Research Article

Landscape Attributes Explain Migratory Caribou Vulnerability to Sport Hunting

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ABSTRACT Human disturbances are increasing in Arctic regions and have been suggested as one of the main factors explaining caribou (Rangifer tarandus) decline. The cumulative effects of disturbances may negatively affect caribou habitat use, survival, and population dynamics. Thus, there is a need to evaluate the impact of various human disturbances, especially those that cause direct mortality (e.g., sport hunting). We evaluated the relative importance of caribou and hunter habitat selection and landscape characteristics on caribou vulnerability to sport hunting in northern Québec, Canada. We used resource selection functions to describe habitat selection of 223 caribou and 87 hunters. We then characterized >169,000 caribou harvest sites recorded over 17 years according to the relative probability of co-occurrence of caribou and hunters, the relative probability of occurrence of hunters only, or the characteristics of the landscape (e.g., distance to human infrastructures, elevation, land cover type). Landscape characteristics better explained caribou vulnerability to sport hunting than habitat selection of caribou and hunters, or their co-occurrence. Caribou were more vulnerable in proximity to hunting infrastructures (e.g., roads, outfitter camps) than elsewhere, but caribou strongly avoided roads. Caribou were also more vulnerable on frozen lakes than in other land cover types. Lakes were, however, avoided by caribou and not selected by hunters. Harvest was more likely in smoother terrain, even if caribou and hunters did not select for this characteristic. We demonstrated caribou were more vulnerable in areas with good accessibility (near roads) or where caribou were easily detectable (lakes, smoother terrain), which also represents areas that were either avoided or not selected by caribou or hunters. This discrepancy between harvest distribution and behaviors of caribou and hunters suggests that harvest may be an opportunistic event where visibility and accessibility increased chances of success for hunters. Managers could use this information to manipulate hunting success according to population estimates and harvest quota by establishing minimal distance to risky areas within which hunting would be prohibited. © 2016 The Wildlife Society.

KEY WORDS game species vulnerability, human disturbances, northern Québec, Rangifer tarandus, resource selection functions, sport hunting.

When facing predation risk, prey may respond by modifying their movement patterns (Stankovich and Blumstein 2005), increasing their vigilance rate (Cherry et al. 2015), or selecting safer habitat (Creel et al. 2005). These responses reduce predation risk but may also have costs, including reduced energy intake (Fortin et al. 2004) with impacts on reproduction (Creel and Christianson 2008). Human disturbances can also trigger anti-predator responses that are similar to those induced by other predators (Frid and Dill 2002). The most common response of animals to human disturbances is avoidance (Fahrig and Rytwinski 2009, Benítez-López et al. 2010) and some studies suggest that avoidance increases with disturbance intensity (Ciuti et al. 2012, Leblond et al. 2013).

Although most human disturbances do not cause direct mortality in animals, hunting is a particular case of human disturbance where anti-predator responses can be invoked and prey mortality can occur. As with natural predation, hunting pressure may lead game species to leave habitat patches providing good foraging opportunities for safer ones (Kilgo et al. 1998, Benhaiem et al. 2008, Proffitt et al. 2009). Unlike most human disturbances, however, there is a real mortality risk associated with hunting, and animals that trade-off foraging to favor safety may increase their probability of survival (Proffitt et al. 2009, Lone et al.

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2015). It was also reported that game species avoid areas with high densities of hunters and roads during the hunting season (Little et al. 2014), whereas hunters are generally associated with hunting infrastructures (e.g., cabins or roads; Brøseth and Pedersen 2000, Diefenbach et al. 2005, Lebel et al. 2012). Consequently, space use overlap between game species and hunters is expected to be low near hunting infrastructures (Millsbaugh et al. 2000), possibly resulting in lower hunting success (Gratson and Whitman 2000). However, some studies have reported that game species were disproportionately harvested in proximity of hunting infrastructures (Foster et al. 1997, Brøseth and Pedersen 2000), especially in open areas (Lebel et al. 2012), suggesting harvest sites were better predicted based on hunters than game species habitat use (Roever et al. 2013).

