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Human disturbance effects and cumulative habitat loss in endangered migratory caribou

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ABSTRACT

As human development intensifies in northern ecosystems, negative impacts of anthropogenic disturbances on wildlife could increase. Many caribou and reindeer populations are declining across the northern hemisphere, and human disturbances have been suggested as a potential cause for these declines. We evaluated the effects of human disturbances in the summer and winter ranges of two migratory caribou herds in northern Québec and Labrador, Canada. We captured and collared 510 caribou between 2009 and 2015. We first assessed caribou avoidance of human disturbances at a large spatial scale by comparing the density of mines, mining exploration sites, power lines, roads and human settlements within seasonal ranges to their density within available ranges. We estimated the area avoided by caribou (ZOI; zone of influence) around disturbances located within seasonal ranges and evaluated the resulting cumulative habitat loss. We also evaluated the barrier effect of roads and their influence on caribou movement rates. The density of many disturbance types was lower within caribou seasonal ranges than within available ranges, suggesting they avoided disturbances over a large spatial scale. Within seasonal ranges, caribou avoided all disturbance types except power lines. ZOIs were highly variable among disturbance types and years, ranging from no avoidance to 23 km. Cumulative habitat loss could reach as much as 30% of seasonal ranges and 38% of high-quality caribou habitat. We demonstrate that human disturbances have broad negative effects on caribou behavior, but whether this could translate into population decline remains to be investigated.

1. Introduction

Human disturbances are encroaching wildlife habitat at an unprecedented rate, especially in northern ecosystems where mining, oil and gas industries are expanding (UNEP, 2001). Adverse effects of human disturbances may affect wildlife distribution, population dynamics, and ability to thrive in changing environments (Trombulak and Frissell, 2000; UNEP, 2001). As many wildlife populations decline, effects of human disturbances on behavior and vital rates are increasingly investigated (Johnson and St-Laurent, 2011).

Human disturbances are generally non-lethal, but can cause risk-averse responses which could lead to fitness costs for animals (Frid and Dill, 2002). These responses have been reported at multiple spatio-temporal scales (Benítez-López et al., 2010; Fahrig and Rytwinski, 2009), ranging from increased vigilance over short periods of time and flight movements of a few meters (Benhaiem et al., 2008; Côté, 1996; Hansen and Aanes, 2014), to avoidance over several km or even desertion of disturbed areas (Harju et al., 2010; Hovick et al., 2014). Disturbances can also disrupt migration routes (Seidler et al., 2015), increase movement rates (Dussault et al., 2007) or delay crossing of linear infrastructures (Wilson et al., 2016), potentially increasing energy expenditure or reducing the time animals spend in suitable habitat. It can also prevent animals from reaching portions of their range (Sawyer et al., 2013), or maintaining synchrony with vegetation availability (Lendrum et al., 2013). The energetic costs of risk-averse responses and habitat loss caused by avoidance may appear insignificant for a single disturbance. At the scale of the animal lifetime or range, however, repeated risk-averse responses and cumulative habitat loss resulting from the avoidance of all disturbances encountered by the animal may be considerable (Bradshaw et al., 1998; Dyer et al., 2001). As negative effects of disturbances accumulate, they may reach a critical point where consequences are observed on fitness, survival and population dynamics (Johnson and St-Laurent, 2011).

Human disturbance was suggested to contribute to the generalized

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decline of caribou and reindeer (*Rangifer tarandus*) across northern regions (Vors and Boyce, 2009). These ungulates could be particularly sensitive to human disturbances and their cumulative effects because of their broad distribution and long-ranging movements (Bergerud et al., 2008). They are reported to consistently avoid human disturbances such as cabins (Polfus et al., 2011), roads (Leblond et al., 2013), resorts (Nellemann et al., 2010), human settlements (Anttonen et al., 2011), and mines (Boulanger et al., 2012). Avoidance of disturbances by caribou and reindeer were found to range from ≤1 km (roads; Dussault et al., 2012; Dyer et al., 2001) to 14 km (diamond mine; Boulanger et al., 2012). Linear features, such as roads, are also known to alter caribou movements or compromise access to portions of their range (Leblond et al., 2013; Wilson et al., 2016). For example, Leblond et al. (2013) showed that 77% of individuals in a forest-dwelling caribou population did not cross a highway, resulting in a potential loss of > 50% of their range and limiting their access to protected areas. In the same study, caribou willing to cross the highway showed increased movement rates within 5 km of the roadway, potentially reducing time spent in risky habitat. Although human disturbances have unequivocal effects on caribou and reindeer behavior and habitat use, quantifying cumulative effects remains a challenge (Gunn et al., 2011).

The study of habitat selection constitutes a powerful tool to assess individual and cumulative effects of human disturbances on wildlife. Distinguishing disturbance effects from environmental effects can, however, be challenging due to their confounding influences on habitat use (Boulanger et al., 2012). If a disturbance is located in low-quality habitat, for example, it may be difficult to determine whether animals are avoiding low-quality habitat or the disturbance. Similarly, animals may avoid crossing a road either because of the absence of suitable habitat on the other side, or because of the human activity on the road. Comparing habitat use near disturbances to predicted use based on habitat quality constitutes a robust approach to untangle environmental and disturbance effects (Polfus et al., 2011; White and Gregovich, 2017).

Here, we evaluated the individual and cumulative effects of human disturbances on an Arctic ungulate, the eastern migratory caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) herds in northern Québec and Labrador. Like most caribou and reindeer herds, the RFH and RGH have been declining in the last decades. In northern Québec, the RFH peaked at > 500,000 individuals around 2001 (Couturier et al., 2004) and declined to ca. 199,000 (± 16,000) individuals in 2016 (Taillon et al., 2016). The RGH, distributed over parts of Québec and Labrador, peaked at ca. 800,000 (± 104,000) individuals in 1993 (Couturier et al., 1994), and rapidly decreased to < 9000 (± 670) individuals in 2016 (MFFP, 2016). In 2017, both herds were listed as endangered by conservation authorities (COSEWIC, 2017), which stressed the importance of caribou sensitivity to human disturbances. Evaluating the effects of human disturbances and their cumulative effects on migratory caribou is thus critical to implement effective management and conservation measures.

Our goal was to evaluate the effects of human disturbances on migratory caribou habitat and space use. Because caribou are sensitive to human disturbances, we hypothesised that they would avoid approaching sites with human activity or infrastructures. We first predicted that caribou would avoid disturbances at a large spatial scale, by establishing seasonal ranges where the density of industrial disturbances (mines, mining exploration), power lines, human settlements and roads was lower than in other potential seasonal ranges. We also predicted that caribou would avoid disturbances at a finer spatial scale, by reducing occupancy around disturbances found within their seasonal ranges, termed the zone of influence or ZOI. We expected that industrial disturbances would be avoided over larger distances than other types of disturbances, due to the use of heavy machinery and the noise they produce. We evaluated cumulative habitat loss for caribou caused by the avoidance of all disturbances in caribou ranges. We finally assessed whether roads could affect caribou movements, by either acting as a barrier to movements or by modifying movement rates during crossing.

2. Study site

The study area is located north of the 51st parallel and encompassed northern Québec and Labrador, including Nunavik and Nunatsiavut territories, Canada (Fig. 1A). Every year, caribou of the RFH and RGH undertake a migration of several hundreds of kilometers between their summer and winter ranges (mean migration distance 2000–2011: RFH = 615 km; RGH = 350 km; Le Corre et al., 2017). Summer ranges are located in the northern part of the herds' annual distribution range and are mainly covered by arctic tundra dominated by shrubs (*Salix* sp. and *Betula* sp.), grasses, herbaceous plants, and terrestrial lichens (Latifovic and Pouliot, 2005). Transition areas between open tundra and taiga forests are composed of shrubs and conifer trees (mainly black spruce, *Picea mariana*), and are also found in the southern part of the summer ranges. Caribou winter ranges, located in the southern portion of their annual distribution, are dominated by black spruce stands with tamarack (*Larix laricina*), interspersed with low vegetation composed of shrubs and lichens. Natural fires occur mainly on winter ranges, and decrease in frequency and size from west to east, as well as from south to north (MRN, 2014). Elevation of the study area ranges from sea level to 1652 m. Arctic and subarctic climates prevail, with short, cool summers followed by long, cold winters. Annual temperatures averaged −3.6 °C (mean of −27.4 °C and 11.0 °C for the coldest and warmest trimesters, respectively; 1981–2010; Berteaux et al., 2018) across the annual range of the RGH and the winter range of the RFH. On the summer range of the RFH, temperatures for the warmest trimester (summer) averaged 9.7 °C. Precipitations averaged 1077 and 718 mm·year^{-1}, for the southern and northern parts of the study area, respectively, with most precipitations falling as snow between October and March.

