed (using ZINB or NBRM) for each of four wolf packs monitored from 2008 to 2010 across the South Peace region of British Columbia, Canada. Sample size used to de...
Murray pack occurred more frequently in HSUs with a high density of cutblocks (count $\beta = 0.025$, $P = 0.030$). Packs occurring in mountainous portions of the study area were absent or rarely occurred in areas near linear features (Upper Murray and Onion Creek) and coal mines (Onion Creek and Upper Sukunka). Wolves from the Chain Lakes pack were uncommon in habitats with a relatively high density of linear features (count $\beta = -0.312$, $P = 0.002$). The location data suggested a similar pattern for wolves from the Onion Creek pack, except that the relationship was non-linear indicating greater occupancy of areas with a very high density of linear features (count $\beta = -0.488$, $P = 0.004$; count $\beta = 0.058$, $P = 0.056$ [quadratic]).

Although wolves from the Upper Sukunka pack rarely had the opportunity to overlap populations of woodland caribou, they demonstrated increased frequencies of use of alpine habitats during late winter—areas potentially occupied by Quintette caribou (count $\beta = 0.911$, $P = 0.003$). Upper Murray wolves had a higher frequency of locations in HSUs representing high-quality habitat for BHRW caribou (count $\beta = 0.214$, $P = 0.001$; Table 5; Appendix S2: Table S5). In contrast, and consistent with the early winter, Onion Creek and Chain Lakes wolves did not

Fig. 6. Differences in the observed (withheld data) and predicted probability of counts of wolf locations within habitat selection units (HSUs) for the Upper Sukunka (A), Upper Murray (B), Onion Creek (C), and Chain Lakes (D) packs residing in the South Peace region of British Columbia, Canada. Predicted data were generated from the most parsimonious zero-inflated (ZINB) or negative binomial regression model (NBRM; Table 3). A value of zero indicated perfect prediction, whereas positive values indicated under-prediction and negative values indicated over-prediction.
frequently occur in habitats selected by caribou in the boreal forest (count $\beta \leq -0.001$, $P = 0.001$; count $\beta = -1.073$, $P \leq 0.001$).

**DISCUSSION**

This study supports the general conclusions of others that the cumulative effects of industrial development influence the distribution of wolves across boreal and mountainous ecosystems (James et al. 2004, Houle et al. 2010, Lesmerises et al. 2012). This is one of only a few studies, however, to quantify and contrast the simultaneous distribution of packs of wolves that occupy both alpine and low-elevation boreal habitats. This is important as the distribution of prey, in this case woodland caribou, can follow an elevation gradient. Caribou from the Quintette herd occupy high-elevation alpine habitat during winter, and the BHRW caribou are found in low-elevation boreal forest during that season. In other portions of their range, woodland caribou are thought to now only persist across high-elevation habitats distant from forested areas with abundant moose, deer, and dependent wolves (Poole et al. 2000). Thus, our results suggest that ecosystem-specific information and knowledge of the processes of predator–prey interactions are essential for understanding the ecological impacts of human-caused landscape change.

We used an innovative combination of field and statistical methods to understand the seasonal distribution of wolves relative to caribou habitat and industrial development. The application of count models to HSUs allowed us to develop statistical relationships that represented the frequency of habitat use, an index of behavior (Nielsen et al.
This differs from more typical species-distribution models that are premised on binary data that contrast resource use relative to the availability of that resource (e.g., RSF; Boyce et al. 2015). However, the number of wolf locations in an HSU may be associated with factors other than the availability of prey and the intensity of human-caused disturbance; predatory behavior, such as hunting and prey handling, the density and type of prey, or the size of pack territories are important considerations (Smith et al. 2004, Hebblewhite et al. 2005, Klaczek et al. 2015). Also, the frequency of wolf locations in any particular HSU could be a product of competitive interactions (Stahler et al. 2006). One may find few locations from monitored animals simply because they are excluded by conspecifics from adjacent packs. We are confident that wolves were collared from all packs within the core of the study area. There is the possibility, however, that distribution of the monitored animals was influenced by non-collared wolves found at the geographic extent of the study area.

**Seasonal distribution and resource use by wolves**

Wolves residing in mountainous regions (Upper Murray and Onion Creek) used pine-dominated forests throughout the year. Unlike caribou, however, wolves infrequently used late-seral forests. During all three seasons, forested areas dominated by broadleaf or mixed-conifer trees and water were important indicators of wolf, but not caribou habitat. Upper Murray and Onion Creek wolves demonstrated some use of habitats selected by BHRW caribou, but in general these results supported our hypothesis that predation risk for caribou was likely related to the occurrence of other prey species, such as moose and deer. As observed in other regions, the distribution of wolves was not consistently associated with boreal or alpine habitats strongly selected by caribou (Courbin et al. 2009, Whittington et al. 2011, Latham et al. 2013).