The Arctic has experienced an increase in human disturbances, partly due to the growth in oil, gas and mineral exploration and extraction in the recent decades (National Research Council 2003, Arctic Monitoring and Assessment Program 2010). These activities may have negative and cumulative effects on wildlife and have been suggested as one of the main reasons for the decline of caribou (*Rangifer tarandus*) in boreal and arctic regions (Vors and Boyce 2009). There is a need to evaluate the impact of several types of human disturbances, especially those that can cause direct mortality (i.e., sport hunting). Few studies, however, have described the landscape of vulnerability created by hunters (Roever et al. 2013, Lone et al. 2014, Norum et al. 2015), despite the fact that hunting can disturb habitat use and directly cause mortality of game species. In addition, industrial development may increase accessibility to remote regions and increase vulnerability to hunting for Arctic wildlife. The Rivière-aux-Feuilles (RAF) migratory caribou herd in northern Québec, Canada, faces an increase in human disturbances in its annual range, mainly through mining exploration and is also hunted by sport hunters in autumn and winter. Disturbances could have cumulative effects and significantly influence caribou habitat use and vulnerability to hunting.

We examined landscape vulnerability of migratory caribou of the RAF herd during winter sport hunting. We evaluated the relative importance of caribou and hunter behaviors, and landscape characteristics in determining caribou vulnerability to sport hunting. More specifically, we investigated whether habitat selection of caribou and hunters could increase caribou vulnerability to sport hunting, or whether harvest was opportunistic and depended mainly on landscape characteristics that favor harvest (e.g., accessibility and visibility). We expected that habitat selection patterns of caribou and hunters would differ greatly during the hunting season because caribou should reduce predation risk by avoiding human infrastructures, whereas hunters should be constrained by access to hunting grounds via roads and outfitter camps. As such, we hypothesized that caribou harvest should be opportunistic, and located in areas that favor visibility and detection rather than in areas where caribou-hunter co-occurrence is high. We also expected hunter accessibility to hunting areas to be highly constrained by roads. Although we hypothesized that caribou vulnerability should not be mainly explained by hunter habitat selection, there must be an encounter between caribou and hunters for a harvest event to happen. We predicted that caribou vulnerability should be higher near roads because of the access constraint of hunters.

**STUDY AREA**

The study area was located in the James Bay region of northern Québec, Canada, in winter hunting zone 22 (Fig. 1). The area was at the limit between the boreal forest and the taiga, and was dominated by conifer forests, transition shrub lands, and open areas with lichens (Latifovic and Pouliot 2005). Forest stands supported black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), with few white spruce (*P. glauca*) and tamarack (*Larix laricina*). The main predator of caribou in the area were grey wolves (*Canis lupus*). Black bears (*Ursus americanus*) were also present but usually hibernated when caribou moved through this area. Moose (*Alces alces*) also occurred in the area at low density (0.5 moose/10 km²; Lefort and Massé 2015). The climate was characterized by cool summers and cold winters, with an annual mean temperature of −2.1°C and a mean winter temperature (Nov–Feb) of −15.5°C (data available from 2005 to 2015, Environment Canada 2016). Mean annual snowfalls totalled 291 cm, with most falling between October and March. The area was mostly flat but included rolling hills where the elevation varied between sea level and 923 m.

The sport hunting of the RAF herd is limited by permits issued by the Québec government and permit numbers are dictated by population estimates. The RAF population peaked in 2001 at >500,000 individuals (Couturier et al. 2004) and decreased afterwards. Population size was estimated at 430,000 individuals in 2011 (Taillon et al. 2016). From 2011 to 2014, the herd was slightly declining. Although caribou of the RAF herd can be hunted in autumn and winter, our study focused exclusively on winter, because a larger proportion of the caribou harvest occurs during this period. The opening and closing dates of the winter sport hunting season varied over time: 15 November to 15 February from 1989 to 2010, 15 November to 15 January in 2011, and 1 December to 31 January from 2012 to 2015. The winter hunting zone was divided into 2 subzones, A and B, where hunting regulations differed (Fig. 1). Accommodations were rare across the study area, and most hunters used outfitter camps or the town of Radisson as starting points. There were only a few roads in the hunting zone, including 2 major roads and a few secondary roads totalling 2,179 km, mostly related to hydroelectric infrastructure. The area was mainly used by aboriginal and sport hunters, and hydro-electric workers.