We focused our analyses on caribou summer and winter ranges. Disturbances were rare in the summer ranges of both herds, but included human settlements located on the coast, mining exploration sites, and mines (Fig. 1B). RFH and RGH winter ranges were more disturbed than summer ranges, and included human settlements, main roads stretching outside settlements, power lines, and mining exploration sites. The Raglan mine (Glencore; 61°41′08″N, 73°40′49″W; Fig. 1C) was the only mine in operation on the summer range of the RFH during our study. The mine operated three to four underground pits, and an airfield during the study period. The RGH summer and winter ranges included one and two mines in operation, respectively, located at the periphery of the ranges. Three major roads crossed caribou ranges (Fig. 1C). The Raglan road connected the Raglan mine to the shipping port (93 km), and crossed the northern portion of the RFH summer range from southeast to northwest. This road was not paved and was mainly used for ore transportation. The Trans-Taiga and the Trans-Labrador roads respectively crossed the RFH and the RGH winter ranges from east to west. The unpaved Trans-Taiga road connected the hydroelectric infrastructures along the La Grande River, and was mainly used by workers, as well as sport and traditional hunters during winter. The Trans-Labrador road was partially paved and served as the only terrestrial link between Labrador and Québec. Human settlements, power lines and roads did not develop significantly in the last decades, but the number of mining exploration sites varied among years and the number of mines increased over the last 15 years (Appendix 1).

3. Methods

3.1. Caribou data

We captured caribou between 2009 and 2015 using a net-gun shot from a helicopter and fitted them with GPS (Vectronic Aerospace, Berlin, Germany) or Argos (Telonics, ARGOS platform, Mesa, Arizona) collars programmed to record a location every 1 h to 7 d (1 h, 2 h, 7 h, 13 h, or 1 to 7 day-schedule). We used location data of 360 individuals of the RFH (113 M, 247 F) and 150 of the RGH (38 M, 112 F). We removed locations with an estimated error > 1500 m (Argos LC score of 0; GPS PDOP score > 10) from analyses (Christin et al., 2015). We only used caribou equipped with a GPS collar recording locations at high frequencies (1 h to

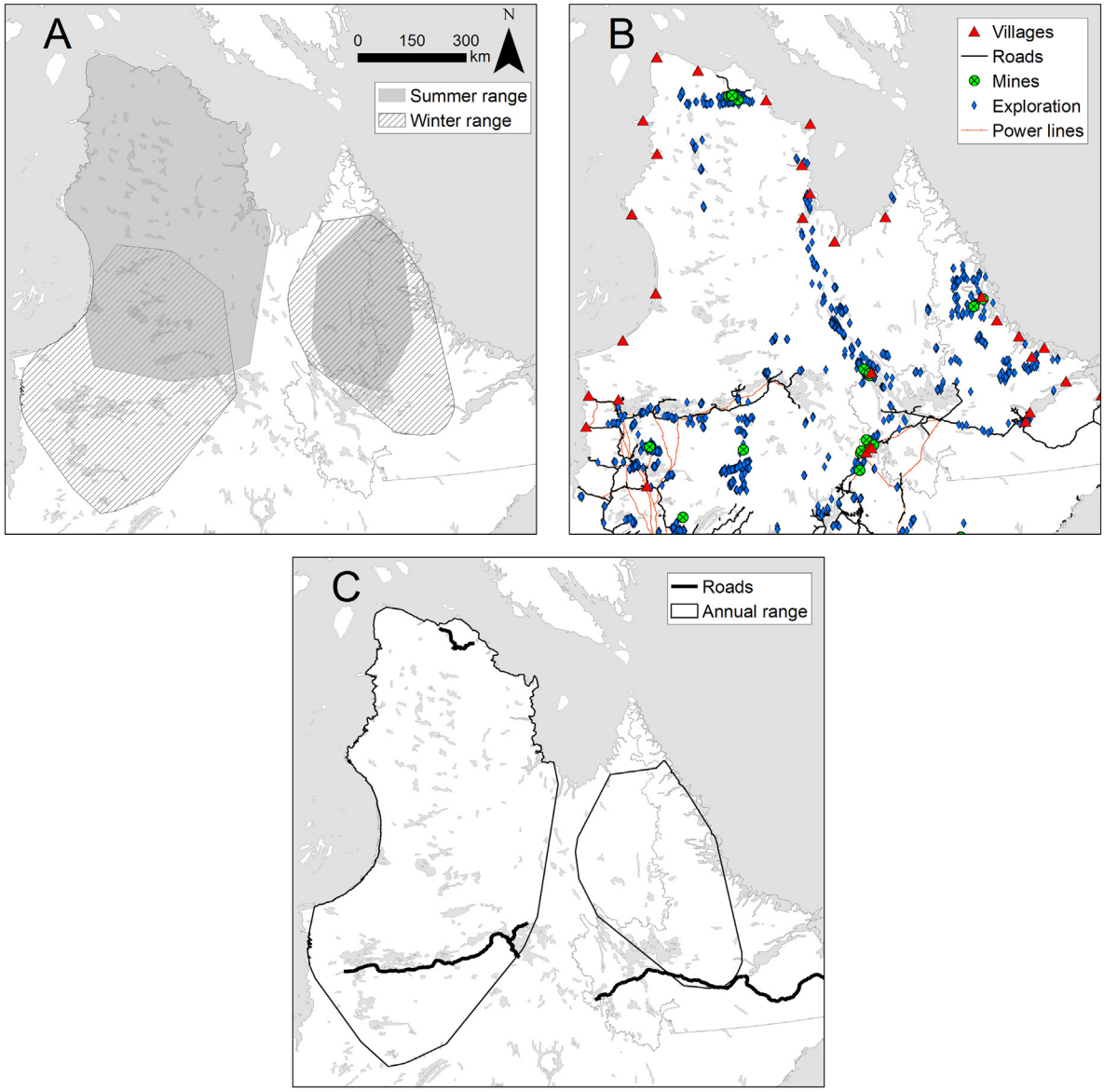

Fig. 1. Annual, summer and winter ranges of the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) migratory caribou herds (A), human disturbances (B) and sections of major roads overlapping caribou seasonal ranges (C) from 2009 to 2016 in northern Québec and Labrador, Canada. Seasonal areas for caribou are represented by 100% minimum convex polygons of all caribou locations in summer (2009–2013) and winter (2009–2016).

7 h; n = 22 F) to evaluate movement rates near and during road crossings events. We subsampled location data to obtain 1 location every 7 to 8 h to ensure movement rates were comparable among individuals.

3.2. Disturbance density in seasonal areas

We first assessed whether caribou avoided human disturbances at a broad spatial scale by comparing disturbance densities in used and available seasonal ranges. We defined used annual seasonal ranges as 95% kernels of all individuals during the summer or winter of a given year (*Kernel density tool* in Arcgis 10.2.2; default bandwidth). We chose 95% kernels instead of 100% MCPs to define seasonal ranges because kernels reflected the actual habitat used by caribou more precisely, and thus better identified disturbances 'available' for caribou within seasonal ranges. We determined the timing of summer and winter seasons using a First-Passage Time model which relied on temporal variations in movements for each individual to differentiate migration movements from summer and winter movements (see Le Corre et al. (2014) for details). We defined the starting and ending dates of summer and winter seasons annually using the mean date for all individuals. Summer began when caribou started moving after calving (June 29th–July 8th), and ended when fall migration started (July 20th–September 1st). Winter began at the end of the fall migration (November 12th–December 13th) and ended when caribou started their spring migration (March 27th–May 4th). We defined available seasonal ranges as all continental areas bounded within the most extreme caribou locations recorded for summer or winter. We calculated the density of mines, mining exploration sites, power lines (winter only), roads and human settlements by dividing the number of disturbances of each type or the length of the infrastructure by the total area of used or available seasonal ranges. We compared mean densities of disturbances across years within used and available seasonal ranges using the non-parametric Mann-Whitney-Wilcoxon test (in R 3.0.3; R Core Team, 2014).

3.3. Assessment of the zones of influence

When human disturbances occurred within a seasonal range, we estimated their ZOI using a method very similar to the one proposed by White and Gregovich (2017). The first step consisted of evaluating

Table 1
Descriptions of habitat classes used to evaluate habitat selection of migratory caribou on summer and winter ranges in northern Québec and Labrador, Canada (see Appendix 2 for more details on the corresponding habitat categories from the original layer from Latifovic et al. (2002), Latifovic and Pouliot (2005)).

Season	Habitat classes used in RSF modelling	Description
Summer	Conifer forest	> 40% of cover composed of needleleaf forest with understory of mosses, shrubs and lichens
	Barren (reference habitat)	Barren ground, snow or ice
	Shrubland	< 40% of cover composed of trees, with understory of shrubs, lichens, herbs or rocks
	Low vegetation	Lichens, herbs, rocks, shrubs
	Water (HF)	Lakes
Winter	Conifer forest with lichens[a]	10%–60% of the cover composed of needleleaf forest with understory of shrubs, lichens, and moss
	Conifer forest without lichen[a]	25% to > 75% of the cover composed of needleleaf or mixed forests
	Open or disturbed areas without lichen	New or old disturbances resulting in open areas, mostly barren, but also regenerating with low vegetation (no lichen)
	Open areas with lichens	< 40% of cover composed of trees, with understory of shrubs, lichens, herbs or rocks
	Low vegetation or barren (reference habitat)	Lichens, herbs, rocks, shrubs or barren grounds
	Water	Lakes and hydroelectric reservoirs

[a] Conifer forest with lichens and conifer forest without lichens were merged into a category named conifer forest when collinearity occurred between the two categories and prevented using them in the same RSF model.

habitat selection based only on habitat characteristics which allowed us to predict habitat use in proximity of disturbances based on the natural components of the environment. We then compared the observed caribou use (number of caribou locations) to the predicted use (based on the habitat selection model) at various distances from the disturbance. If observed use was lower than predicted, we considered that animals were avoiding the area because of the disturbance. We established the ZOI as the distance at which habitat use was no longer influenced by the disturbance. This method is comparable to a quasi-treatment-control experiment, where habitat use before disturbance is unknown but can be predicted based on habitat selection patterns where disturbances are absent (White and Gregovich, 2017).