Investigations of mortality sites corroborated the results from the count models as caribou accounted for only 1.3% of identified remains at wolf kill sites, although we likely underrepresented the mortality of young, small-bodied ungulates, including caribou. However, the data suggest that caribou are a minor prey item for wolves, but even incidental predation can result in the mortality of 5–10% of adult caribou in these populations (Seip and Jones 2014). These results are comparable with past studies suggesting that wolf populations in western North America are typically supported by prey other than caribou (i.e., moose, deer, beaver (*Castor canadensis*), other small mammals; Seip 1992, Gustine et al. 2006, Latham et al. 2011b, 2013, Milakovic and Parker 2011, Serrouya et al. 2011). Although our data suggest that wolves are not using habitat selected

| Variables                | Upper Sukunka | Upper Murrey | Onion Creek | Chain Lakes |
|--------------------------|---------------|--------------|-------------|-------------|
| S                        | A             | A            | A           | A           |
| Alpine                   |               |              |             |             |
| Black spruce             |               |              |             |             |
| No VRI                   | C             | C            |             |             |
| Other                    | C             | C            |             |             |
| Pine                     | C             | B            |             |             |
| Spruce                   |               |              |             |             |
| Tamarack                 |               |              |             |             |
| Broadleaf                |               |              | B           | C           |
| Tree—other               | C             | C            |             |             |
| No age                   |               |              |             |             |
| YG (0–80 yr)             |               |              |             |             |
| YGM (0–120 yr)           |               |              |             |             |
| Young                    |               |              |             |             |
| Growing                  |               |              |             |             |
| Mature                   |               |              |             |             |
| Old                      |               |              | B           |             |
| Water†‡                  | C             | C            | C           |             |
| RSF_BHRW                 |               |              |             |             |
| RSF_Quintette            |               |              |             |             |
| Road†‡                   | C             | B            | B           | C           |
| SeisPipln†‡              | C             | B            | C           |             |
| Ctblk†‡                  |               |              |             |             |
| OG†‡                     |               |              |             |             |
| Mine†‡                   | C             | C            | B           |             |
| MOG_Dens‡                |               |              |             |             |
| FOR_Dens‡                |               |              |             |             |
| LF_Dens‡                 |               |              |             |             |

Notes: Presence or absence (B; binary) and the frequency of habitat use (C; count) within a habitat selection unit were determined using β coefficients from count models for each pack of wolves. Model covariates are explained in Table 1.

† Covariate measuring distance (km) to a feature; selection is therefore represented by a − β coefficient, and avoidance is represented by a + β coefficient.

‡ Either a Gaussian (squared) or linear term was used in the top model.

| Variables | Upper Sukunka | Upper Murrey | Onion Creek | Chain Lakes |
|-----------|---------------|--------------|-------------|-------------|
| S         | A             | A            | A           | A           |
| A         |               |              |             |             |

2005, Sawyer et al. 2006). This differs from more typical species-distribution models that are premised on binary data that contrast resource use relative to the availability of that resource (e.g., RSF; Boyce et al. 2015). However, the number of wolf locations in an HSU may be associated with factors other than the availability of prey and the intensity of human-caused disturbance; predatory behavior, such as hunting and prey handling, the density and type of prey, or the size of pack territories are important considerations (Smith et al. 2004, Hebblewhite et al. 2005, Klaczek et al. 2015). Also, the frequency of wolf locations in any particular HSU could be a product of competitive interactions (Stahler et al. 2006). One may find few locations from monitored animals simply because they are excluded by conspecifics from adjacent packs. We are confident that wolves were collared from all packs within the core of the study area. There is the possibility, however, that distribution of the monitored animals was influenced by non-collared wolves found at the geographic extent of the study area.

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Investigations of mortality sites corroborated the results from the count models as caribou accounted for only 1.3% of identified remains at wolf kill sites, although we likely underrepresented the mortality of young, small-bodied ungulates, including caribou. However, the data suggest that caribou are a minor prey item for wolves, but even incidental predation can result in the mortality of 5–10% of adult caribou in these populations (Seip and Jones 2014). These results are comparable with past studies suggesting that wolf populations in western North America are typically supported by prey other than caribou (i.e., moose, deer, beaver (*Castor canadensis*), other small mammals; Seip 1992, Gustine et al. 2006, Latham et al. 2011b, 2013, Milakovic and Parker 2011, Serrouya et al. 2011). Although our data suggest that wolves are not using habitat selected
by caribou, the level of spatial separation between the primary prey of wolves and caribou remains greatest for the Quintette herd that is found across high-elevation habitats. Wolves ranging across the boreal forest have increased opportunities to encounter BHRW caribou, especially during winter. The Quintette herd has the lowest rate of population decline in the study area \( \frac{k}{C} = 0.90 \), whereas the BHRW population is declining rapidly \( \frac{k}{C} = 0.812 \); Johnson et al. 2015).