**METHODS**

**Data**

We first assessed habitat selection patterns for caribou and hunters to evaluate their relative importance on caribou vulnerability to hunting. We used a long-term database of global positioning system (GPS) and Argos locations from caribou of the RAF herd. Between 1990 and 2015, we captured caribou by net-gunning from a helicopter
(Bookhout 1996) and fitted them with satellite collars as part of long-term monitoring. We programmed collars to record locations every 2 hr to 7 days. We removed caribou locations with large spatial errors (Argos LC score of 0 (>1.5 km); GPS positional dilution of precision score > 10 qualified as moderate quality). We also restricted our analyses to caribou that were susceptible to harvest by selecting individuals with ≥10 locations in hunting zone 22 during the winter hunting season. Individuals removed were mainly equipped with Argos collars, which did not allow us to collect the 10 necessary locations (frequency of 1 location every 4–7 days). Preliminary analyses indicated that 10 locations were the minimum required to parameterize the random effect of individuals. We also excluded individuals from the analyses that were not vulnerable to sport hunting because of their avoidance of the hunting zone during the hunting period. Our conclusions only apply to caribou available to hunters because they were within the hunting zone. In addition, most individuals that we removed from our analyses because of their avoidance of the hunting zone for a particular year did not avoid it for ≥1 year (81% of avoidance events), suggesting that this behavior was not recurring. We focused our analyses on the 1997–2015 period (n = 223 individuals) because of the low number of marked animals before 1997. We also verified whether caribou habitat selection behaviors observed during the hunting season were attributable to hunting risk by identifying changes in habitat selection triggered by the opening and closing of the hunting season (Supplemental Appendix A, available online in Supporting Information). All capture and handling procedures were approved by the animal care committee of Université Laval and the Ministère des Forêts, de la Faune et des Parcs.

To evaluate hunter habitat selection, we surveyed 87 hunters from 2 outfitter camps: Kiskimaastakin (54°15′57″N, 72°52′31″W) and Mirage (53°46′28″N, 72°52′31″W). Both camps were located in hunting zone 22B (Fig. 1). Hunters were allowed to hunt everywhere in hunting zone 22B, except in a 1-km radius around camps because of safety concerns. We equipped hunters with handheld GPS devices (Garmin eTrex 20, Olathe, KS, USA) during the 2013–2014 and 2014–2015 winter hunting seasons. We programmed GPS devices to record locations every 30 seconds. On any given day, we equipped only 1 hunter per group with a GPS device to avoid pseudo-replication. We also excluded all locations that were taken outside legal hunting hours or after the hunter had harvested his quota.

To evaluate the spatial distribution of harvested caribou, we used a large database of harvest reports from 1997 to 2014 (n = 169,835 harvest sites). In Québec, reporting of any large animal harvested is mandatory. Hunters were asked to

![Figure 1. Caribou winter sport hunting zone 22, James Bay region, northern Québec, Canada. Hunting zone 22 is subdivided into subzones A and B where hunting legislation differs. Outfitter camps that were open ≥1 year during 1997–2015 are represented by triangles.](image-url)
position their kill site on a gridded map with a resolution of 10 × 10 km. Precision of caribou harvest sites varied from a few meters to 5 km; most harvest sites were reported at the center of the 10 × 10-km cells. We used caribou harvest sites registered in hunting zones 22A and 22B. We also used all harvest sites although there was sometimes >1 caribou harvested at the same location.