3.4. Habitat selection model

We evaluated caribou habitat selection using only natural habitat components (no disturbance covariates) during summer (2009–2013) and winter (2009–2016). We used a shorter period for summer habitat selection because data on vegetation productivity were not available after 2013. We evaluated habitat selection within individual seasonal ranges (third-order selection; Johnson, 1980), defined as the 100% minimum convex polygon (MCP) of all locations from an individual-season. For the RFH, we considered two distinct winter periods according to the occurrence of winter sport hunting because the risk associated with hunters near infrastructures can exacerbate avoidance responses (Paton et al., 2017). Opening and closing dates of the hunting season varied through time (November 15th to February 15th in 2009–2010, November 15th to January 15th in 2011, and December 1st to January 31st from 2012 to 2015). During hunting, we only included caribou locations within the winter sport hunting zone in our analyses. To evaluate habitat selection outside the hunting season, we considered only the period after hunting due to the short period, and therefore low sample size, between the end of the fall migration and the beginning of the hunting season. For the RGH, sport hunting either occurred during the entire winter season and over the entire winter range (2009–2011) or was prohibited (2012–2015). Subsistence harvest occurred year-round on both herds.

We evaluated caribou habitat selection using resource selection functions (RSF; Manly et al., 2002). The RSF compared used resources, found at caribou locations, to available resources, found at random locations drawn within individual seasonal ranges. We used a 1:1 ratio of used and available locations (Barbet-Massin et al., 2012). We evaluated habitat characteristics within a circular buffer of 1.5-km radius around caribou and random locations to account for the largest location error in the data (1.5 km for Argos locations), but also to better describe habitat characteristics perceived by a highly mobile animal such as caribou. We calculated the proportion of each vegetation cover type, mean vegetation productivity in summer, and mean elevation within buffers. We also evaluated the effect of the proximity to the coast in summer, because strong winds in coastal areas could provide relief from insect harassment (Haskell et al., 2006). We identified vegetation cover using an advanced high-resolution radiometer AVHRR land cover map of 1 × 1 km resolution updated in 1990, 1995, 2000, and 2005 (Latifovic and Pouliot, 2005). These maps originally had 31 vegetation classes which we merged into 6 classes for RFH and RGH summer areas, and RGH winter areas, and 7 classes for RFH winter areas. We based this classification on the type of food available for caribou (mainly shrubs, grasses, lichens and herbaceous plants in summer; lichens in winter), protective cover, and natural disturbances (Table 1, Appendix 2). The proportion of vegetation cover always summed to 1 within a location buffer, which resulted in high collinearity between vegetation classes. To reduce collinearity, we used an additive log-ratio transformation (Aitchison, 1994):

$$new\%vegetation\ cover_i = log\frac{\%vegetation\ cover_i}{\%vegetation\ cover_{ref}}$$

where vegetation cover$_i$ represented the ith vegetation class and vegetation cover$_{ref}$ represented the vegetation cover type used as reference in the RSF analysis (see Table 1). We used the Normalized Difference Vegetation Index (NDVI) during summer as a proxy of vegetation productivity, based on a series of 10-day composite AVHRR images of 1 km × 1 km resolution. NDVI is a good proxy of vegetation productivity when vegetation is sparse like in our study area (Pettorelli, 2013). For each location, we assessed vegetation productivity using the NDVI values of the composite AVHRR image corresponding to the time when each location was recorded. Finally, we estimated elevation using a digital elevation model with a resolution of 100 m × 100 m. We standardized mean elevation within buffers (centered on 0 and rescaled relative to the standard deviation) to minimize RSF convergence problems. We conducted spatial analyses with ArcGIS 10.2.2 (ESRI, 2014) and Geospatial Modelling Environment (GME; Beyer, 2012).

We evaluated resource selection functions with a mixed logistic regression (PROC GLIMMIX; SAS Institute Inc., 2011) of the form:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k + \gamma_{0ij})$$

where β_0 represented the intercept for the population, β_k was the selection coefficient for the kth habitat characteristic and γ_{0ij} was the random intercept for the ith year and the jth individual. To account for autocorrelation among locations and years, and unbalanced sample size, we used the individual and year as random effects, and robust empirical standard errors (Gillies et al., 2006). We compared resource selection models including different combinations of habitat characteristics with the Akaike's information criterion (AIC) and selected the most parsimonious model (lowest AIC) to predict seasonal habitat use by caribou (Table 2). We then assessed the predictive performance of the best RSF models using a 10-fold cross validation repeated 50 times, and the mean Spearman correlation score ($r_{spearman}$ calculated in R 3.0.3; Boyce et al., 2002). When predictive performance of the best

Table 2
Candidate models and model selection results for summer (2009–2013) and winter (2009–2015) habitat selection of caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) herds in northern Québec and Labrador, Canada. We chose the most parsimonious model to predict caribou habitat use surrounding human disturbances.

Herd	Season	Model	AIC	Delta AIC	Akaike weight
RFH	Summer	Vegetation + NDVI + distance to coast + elevation	57,833.0	0.0	1.0
		Vegetation + NDVI + distance to coast	57,931.2	98.3	0.0
		Vegetation + NDVI	58,520.8	687.8	0.0
		Vegetation	58,558.3	725.3	0.0
		Distance to coast	59,592.3	1759.3	0.0
		NDVI	59,981.0	2148.0	0.0
		Elevation	60,184.7	2351.7	0.0
	Winter (hunting)	Vegetation + elevation	110,918.8	0.0	1.0
		Vegetation	111,324.3	405.5	0.0
		Elevation	112,256.5	1337.7	0.0
	Winter (no hunting)	Vegetation + elevation	163,724.1	0.0	1.0
		Vegetation	164,517.2	793.1	0.0
		Elevation	169,928.3	6204.2	0.0
RGH	Summer	Vegetation + NDVI + distance to coast + elevation	27,064.8	0.0	1.0
		Vegetation + NDVI + distance to coast	27,171.6	106.8	0.0
		Vegetation + NDVI	27,202.8	137.9	0.0
		Vegetation	27,299.4	234.6	0.0
		Distance to coast	28,230.2	1165.4	0.0
		Elevation	28,359.4	1294.5	0.0
		NDVI	28,533.1	1468.3	0.0
	Winter	Vegetation + elevation	121,540.9	0.0	1.0
		Vegetation	121,996.3	455.4	0.0
		Elevation	126,974.7	5433.8	0.0

RSF model was good (10-fold cross validation with $r_{spearman} > 0.70$), we used it to predict caribou use within a circular area of 50 km-radius around disturbances. We predicted caribou use annually for each season to account for variation in vegetation cover and vegetation productivity, but also to account for annual occurrence of disturbances within seasonal ranges. Multicollinearity among RSF variables was verified with a maximum variance inflator factor (VIF) score. Multicollinearity was negligible for all variables included in summer and winter RSF models (VIF < 4; Zuur et al., 2010), and was moderated for disturbed vegetation cover in winter for the RGH (VIF = 5.9).

3.5. Zones of influence and cumulative habitat loss

We evaluated the ZOIs of human settlements, roads, power lines, mines, and mining exploration sites. We only estimated ZOIs of disturbances that were available for caribou (i.e. that overlapped with their seasonal ranges; kernels 95%). For mining exploration, we evaluated the ZOI for projects that we considered most likely to disturb caribou (i.e. those including heavy machinery, and performing drilling, trenching, or stripping activities). For roads, we evaluated the ZOI only for segments stretching outside human settlements and overlapping the 95% kernel seasonal ranges. Many power lines were along roads. To avoid confounding the effects of roads and power lines, we restricted our ZOI evaluation to sections of power lines that were separated from roads.

We limited our analyses to areas within 50 km from disturbances because caribou habitat selection is unlikely to be affected by disturbances at greater distances (Boulanger et al., 2012; Johnson and Russell, 2014). We drew buffers at 1-km intervals, from 1 km to 50 km surrounding the disturbances. We counted the number of caribou locations within the 50 1-km buffers and calculated observed use within each buffer:

$$\textit{Observed use in the } i^{th} \textit{ buffer} = \frac{\textit{Number of caribou locations in the } i^{th} \textit{ buffer}}{\textit{Number of caribou locations in all buffers}}$$

We summed the relative probability of use predicted for caribou within each buffer (RSF volume) and calculated predicted use within each buffer:

$$\textit{Predicted use in the } i^{th} \textit{ buffer} = \frac{\textit{RSF volume in the } i^{th} \textit{ buffer}}{\textit{RSF volume in all buffers.}}$$

We then calculated buffer-specific selection ratios (observed use in the *i*th buffer/predicted use in the *i*th buffer). Predicted use could be systematically lower or higher than observed use in all buffers simply because of differences in habitat composition surrounding the disturbance compared to the seasonal ranges (White and Gregovich, 2017). To account for this, we compared buffer-specific selection ratios to the median selection ratio (selection ratio buffer_i – median selection ratio for all buffers) to obtain relative selection ratios. This ensured that selection ratios, and thus the ZOI, were evaluated relatively to a site-specific measure of central tendency (White and Gregovich, 2017). We identified the ZOI as the distance at which relative selection ratios first became greater than zero, indicating that observed use equalled expected use based on natural habitat components. To determine whether the ZOI truly corresponded to a threshold in caribou behavior, we ensured that the relative selection ratios reached an asymptote, or peaked and reached an asymptote after the first positive value. We also ensured that the ZOI identified was not a statistical artefact by performing a sensitivity analysis where we sequentially included caribou locations at increasing distances from the disturbance (see Appendix 3 for details). If the ZOI did not stabilize with the inclusion of further locations or if the relative selection ratios did not reach an asymptote, we considered the ZOI undefinable.