### Behavioral responses of wolves to industrial disturbances

Wolves across the study area demonstrated considerable variability in their response to the occurrence or density of industrial features. Similarly, Latham (2009) reported a differential response of eight packs to recent wildfire burns, anthropogenic features, and new clearcuts. In general, wolves in our study spent relatively little time, as indexed by the number of locations, in HSUs characterized by roads and other linear features. Only one pack (Upper Murray) was observed frequently using habitats near roads during the non-winter season. These findings paralleled similar studies that reported avoidance of linear corridors or other areas frequently used by people (Thurber et al. 1994, Mladenoff et al. 1999, Whittington et al. 2005, Hebblewhite and Merrill 2008, Houle et al. 2010, Lesmerises 2012).

| Variables | Early Winter | Late Winter |
|-----------|--------------|-------------|
|           | Upper Sukunka | Upper Murrey | Onion Creek | Chain Lakes | Upper Sukunka | Upper Murrey | Onion Creek | Chain Lakes |
| Alpine    | S            | S            | S            | A            | S            | S            | S            | A            |
| Black spruce | C            | C            | C            | C            | C            | C            | C            | C            |
| No VRI    | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| Other     | C            | C            | C            | C            | C            | C            | C            | C            |
| Pine      | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| Spruce    | C            | C            | C            | C            | C            | C            | C            | C            |
| Tamarack  | C            | C            | C            | C            | C            | C            | C            | C            |
| Broadleaf | C            | C            | C            | C            | C            | C            | C            | C            |
| Tree—other | B            | B            | B            | B            | B            | B            | B            | B            |
| No age    | C            | C            | C            | C            | C            | C            | C            | C            |
| YG (0–80 yr) | C            | C            | C            | C            | C            | C            | C            | C            |
| YGM (0–120 yr) | C            | C            | C            | C            | C            | C            | C            | C            |
| Young     | C            | C            | C            | C            | C            | C            | C            | C            |
| Growing   | C            | C            | C            | C            | C            | C            | C            | C            |
| Mature    | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| Old       | C            | C            | C            | C            | C            | C            | C            | C            |
| Water†‡   | B            | B            | B            | B            | B            | B            | B            | B            |
| RSF_BHRW  | B            | B            | B            | B            | B            | B            | B            | B            |
| RSF_Quintette | B        | B            | B            | B            | B            | B            | B            | B            |
| Road†‡    | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| SeisPipln†‡ | B, C       | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| Ctblk†‡   | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| OG†‡      | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| Mine†‡    | B            | B            | B            | B            | B            | B            | B            | B            |
| MOG_Dens†‡ | B, C       | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| FOR_Dens†‡ | B, C       | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |
| LF_Dens†‡ | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         | B, C         |

**Notes:** Presence or absence (B; binary) and the frequency of habitat use (C; count) within a habitat selection unit were determined using \( \beta \) coefficients from count models for each pack of wolves. Model covariates are explained in Table 1.

† Covariate measuring distance (km) to a feature; selection is therefore represented by a \( (-\beta) \) coefficient, and avoidance is represented by a \( (+\beta) \) coefficient.

‡ Either a Gaussian (squared) or linear term was used in the top model.
et al. 2012). Others, however, found that wolves used linear features, such as roads and seismic lines, as movement corridors to transit seasonal ranges (James and Stuart-Smith 2000, Latham et al. 2011a, Whittington et al. 2011). Typically, such behaviors occur in areas where the risk of mortality from hunting, trapping, and vehicular collisions is low or human activities are limited (Mech et al. 1988, Merrill 2000, Whittington et al. 2005, Person and Russell 2008). When wolves in our study area were near or used linear features, their movements were typically straighter and faster, suggesting that this type of feature can facilitate access to and movement through caribou range (Ehlers et al. 2014).

Features associated with the development of natural gas deposits also had a variable effect on the behavior of wolves across the study area. The Onion Creek and Upper Murray packs avoided areas of their range that were in the vicinity of natural gas features during the non-winter seasons. In contrast, wolves in the Sukunka Valley demonstrated a non-linear response to habitats within close proximity to natural gas features. These patterns of selection suggest that levels of human activity associated with natural gas development vary across the territories of collared wolves, or some wolves have developed strategies to accommodate disturbance stimuli (Hebblewhite and Merrill 2008).