**Resource Selection Functions**

We used resource selection functions (RSFs; Manly et al. 2002) to evaluate the spatial distribution of caribou harvest and the habitat selection of caribou and hunters according to landscape characteristics. We assessed habitat selection at the population level and at the landscape scale (i.e., second-order selection; Johnson 1980). We used circular buffers with a 5−km radius around harvest, caribou, and hunter locations to assess landscape variables. This enabled us to account for the precision of the less precise locations (i.e., harvest sites) and standardize the spatial scale of all analyses. Although the accuracy of caribou and hunter locations was adequate to evaluate habitat selection at a fine spatial scale, it would have been inappropriate to compare selection by caribou or hunters at a fine scale to the harvest distribution, evaluated at a coarser scale. We thus used the same spatial scale for analyzing caribou and hunter data and the distribution of caribou harvest sites. We used a 1:1 ratio of used and available locations (Manly et al. 2002). We drew available harvest sites randomly throughout hunting zone 22. For caribou, we drew available locations within the 100% minimum convex polygon (MCP) of all recorded locations (i.e., used) in hunting zone 22 from 1997 to 2015. For hunters, we drew available locations within the 100% MCP of all recorded locations for all hunters in subzone 22B, because subzone 22A was not available for surveyed hunters.

**Environmental characteristics.**—At each location (i.e., harvest, caribou, hunter), we characterized land cover, mean elevation, and altitudinal range. We used land cover maps with a 1 × 1−km resolution (Latifovic and Pouliot 2005). We used 3 land cover maps respectively updated in 1995, 2000, and 2005 to track changes in land cover during our study. The maps originally had 31 land cover classes that we grouped into 5 classes according to the openness of the canopy and the presence of lichens, the major food source for caribou during winter (Klein 1991, Joly et al. 2010; Table 1). We considered lakes available for caribou and hunters because they were frozen during the winter hunting season. We computed the proportion of each land cover type within the buffer surrounding each location. The proportions of each land cover type were compositional data because they always summed to 1 within a given buffer area. To remove the resulting correlation between proportions of the different land cover types, we used an additive log-ratio transformation of the form:

\[
\text{new % land cover type}_i = \log \left( \frac{\text{% land cover type}_{i}}{\text{% land cover type}_{ref}} \right)
\]

where land cover type ref was the land cover type used as reference cover in the RSF analysis (Aitchison 1994). Preliminary analysis suggested that conifer forests without lichens were used by caribou proportionally to their availability. We used this land cover type as the reference in all RSFs (i.e., harvest, caribou, hunter). We computed mean elevation (m) and altitudinal range (m) using a digital elevation model with a 100 × 100−m resolution. We defined altitudinal range as the range of elevation values (max.–min.) within the buffer. We centered and scaled mean elevation and altitudinal range values to minimize model convergence problems using the equations:

- **Centered variable** = \( x_i - \text{mean}(x_i) \)
- **Scaled variable** = \( \frac{\text{Centered } x_i}{\text{Standard deviation}(x_i)} \)

**Human infrastructures.**—We also characterized harvest, caribou, and hunter locations according to their proximity to human infrastructures (i.e., roads, outfitter camps, buildings, power lines). We obtained geographic information regarding human infrastructures from online databases (GeoGratis, Natural Resources Canada). Most roads in the study area were built during the development of hydroelectric infrastructure in the James Bay region during the 1970s and 1980s, and no major development occurred since then. We used the same network of roads and power lines throughout the studied period. We considered outfitter camps only during the period when they were in operation; they were otherwise classified as buildings. We calculated the distances to infrastructure (in km) as the Euclidian distances between each location and the nearest infrastructure of each type. To account for a possible decrease in the impact of infrastructure with increasing distance (Aue et al. 2012), we used a decay function of the form:

\[
\text{decay distance} = e^{-d/\alpha}
\]

where \( d \) is the distance from the nearest infrastructure and \( \alpha \) is the decay value (Carpenter et al. 2009). In a preliminary

<table>
<thead>
<tr>
<th>Land cover type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conifer forests with lichens</td>
<td>10–60% of the cover composed of needle leaf forest with an uncover of moss, lichens, and shrubs</td>
</tr>
<tr>
<td>Conifer forests without lichen (reference habitat)</td>
<td>25% to &gt;70% of the cover composed of needle leaf forest with an uncover dominated by mosses and shrubs</td>
</tr>
<tr>
<td>Open or disturbed areas without lichen</td>
<td>Old and new disturbances with most of the ground as barren (e.g., burnt areas)</td>
</tr>
<tr>
<td>Open areas with lichens</td>
<td>Lichens, shrubs, herbaceous, rocks, and barren ground</td>
</tr>
<tr>
<td>Lakes</td>
<td>Natural lakes and hydroelectric reservoirs</td>
</tr>
</tbody>
</table>