To evaluate cumulative habitat loss for caribou, we calculated the proportion of seasonal ranges lost due to avoidance of disturbances. On an annual basis, we calculated the proportion of seasonal ranges covered by the ZOI for all disturbance types, and the proportion of high quality habitat within the ZOI. When we were unable to identify the ZOI for a given disturbance type in a given year, we calculated cumulative habitat lost for that year using the mean ZOI of the disturbance type in all other years. We defined high-quality habitat with a contrast validation index (CVI; Fedy et al., 2014), which identifies habitat quality threshold (minimal RSF score) that included the most caribou locations within the smallest area.

3.6. Effect of roads on movements

We evaluated the effect of the Raglan, Trans-Taïga, and Trans-Labrador roads on caribou propensity to cross them (barrier effect), and on caribou movement rates. Caribou had to cross the Raglan road to reach the northernmost portion of their summer range, while the Trans-Taïga, and Trans-Labrador roads had to be crossed to reach southernmost portions of

winter ranges. We measured the barrier effect of roads by comparing observed caribou use to the use predicted by RSF models based on natural habitat components within 10 km on both sides of the roads. This allowed us to control for different habitat composition on both sides of the roads which could influence caribou propensity to cross. We calculated mean selection ratios across years for both sides of roads, and compared mean selection ratios of the southern side to those of the northern side of the roads (all roads were in a west-east axis) with a *t*-test. We also tested whether caribou increased their movement rate ($m \cdot h^{-1}$) when crossing a road. We compared the movement rates during the 5 steps preceding and following the crossing event to the movement rate during the crossing step (Leblond et al., 2013). A step was defined as the straight-line movement between two consecutive locations. We calculated movement rate between two consecutive locations by dividing the distance travelled by the interval of time between these locations. We assessed differences in movement rate between steps before, during and after a crossing event with a generalized linear model (*lmer* in R 3.0.3), and controlled for unequal sample size among individuals by setting individual identity as a random effect (Gillies et al., 2006).

4. Results

4.1. Habitat selection by caribou

For both RFH and RGH, the best candidate models describing habitat selection during summer included vegetation cover, NDVI, distance to coast and elevation, whereas vegetation cover and elevation best described habitat selection during winter (Table 2). The best-performing candidate models had a good predictive power (mean $r_{spearman}$; $RFH_{summer} = 0.97$, $RGH_{summer} = 0.95$, $RFH_{winter\ hunting} = 0.83$, $RFH_{winter\ no\ hunting} = 0.86$, $RGH_{winter} = 0.80$). During summer, caribou selected habitats with higher abundance of summer food resources (shrublands) and avoided areas with lower abundance of food (lichens or low vegetation; Table 3). Caribou of the RFH also selected for more productive areas (higher NDVI values), whereas caribou of the RGH selected for less productive areas. Caribou of the RFH appeared to select for windier areas by selecting proximity to the coast, whereas caribou of the RGH used areas inlands, far from the coast. During winter, habitat selection patterns of both herds suggested avoidance of risky habitats when sport hunting occurred. Caribou selected habitats offering dense (conifer forest, with or without lichens) or sparse protective cover (shrublands) and avoided open areas (lakes). Caribou of the RFH also selected for areas with higher abundance of winter food resources (lichens), but caribou of the RGH did not. For the RFH, habitat selection during and outside the winter sport hunting season was similar, except the selection of conifer forest without lichens that switched from being selected during the hunting period to avoided outside. Caribou of the RFH and RGH generally avoided higher elevation, except RFH during summer for which elevation had no effect on habitat selection.

4.2. Avoidance of human disturbances

The density of many disturbance types was lower within seasonal ranges than within the available ranges, suggesting avoidance of these disturbances at a large spatial scale (Table 4). We found, however, that none of the disturbance types were consistently avoided across herds or seasons.

When disturbance occurred within seasonal ranges, we found that all disturbance types could be avoided by caribou (Table 5; see Appendix 3 for curves of relative selection ratios). The ZOIs were highly variable among disturbance types and years. On the RFH summer range, the Raglan mine and its road respectively decreased caribou habitat use as far as 23 km (19–23 km) and 8 km (0–8 km). Mining exploration rarely overlapped seasonal ranges of the RFH and RGH, but when it did, the ZOI ranged from 2 to 4 km in summer, and could reach as much as 21 km in winter (3–21 km). Avoidance of human settlements was more important in winter (RFH: 2–18 km) than in summer (RFH: 2–4 km). The ZOIs of other roads were highly variable from year to year, ranging from no avoidance to 15 km. Power lines were avoided over 5 km by the RFH in winter 2009, but not in other years.

4.3. Cumulative habitat loss

Cumulative habitat loss for caribou was larger in winter than in summer. The RFH lost between 0.9% and 1.8% (1827–3130 km^2) of its summer range, and between 1.2% and 2.7% (1678–2043 km^2) of the

Table 3
Resource selection functions (estimates, standard errors [SE] and 95% confidence intervals [CI]) for caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) herds on summer (2009–2013) and winter ranges (2009–2016), northern Québec and Labrador, Canada. Models had a high predictive power (mean r_s $RFH_{summer} = 0.97$; $RGH_{summer} = 0.93$; $RFH_{winter\ hunting} = 0.81$; $RFH_{winter\ no\ hunting} = 0.93$; $RGH_{winter} = 0.88$).

Season	Covariate	RAF herd				RG herd			
		Estimate	SE	Lower CI	Upper CI	Estimate	SE	Lower CI	Upper CI
Summer	Conifer forest	−0.06	0.02	−0.09	−0.02	0.00	0.02	−0.04	0.04
	Shrublands	0.07	0.01	0.05	0.08	0.08	0.01	0.06	0.11
	Low vegetation and natural disturbance	0.01	0.01	−0.01	0.02	−0.06	0.02	−0.10	−0.02
	Lakes	−0.05	0.01	−0.07	−0.03	−0.05	0.02	−0.10	0.00
	Lichens	−0.03	0.01	−0.05	−0.02	−0.06	0.03	−0.11	−0.01
	NDVI	1.52	0.25	1.03	2.01	−1.16	0.29	−1.72	−0.60
	Distance to coast	−0.003	0.000	−0.005	−0.003	0.004	0.001	0.002	0.006
	Elevation	0.11	0.06	−0.01	0.22	−0.26	0.09	−0.44	−0.08
Winter (hunting)	Conifer forests	–[a]	–	–	–	0.14	0.02	0.09	0.18
	Conifer forests with lichens	0.04	0.01	0.02	0.07	–[a]	–	–	–
	Conifer forests without lichens	0.06	0.02	0.02	0.10	–[a]	–	–	–
	Natural disturbance	−0.01	0.01	−0.03	0.00	−0.04	0.02	−0.09	0.01
	Shrublands	0.02	0.01	0.01	0.04	0.08	0.02	0.04	0.11
	Lakes	−0.04	0.01	−0.06	−0.02	−0.11	0.02	−0.15	−0.07
	Lichens	0.03	0.01	0.01	0.05	0.03	0.02	−0.01	0.06
	Elevation	−0.15	0.06	−0.28	−0.03	−0.21	0.07	−0.35	−0.07
Winter (no hunting)	Conifer forests with lichens	0.02	0.01	−0.01	0.04	–	–	–	–
	Conifer forests without lichens	−0.13	0.03	−0.18	−0.08	–	–	–	–
	Natural disturbance	−0.05	0.01	−0.07	−0.03	–	–	–	–
	Shrublands	0.01	0.01	−0.01	0.03	–	–	–	–
	Lakes	−0.03	0.01	−0.05	−0.01	–	–	–	–
	Lichens	0.15	0.02	0.12	0.18	–	–	–	–
	Elevation	−0.24	0.07	−0.37	−0.11	–	–	–	–

[a] Variable not included in the best-performing model.

Table 4
Density of roads, mining exploration sites, mines, human settlements and power lines (winter only) in used and available seasonal ranges (summers of 2009–2013; winters of 2009–2015) for caribou of the Rivière-aux-Feuille (RFH) and Rivière-George (RGH) herds, northern Québec and Labrador, Canada.