The Upper Murray, Upper Sukunka, and Onion Creek packs occupied mountainous territories adjacent to, but were infrequently located near coal mines. As wolves focus on the rearing of pups, the high levels of human activity and vehicular traffic associated with mine sites might deter them from frequenting those areas (Person and Russell 2008, Lesmerises et al. 2012). During winter, wolves may naturally avoid higher-elevation industrial features, such as coal mines, if they continue to hunt primary prey in the valley bottoms. Coal mines occurred only within the range of the Quintette herd. These caribou avoided mines during calving and throughout the summer and fall months, but during winter they occupied elongated ridges adjacent to mines (Johnson et al. 2015).

Wolves in boreal and mountainous habitats occurred in areas closer to or with a higher density of cutblocks during the non-winter season. Across the packs we monitored, this was the most consistent response to human developments. Wolves may be advantageously selecting these habitats for increased hunting opportunities of moose and deer (Peters et al. 2013, Ehlers et al. 2014). Unlike early winter, wolves did not select for or avoided (Onion Creek) cutblocks during the late-winter months—the time of year when forestry, oil, and gas industries are most active and when deep snow begins to restrict moose from foraging in those areas (Courtois et al. 2002).

As with road density, there may be a non-linear response of wolves to the increasing occurrence of cutblocks. Houle et al. (2010) and Lesmerises et al. (2012), for example, found that wolf occurrence decreased as cutblock density increased in Quebec. Wolves in the South Peace may be responding to the cumulative influence of roads and cutblocks at both a home range and regional scale (inter-pack). Also, there is often little browse for moose in newly harvested areas (Nielsen et al. 2005). The infrequent occurrence of wolves could indicate a relatively large proportion of recent cutblocks, and their associated roads, in some territories as opposed to those with older regenerating cutblocks containing more suitable habitat for moose (Courtois et al. 1998).

**Cumulative impacts of resource extraction and development**

The cumulative impacts of anthropogenic activities are now recognized as one of the most pressing problems facing the conservation and management of wildlife (Johnson et al. 2005, 2015, Vors et al. 2007, Krausman and Harris 2011). Habitat alterations from large-scale forestry, natural gas, and mineral exploration are resulting in dramatic transformations that continue to threaten the ecological integrity of the South Peace region (Nitschke 2008). Human-caused disturbance in combination with altered vegetation communities leads to compounding instabilities for populations of caribou: increased movement and vigilance, displacement from portions of the range, and altered predator–prey dynamics (Vistnes and Nellemann 2001, Cameron et al. 2005, Faille et al. 2010, Latham et al. 2011b, Johnson et al. 2015). Furthermore, these relationships are complex and may be confounded by ecological sinks and lag effects (Vors et al. 2007).
Habitat and movement analyses (Ehlers et al. 2014), in addition to field investigations of wolf kill sites, suggest that the co-occurrence of caribou and wolves is rare across this study area. In general, wolf packs did not frequently use habitats that were ranked as high quality for either herd of caribou. Also, some wolves avoided roads, seismic lines, and/or pipelines, but used areas within close proximity to non-linear features (e.g., cutblock, well site), where early-successional forests suggested the presence of ungulates other than caribou. Although caribou kills from wolves were infrequently identified during field investigations, slight increases in the rate of adult mortality from predation can have significant impacts on the stability of small herds of caribou (Wittmer et al. 2005, Hervieux et al. 2013, Seip and Jones 2014). In the absence of spatial refugia for caribou, this increase in mortality could be facilitated by larger and more broadly distributed populations of wolves regardless of a functional response in predation rates, as facilitated by human developments.

A challenge for resource managers working in the South Peace region is to balance the demand for coal mines, wind farms, and the development of natural gas reserves with sudden and unanticipated changes in the distribution and abundance of caribou populations. Current declines in these populations, including observed extirpation, has led to controversial stop-gap measures such as lethal wolf control and the penning and protection of newborn calves (Ray et al. 2015). Further development, and the resulting loss of contiguous habitat, will increase the threats to already small and declining populations and make for more desperate and expensive conservation actions (Johnson et al. 2015).

As our results suggest, the interactions among predators, caribou, and land use are not easily predicted or temporally static. Theory and past findings suggest that early-successional habitats will result in a numerical response of wolves and a greater per capita rate of predation for caribou. Our data, however, did not reveal strong spatial overlap between caribou and wolves nor consistent selection by wolves for industrial features that facilitate movement and that are correlated with the distribution of other deer species. Clearly, apparent competition between moose and caribou makes for a complex, non-equilibrium predator–prey relationship that is difficult to link directly to landscape change and ultimately management. A full understanding of this complex dynamic is necessary if we are to minimize environmental changes that permanently alter the ability of landscapes to support populations of woodland caribou.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1600/full