Herd-season	Disturbance type	Mean density in seasonal area (/10,000 km^2)	Mean density in available area (/10,000 km^2)	p-Value and interpretation of the Mann-Whitney-Wilcoxon test
RFH winter	Roads	61.1 km	87.7 km	No avoidance (p = 0.68)
	Mining exploration	0 site	0.5 site	Avoidance (p = 0.03)
	Mines	0 mine	0.01 mine	No avoidance (p = 0.17)
	Human settlements	0.05 settlement	0.15 settlement	Avoidance (p = 0.02)
	Power lines	116.2 km	103.8 km	No avoidance (p = 0.83)
RGH winter	Roads	28.3 km	74.6 km	Avoidance (p = 0.02)
	Mining exploration	0.3 site	0.7 site	No avoidance (p = 0.18)
	Mines	0.09 mine	0.05 mine	No avoidance (p = 0.19)
	Human settlements	0.09 settlement	0.3 settlement	Avoidance (p = 0.02)
	Power lines	14.5 km	23.6 km	No avoidance (p = 0.18)
RFH summer	Roads	7.6 km	9.4 km	Avoidance (p = 0.01)
	Mining exploration	1.1 site	1.1 site	No avoidance (p = 0.29)
	Mines	0.2 mine	0.09 mine	No avoidance (p = 0.14)
	Human settlements	0.2 settlement	0.3 settlement	No avoidance (p = 0.23)
RGH summer	Roads	0 km	2.5 km	Avoidance (p < 0.005)
	Mining exploration	1.4 site	2.3 sites	No avoidance (p = 0.27)
	Mines	0 mine	0.05 mine	Avoidance (p < 0.005)
	Human settlements	0 settlement	0.3 settlement	Avoidance (p < 0.005)

available high-quality habitat. In comparison, the RFH lost between 0% and 30.3% (0–6351 km^2) of its winter range and between 0% and 37.9% (0–1893 km^2) of high-quality winter habitat during the hunting season. Cumulative habitat loss was less pronounced outside the hunting season, ranging from 4.6% to 6.7% (1354–3192 km^2) of the winter range and from 3.7% to 7.3% (1430–1508 km^2) of high-quality habitat. Due to limited overlap between the RGH and disturbances, the evaluation of cumulative habitat lost relied only on a few disturbances. In 2009, the RGH summer range overlapped only with mining exploration and cumulative habitat lost was estimated at 0.11% (91 km^2) of the range, and 0.02% (9 km^2) of high-quality habitat. When sport hunting occurred on the RGH (2009–2010), caribou lost at most 3.1% (555 km^2) of their winter range and 4.5% (307 km^2) of their high-quality habitat. In 2014, when no sport hunting occurred on the RGH, we estimated that caribou did not lose access to any part of their winter range or high-quality habitat.

4.4. Effect of roads on movements

We found a strong barrier effect of the Raglan road based on the habitat use of the RFH in summer. After controlling for habitat composition on both sides of the road, we found that selection ratio was 3.7 times lower north (crossing required) than south (no crossing) of the road (mean $sr_{north} = 0.45$, mean $sr_{south} = 1.52$, $p = 0.004$). The barrier effect of the Raglan road was detected in all years between 2009 and 2013, except in 2010 (Fig. 2A), when the Raglan road also had a ZOI of 0 km. On the RFH winter range, we found no barrier effect of the Trans-Taïga road (mean $sr_{north} = 1.11$, mean $sr_{south} = 0.90$, $p = 0.39$). During 3 of the 6 years when the Trans-Taïga road overlapped the RFH winter range, selection ratios were higher south of the road (crossing required) than north of it (Fig. 2B). We found no statistical difference in habitat used by caribou between both sides of the Trans-Labrador road when it overlapped the RGH winter range in 2009 and 2010 (mean $sr_{north} = 1.80$, mean $sr_{south} = 0.37$, $p = 0.12$). Selection ratios, however, were systematically larger north of the road (no crossing required) than south, especially in 2010, when the selection ratio was 73 times higher north of the road than south of it (Fig. 2C).

We could not evaluate movement rates during crossing events of the Raglan and the Trans-Labrador roads due to the low number of individuals equipped with a GPS collar with a fix-rate < 7 h that crossed these roads (Raglan n = 3; Trans-Labrador n = 3). On the RFH winter range, 21 individuals crossed the Trans-Taïga road (55 crossing events). Caribou of the RFH moved 1.2 to 1.3 times faster when crossing the Trans-Taïga road ($mean_{cross} = 371\ m \cdot h^{-1}$) than during the steps before ($mean_{before} = 277\ m \cdot h^{-1}$, $t = -3.88$, $p < 0.001$) or after ($mean_{after} = 316\ m \cdot h^{-1}$, $t = -2.27$, $p < 0.001$). Movement rates following road crossing were slightly higher than movement rates preceding road crossing ($p = 0.005$) (Fig. 3).

5. Discussion

Migratory caribou populations have fluctuated in the past across their circumpolar distribution, but the recovery of these populations in the context of climate change and increased human development in northern ecosystems is questioned (Festa-Bianchet et al., 2011). In recent decades, many studies provided compelling evidence that caribou and reindeer are sensitive to human disturbances (Cameron et al., 2005; Vistnes and Nellemann, 2008; Wolfe et al., 2000). In northern Québec and Labrador, the eastern migratory caribou reacted to human disturbances at multiple spatial scales, suggesting broad effects on caribou behavior. On several occasions, we observed that caribou established their seasonal ranges in areas with fewer human disturbances than the available area, suggesting avoidance at a large spatial scale. When disturbances were present in caribou seasonal ranges, we identified zones with reduced caribou occupancy for almost all types of disturbances. Roads were avoided by caribou, but also impacted their movements, either by limiting their access to certain areas or by increasing their movement rates.

At a large spatial scale, we observed that the RGH completely excluded mines, roads and human settlements from their summer ranges. This exclusion was not observed in winter for the RGH or in any season for the RFH. The decline of the RGH in the last decades was accompanied by a significant reduction of its annual range, which raises the question of whether avoidance at this scale could be an artefact of population decline instead of an active avoidance of disturbed areas (Messier et al., 1988; Reimers et al., 2007; Taillon et al., 2012). As suggested by the ideal free distribution theory, population density may affect habitat selection by individuals, making sub-optimal habitat less attractive as density decreases (Fretwell and Lucas, 1970). Because caribou gradually redistributed themselves away from disturbances as the RGH declined, the avoidance of human disturbances may have contributed to shape the actual range of the RGH.

At a finer spatial scale, we found that caribou reduced habitat use in the surroundings of all types of disturbances. Reported effects of power lines on reindeer behavior in Scandinavia ranged from no effect (Colman et al., 2017; Reimers et al., 2007) to avoidance of several km

Table 5
Zones of influence (ZOI) of human disturbances and cumulative habitat loss (% of seasonal ranges) for migratory caribou of the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) herds in northern Québec and Labrador, Canada, during summer (2009–2013) and winter (hunting/no hunting; 2009–2016). We could not evaluated ZOIs when disturbances did not overlap caribou seasonal ranges (——) or when inter-individual variations in behavior was too high to accurately identify a ZOI (Undetermined).

Season	Herd	Year	Zones of influence (km)					Cumulative habitat loss (%)	
			Mines	Roads	Mining exploration	Human settlements	Power lines	Total area	Prime habitat
Summer	RF	2009	N loc insufficient	5	——	3	——	0.86	1.18
		2010	20	0	——	4	——	1.53	2.57
		2011	23	Undetermined	2	2	——	1.40	2.71
		2012	Undetermined	Undetermined	——	Undetermined	——	1.21	1.91
		2013	21	8 km	——	4	——	1.76	1.96
	RG	2009	——	——	4	——	——	0.11	0.02
Winter (hunting)	RF	2009	——	4	3–21	2–12	5	26.55–29.97	34.09–37.90
		2010	——	0	——	——	0	0.00	0.00
		2011	——	12	——	13	——	2.36	7.98
		2012	——	15	——	9	——	7.44	16.77
		2013	——	Undetermined	——	18	0	12.86	20.69
		2015	——	14	——	Undetermined	0	30.33	34.89
	RG	2009	——	2	——	——	——	3.06	4.51
		2010	——	Undetermined	——	——	——	1.07	1.89
Winter (no hunting)	RF	2009	——	Undetermined	——	——	——	6.64	7.19
		2013	——	3	Undetermined	Undetermined	——	4.59	13.65
		2015	——	2	——	2	——	5.01	5.19
	RG	2014	——	0	——	Undetermined	——	0.00	0.00
		2015	——	——	——	Undetermined	——	NA	NA

(Nellemann et al., 2001; Vistnes and Nellemann, 2001) and strong barrier effect (Vistnes et al., 2004). Our results, however, suggest that power lines alone are not a major disturbance for caribou. Avoidance of other disturbances by caribou of the RFH and RGH was highly variable among years and disturbances types. Caribou were especially sensitive to industrial development, with the largest ZOI identified for the Raglan mine and mining exploration sites. The ZOI we reported for the Raglan mine (19–23 km) is larger than those reported for other species or other caribou ecotypes (2–14 km; Boulanger et al., 2012; Johnson et al., 2015; Polfus et al., 2011; Weir et al., 2007; 1–1.8 km; White and Gregovich, 2017). Dust deposition from mining activities is unlikely to explain such large avoidance. The Raglan mine operated mainly underground, and dust deposition as far as 21 km is unlikely (Boulanger et al., 2012: < 14 km; Chen et al., 2017: < 1 km). Alternatively, the open tundra surrounding the Raglan mine could ease visual and acoustic detection of vehicles and heavy machinery over large distances, thereby increasing the risk perceived by caribou, and exacerbating their responses towards the mine (Benítez-López et al., 2010;

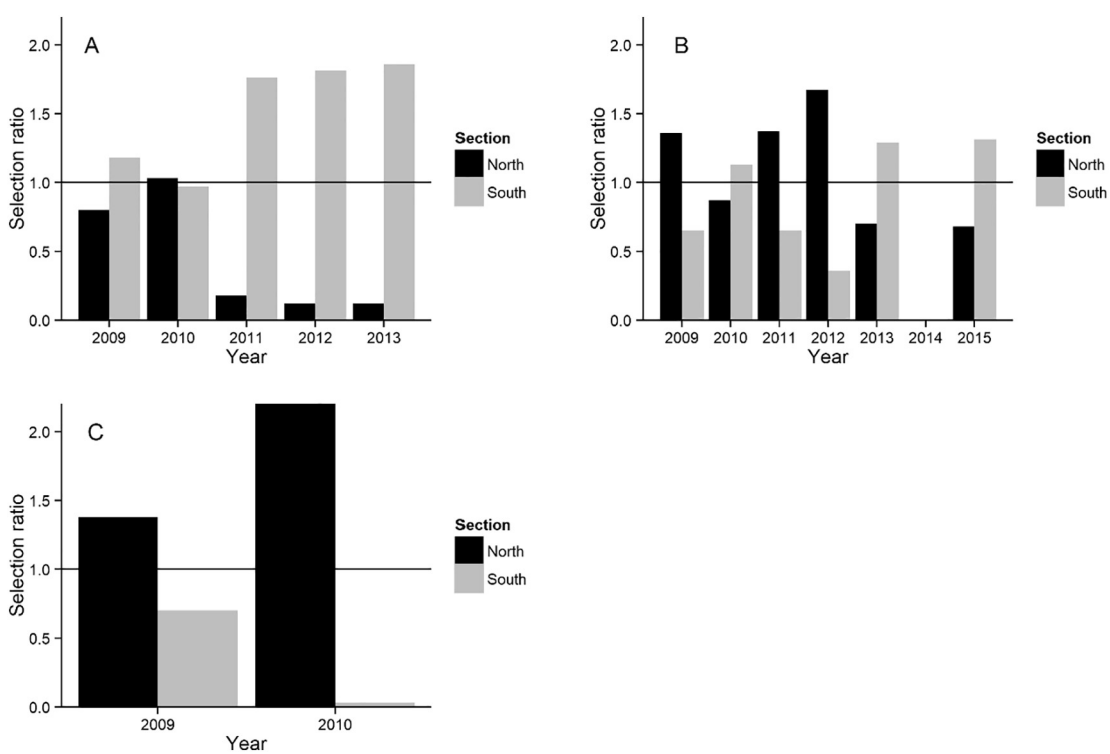

Fig. 2. Selection ratios for habitat on the northern and southern sides of the Raglan road (A), the Trans-Taïga road (B) on the Rivière-aux-Feuilles herd range, and the Trans-Labrador highway (C) on the Rivière-George herd range. See Fig. 1C for the location of the roads. Selection ratio > 1 indicates selection by caribou, whereas selection ratio < 1 indicates avoidance.

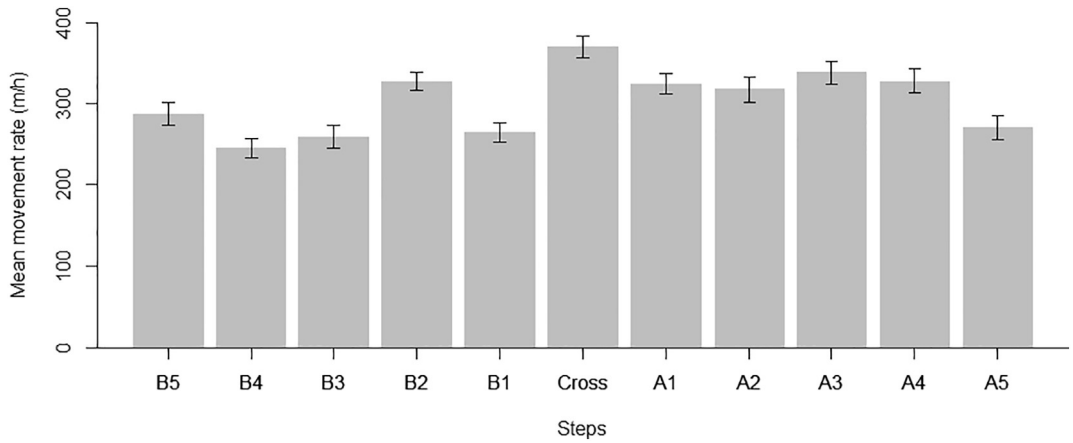

Fig. 3. Mean movement rates of caribou from the Rivière-aux-Feuilles herd when crossing the Trans-Taïga road (Cross), during the 5 steps before (B5 to B1), and after (A1 to A5) the crossing event. A step was defined as the straight-line movement between two consecutive locations.

Bonnot et al., 2013). Avoidance of mining exploration was mostly limited to a few km around drill or trench sites, but could extend as far as 21 km on the winter range of the RFH. We detected, however, two peaks in the selection ratio curve, suggesting that certain individuals avoided, or certain exploration sites were avoided over 3 km, but this avoidance reached 21 km in other cases. We also found that the additional predation risk associated with human hunters can exacerbate risk-averse behaviors (Lone et al., 2015; Paton et al., 2017). Outside the hunting season, for example, the ZOIs for roads and human settlements were similar to other ungulate populations (Anttonen et al., 2011; Laurian et al., 2012; Leblond et al., 2013), while they were larger during the hunting season. Roads and human settlements are known to provide access to hunters and constitute risky environments for migratory caribou (Plante et al., 2017).

Human developments, especially linear features, can disrupt wildlife movements (Dyer et al., 2002; Lendrum et al., 2013; Sawyer et al., 2013). Migration, for example, enables individuals to track high-quality food resources and escape predation (Fryxell et al., 1988; Hebblewhite and Merrill, 2007), so any disturbance of movements could reduce population ability to persist in changing environments (Berger, 2004; Bolger et al., 2008; Sawyer et al., 2013). In northern Québec and Labrador, roads affected range use and movement by migratory caribou. We observed very few crossings of the Trans-Labrador road, suggesting that the road acted as a barrier to movements for the RGH, but again, we should consider the role of population decline, and associated reduction in range size, on habitat use in the vicinity of this road (Bergerud et al., 1984; Messier et al., 1988). On the RFH summer range, the Raglan road represented a barrier to movements, preventing most individuals to reach the tip of the Ungava peninsula. Heavy traffic on the road could deter caribou to cross and the relatively small size of the habitat patch available on the other side may not be worth the risk. Females also had calves at heel during summer, which can make them less tolerant to disturbances (Nellemann and Cameron, 1998; Weir et al., 2007). On their winter range, caribou of the RFH crossed the Trans-Taiga road, despite avoiding that same road over as much as 15 km in some years, and facing an increased risk of predation by sport hunters when using the road. Conifer forest surrounding the road provided good visual obstruction, and animals could be more inclined to cross roads in these conditions (Dussault et al., 2007; Stankowich, 2008). In addition, caribou gained access to a much larger area by crossing the Trans-Taiga than the Raglan road, which could further increase the incentive to cross. Crossing the Trans-Taiga, however, was not without a cost, because caribou increased their movement rate during crossing, as reported elsewhere for other species (*Alces alces*; Dussault et al., 2007; *Odocoileus hemionus*; Lendrum et al., 2013; *Cervus elaphus*; Prokopenko et al., 2017a; Sawyer et al., 2013). Although crossing the road enabled caribou to maintain connectivity on their winter range, the road may represent a semi-permeable barrier hindering movements and influencing individual fitness (Sawyer et al., 2013). Nevertheless, we consider that the access to RFH and RGH seasonal ranges was not imperiled by roads since they were located on the outer fringe of seasonal ranges. We do not exclude, however, that further developments could threaten and limit access to traditional areas for these herds (Bolger et al., 2008).

The large inter-annual variations we observed in the ZOI and barrier effects suggest that other factors may contribute to caribou responses towards disturbances. In 2010, for example, caribou of the RFH did not avoid the Raglan or the Trans-Taiga roads. The same year, these roads did not represent a barrier to caribou movement. Body condition and environmental conditions, such as snow cover or insect harassment, could affect tolerance towards disturbances (Sawyer et al., 2017; Skarin et al., 2004) and modify the cost-benefit ratio of crossing roads. In 2010, temperatures were the warmest recorded since 1991, and the area experienced a negative phase of the North Atlantic Oscillation (NAO), which is associated with more snow precipitations (Le Corre et al., 2017). Negative NAO phases have been linked with poor body condition for caribou (Couturier et al., 2009), and individuals in poor condition may take more risk to acquire food resources near roads or cross them to reach resources (Beale and Monaghan, 2004; Crosmary et al., 2012). The absence or reduced avoidance of disturbances may not indicate the absence of adverse effects, but could rather suggest that animals are forced to use disturbed areas (Gill et al., 2001; Leblond et al., 2011; Prokopenko et al., 2017b).

We demonstrated that avoidance of individual disturbances could lead to significant cumulative effects. Cumulative habitat lost due to the avoidance of disturbances reached as much as 30% of caribou winter range and precluded access to over 37% of high-quality winter habitat in some years. As mining activities expand on the landscape, disturbance density may reach a threshold where rapid changes in animal behavior may be observed. Risk-averse behaviors have been observed for disturbance densities as low as one road or 0.3–1.5 $km \cdot km^{-2}$ (Frair et al., 2008; Nellemann and Cameron, 1998; Wilson et al., 2016). We also showed that a single road could preclude or hinder movements, supporting suggestions that even low density of disturbances may trigger behavioral responses. We suspect that the large ranges used by migratory caribou and their relative fidelity to seasonal ranges and migration routes could make them particularly vulnerable to cumulative effects of human disturbances (Bolger et al., 2008). If human disturbances have impacts on survival, traditional areas or routes could become ecological traps for caribou as they become more disturbed (Faille et al., 2010; Tablado and Jenni, 2017). We also question the potential for migratory caribou to habituate to disturbances. Habituation has been demonstrated for behavioral responses at small spatio-temporal scales (Hansen and Aanes, 2014; Haskell and Ballard, 2008),

but for *Rangifer* populations, avoidance generally prevails at large spatiotemporal scales (Johnson and Russell, 2014; Nellemann et al., 2010), even for domesticated reindeer (*R. tarandus tarandus*; Skarin and Åhman, 2014). In our study, caribou avoided long-established infrastructures, suggesting that long-term habituation is unlikely.

We studied the effects of human disturbances during the declining phase of two herds of migratory caribou, when population abundance was relative low compared to population peaks. Because population density may influence range use and habitat selection of animals (Rosenzweig and Abramsky, 1985), it is possible that the reaction of caribou towards human disturbance was also related to population size. At low density, animals could display higher selectivity due to reduced intraspecific competition and stronger avoidance of human disturbances. On the opposite, high densities could lead animals to use sub-optimal or sink habitats and be more tolerant of human disturbances (Gill et al., 2001). Future studies should investigate the influence of population density on the degree of avoidance of human disturbances. The legacy effects of past disturbances on current habitat use by caribou are also unknown. We were unable to assess the effect of past disturbances due to their proximity to current ones. If the effect of past disturbances on habitat use persists in time, cumulative habitat loss for caribou could be higher than the one assessed in our study. Our results concerning the cumulative habitat loss should therefore be seen as conservative because we have possibly not mapped all the sources of human disturbance. Nevertheless, the statistical approach we used here would be particularly useful to evaluate legacy effects where past disturbances can be isolated from current disturbances. This approach would allow, for example, to untangle the effect of remaining fear associated with past activity from the effect of habitat alteration that can persist over time.

6. Conclusions and recommendations

The future of migratory caribou populations is uncertain with the increasing threat of climate change and human developments (Festa-Bianchet et al., 2011). We showed that disturbances can have substantial individual and cumulative effects on caribou behavior, but we still do not know whether these negative effects could contribute to the recent decline of the caribou herds in northern Québec and Labrador. Further research is needed to quantify fitness costs of risk-averse behaviors towards disturbances and the influence of cumulative habitat loss on population dynamics. Protected areas may fail to track changes in habitat use by caribou, thus pressing the importance of establishing spatially dynamic conservation measures (Taillon et al., 2012). As human developments continue to encroach into northern ecosystems, it may become unfeasible to create protected areas with disturbance density sufficiently low to provide adequate habitat for caribou. Conservation measures should thus focus on maintaining the integrity and functions of ecological systems across caribou ranges, for example by identifying the maximum level of human disturbance that caribou could tolerate without negative consequences on fitness or population dynamics (Johnson, 2013; Sorensen et al., 2008). The conservation of migratory caribou needs to be considered when planning the development of human activities in northern regions. We thus suggest to focus conservation efforts on developing long-term planning minimizing the cumulative effects of multiple disturbances at the scale of caribou ranges.

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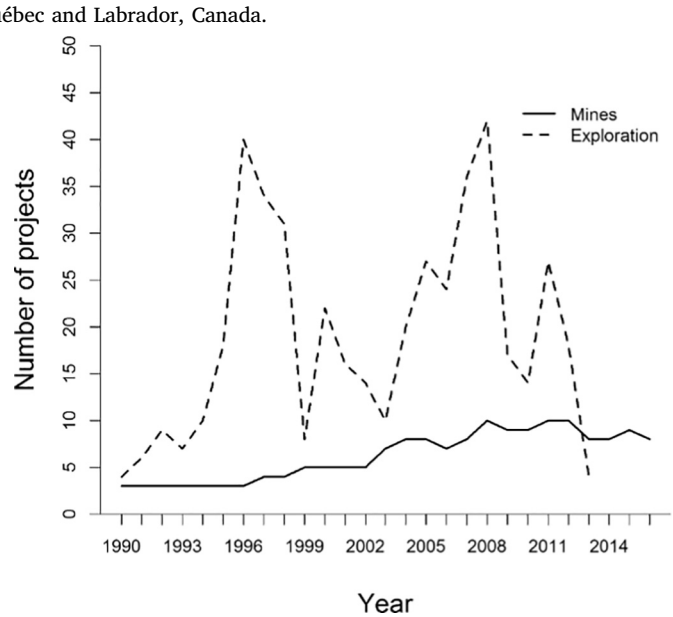
Appendix 1

Number of active mines and mining exploration projects between 1990 and 2013 in the distribution range of the Rivière-aux-Feuilles and Rivière-George caribou herds in northern Québec and Labrador, Canada.



Appendix 2. Habitat selection by caribou

Table 1
Habitat classes used to evaluate habitat selection of migratory caribou on summer and winter ranges in northern Québec and Labrador, Canada, and corresponding habitat classes and raster values from the original layer from Latifovic et al. (2002), Latifovic and Pouliot (2005).

Season	Habitat classes used in RSF model	Description	Raster value and description of the Latifovic et al. 31 vegetation classes	
			Value	Description
Summer	Conifer forest	> 40% of cover composed of needleleaf forest with understory of mosses, shrubs and lichens	1	High density needleleaf forest: old evergreen forest (75% cover) or evergreen open canopy (40–60% cover) with moss-shrub understory
			2	Medium density needleleaf forest: evergreen open canopy (40–60% cover) with lichen-shrub understory
			3	Medium density northern forest: evergreen open canopy (40–60%) with lichen-rock understory
			4	Low density southern forest: young evergreen forest (> 75% cover) or evergreen open canopy (25–40% cover) with shrub-moss understory
			5	Low density northern forest: evergreen open canopy (25–40% cover) with lichen-rock understory
	Barren (reference habitat)	Barren ground, snow or ice	22	Barren lands
			31	Snow or ice
	Shrubland	< 40% of cover composed of trees, with understory of shrubs, lichens, herbs or rocks	13	Transition tree shrubland: sparse conifer trees (10–25%) with herbs, shrubs and lichens
			14	Wetland tree shrubland: deciduous shrubs (> 75% cover) and wetlands
			15	Wetland medium density shrubs: closed shrubland
			18	Shrubs and lichens: shrubs, herbs, lichens with patches of barren grounds and water
	Low vegetation	Lichens, herbs, rocks, shrubs	11	New disturbance: recent burns or mostly bare disturbed areas (cutovers)
			12	Old disturbance: low vegetation cover
			19	Heather and herbs: shrub, herbs, lichens and bare areas
			20	Low vegetation cover nonforest: low vegetation cover with snow
			21	Very low vegetation cover nonforest: rock outcrop, low vegetation cover
	Water (HF)	Lakes	0	Water
Winter	Conifer forest with lichens**	10%–60% of the cover composed of needleleaf forest with understory of shrubs, lichens, and moss	2	Medium density needleleaf forest: evergreen open canopy (40–60% cover) with lichen-shrub understory
			3	Medium density northern forest
			5	Low density northern forest: evergreen open canopy (25–40% cover) with lichen-rock understory
	Conifer forest without lichen**	25% to > 75% of the cover composed of needleleaf or mixed forests	1	High density needleleaf forest: old evergreen forest (75% cover) or evergreen open canopy (40–60% cover) with moss-shrub understory
			4	Low density southern forest: young evergreen forest (> 75% cover) or evergreen open canopy (25–40% cover) with shrub-moss understory
			7	Mixed needleleaf forest
			9	Mixed heterogenous forest: young to old mixed coniferous forest (50–70% cover) or mixed deciduous forest (25–60% cover)
			10	Mixed broadleaf forest: deciduous open canopy (25–60% cover), low regenerating to young broadleaf cover
	Open or disturbed areas without lichen	New or old disturbances resulting in open areas, mostly barren, but also regenerating with low vegetation (no lichen)	11	New disturbance: recent burns or mostly bare disturbed areas (cutovers)
			12	Old disturbance: low vegetation cover
			NA	Fires: rasterized fire polygons from the Canadian National Fire Database, Natural Resource Canada
	Open areas with lichens	< 40% of cover composed of trees, with understory of shrubs, lichens, herbs or rocks	13	Transition tree shrubland: sparse conifer trees (10–25%) with herbs, shrubs and lichens
			14	Wetland tree shrubland: deciduous shrubs (> 75% cover) and wetlands
			15	Wetland medium density shrubs: closed shrubland
	Low vegetation or barren (reference habitat)	Lichens, herbs, rocks, shrubs or barren grounds	19	Heather and herbs: shrub, herbs, lichens and bare areas
			20	Low vegetation cover nonforest: low vegetation cover with snow
			21	Very low vegetation cover nonforest: rock outcrop, low vegetation cover
			22	Barren lands
	Water	Lakes and hydroelectric reservoirs	0	Water

** Conifer forest with lichens and conifer forest without lichens were merged into a category named conifer forest when collinearity occurred between the two categories and prevented using them in the same RSF model.

Appendix 3. Determination of the ZOI and sensitivity analyses

We used two complementary approaches to identify the zones of influence (ZOI) of human disturbances and determine whether ZOIs could be accurately identified. We first identified a ZOI by determining the distance from the infrastructure at which the relative selection ratio became positive (observed use ≥ predicted use). We then visually inspected the relation between relative selection ratios and the distance from infrastructure to confirm the occurrence of a threshold in caribou habitat use. We expected three possible relationships between the distance from infrastructure and relative selection ratios (Fig. 1). Caribou avoiding the infrastructure within a given distance could distribute themselves evenly outside the ZOI (Fig. 1A), or aggregate just beyond the ZOI (Fig. 1B). If the ZOI was larger than 50 km or if behaviors among individuals were highly variable, the relative selection ratios would not reach an asymptote (Fig. 1C). In that case, the first positive relative selection ratio would be around 25 km because we compared buffer-specific selection ratios to the median selection ratio (selection ratio buffer_i – median selection ratio for all buffers) to obtain relative selection ratios. The ZOI identified would thus be an artefact of the statistical method. To ensure that the ZOIs were accurately identified when equal or near 25 km, we performed a sensitivity analysis, where we sequentially included caribou locations at increasing distances from the disturbance, and evaluated the ZOI at each step. If the ZOI did not stabilize with the inclusion of further locations, we considered that the ZOI was undetermined. High variability in avoidance behavior among individuals, for example, could generate this pattern. In most cases, ZOIs were easily determined (Fig. 2). When ZOIs were not obvious, we relied on the sensitivity analysis to identify them (Fig. 3).

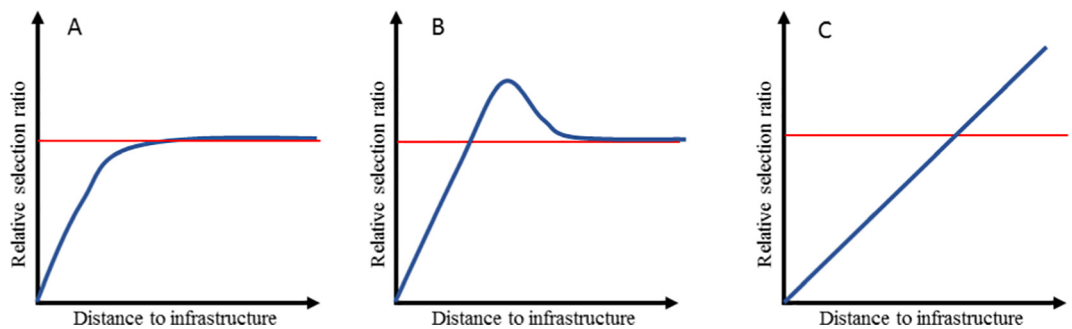


Fig. 1. Potential relationships between relative selection ratio and distance to infrastructure. Relative selection ratio < 0 (below the horizontal line) indicates avoidance by caribou, whereas relative selection ratio = or > 0 indicates neutral or positive selection by caribou.

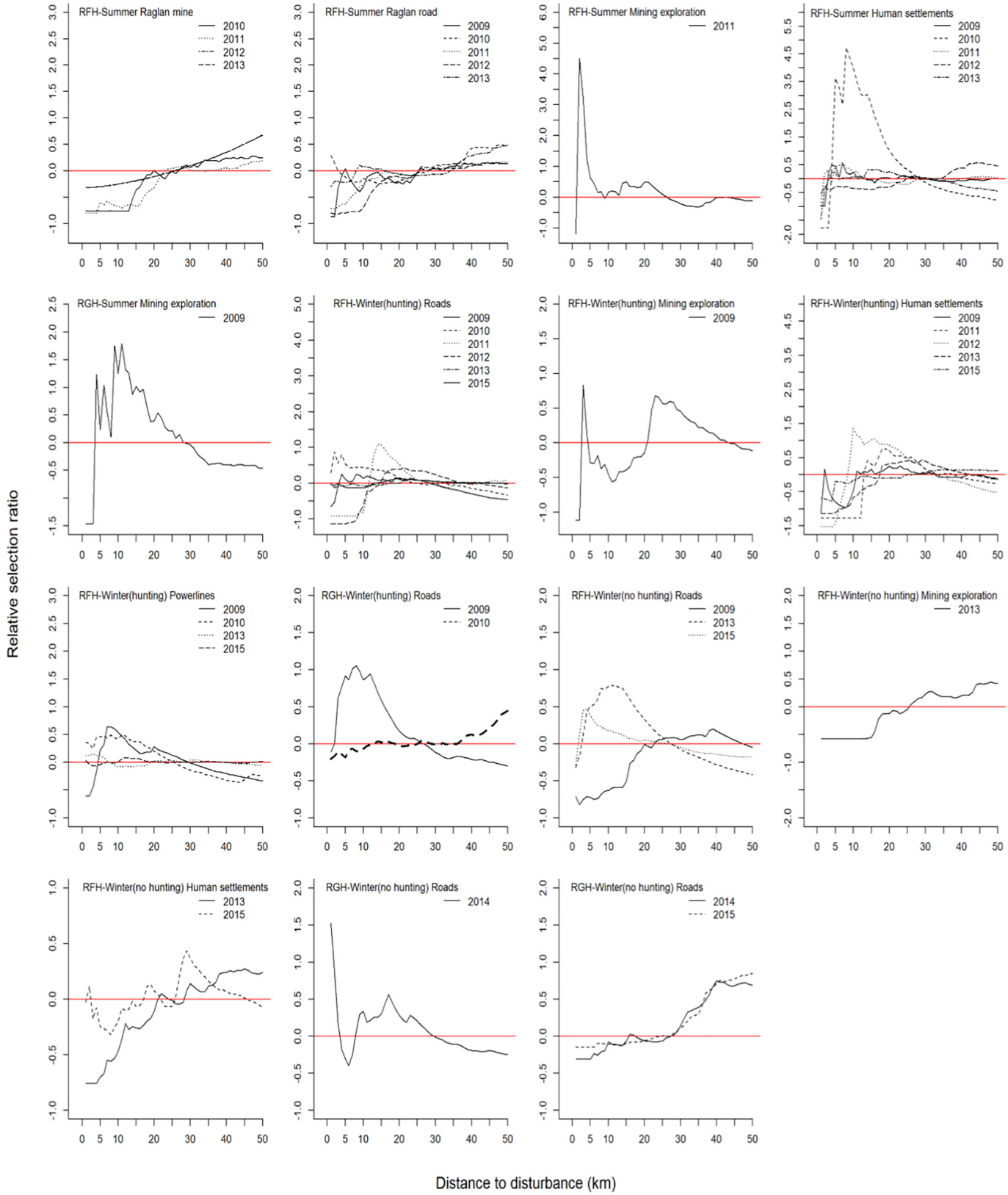


Fig. 2. Relations between the relative selection ratios and distances from disturbance for the Rivière-aux-Feuilles (RFH) and Rivière-George (RGH) caribou herds. Relative selection ratios < 1 suggest avoidance by caribou, whereas ratios = or > 0 respectively suggest absence of selection or positive selection. The ZOI was identified as the distance corresponding to the first positive relative selection ratio.

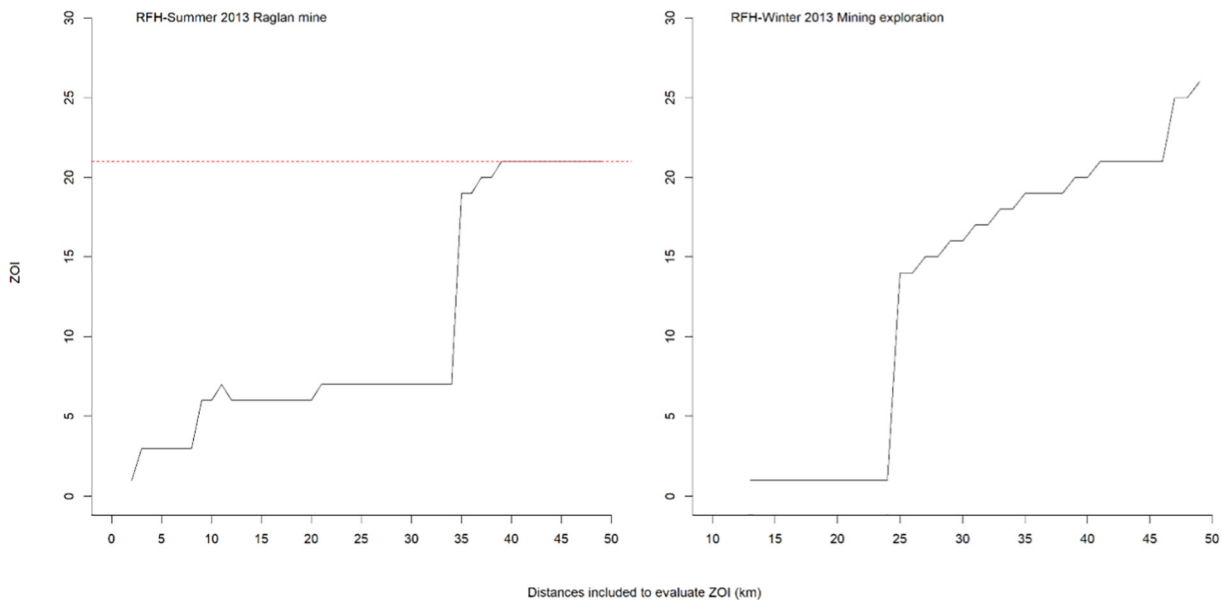


Fig. 3. Examples of ZOI sensitivity plots for caribou of the Rivière-aux-Feuilles herd (RFH). A clear ZOI at 21 km was identified for the Raglan mine in summer of 2013, but we were unable to identify a clear ZOI for mining exploration in winter of 2013 (no hunting).

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