Table 1. Description of the land cover types used to evaluate the spatial distribution of caribou harvest sites and the habitat selection of caribou and hunters during the winter sport hunting season on the Rivière-aux-Feuilles herd in the James Bay region, northern Québec, Canada.
step, we tested the effect of decay values of 0.05, 0.1, 0.25, 0.5, 1, 2, 5, 10, and 15 km on the relative probability of harvest and relative probability of use by caribou and hunters using logistic regression. We limited the possible distance of impact of infrastructures to 15 km because all the studies we reviewed reported that the influence of infrastructures on caribou did not exceed this range (Wilson et al. 2016; Supplemental Appendix B, available online in Supporting Information). We chose the best decay value using model selection and used this value in subsequent analyses (Leblond et al. 2011; Supplemental Appendix C, available online in Supporting Information). Resulting decay distances ranged from 0 to 1, 1 being at the infrastructure and 0 being at a distance larger than the modeled decay value. We evaluated possible effects of land cover on road selection by caribou and hunters, or the distribution of harvest sites by testing the interaction between land cover type and decay distance to the nearest road. We did not include infrastructure density in our RSF models because infrastructures were rare in the James Bay region and variation in infrastructure density throughout our study area was too low to be tested. Additionally, power lines were virtually absent from the area used by surveyed hunters, so we removed distance to power lines from the hunter RSF.

Caribou and hunter occurrence.—In addition to landscape characteristics and proximity to human infrastructures, we characterized caribou locations with the relative occurrence probability of hunters. We also characterized harvest sites with the caribou and hunters’ relative occurrence probability, as well as their probability of co-occurrence. The probability of co-occurrence was estimated as:

$$\rho_{\text{co-occurrence}} = \frac{\rho_{\text{occurrence}}_{\text{caribou}} \times \rho_{\text{occurrence}}_{\text{hunters}}}{1 - \rho_{\text{occurrence}}_{\text{caribou}} - \rho_{\text{occurrence}}_{\text{hunters}}}$$

where we obtained the relative probabilities of occurrence for caribou and hunters from the best RSF models for each species and rescaled them between 0 and 1. We also rescaled the probability of co-occurrence between 0 and 1. We estimated the relative probability of occurrence of hunters across the study area using the best RSF model for hunters. We assumed that hunter behavior did not change spatially or temporally. Spatial distribution of outfitter camps and type of transportation used by hunters, mostly trucks and snowmobiles, were similar throughout the study period according to guides and outfitters. We used the hunter RSF model parametrized for 2013–2015 to assess the relative probability of occurrence of hunters within hunting zone 22 for 1997–2015. The predicted probability of occurrence of hunters could then fit the spatial and temporal extent of caribou and harvest data.

Statistical Analyses
We created RSFs of the form:

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

where $\beta_0$ is the population intercept, $\beta_k$ is the selection coefficient for the $k^{th}$ landscape characteristic and $\gamma_{0ij}$ is the random intercept for the $i^{th}$ year and the $j^{th}$ individual (Boyce et al. 2002). We used a generalized linear mixed model with the individual nested in year (caribou and hunters) or only the year (harvest) as random effects. This accounted for potential autocorrelation and unbalanced sample sizes among individuals and years (Gillies et al. 2006). We also used robust standard errors to account for the non-independence among locations from the same individual (Fieberg et al. 2010). We assessed multicollinearity between covariates using a variance inflator factor (VIF) test on the most parameterized RSF model for harvest, caribou, and hunters. Variance inflation factors were $<3$ for all RSFs, suggesting limited multicollinearity among variables within our models (Graham 2003). For all RSFs, we selected the most parsimonious models based on Akaiki’s Information Criterion ($\Delta AIC > 2$; Burnham and Anderson 2002). We tested the validity of the most parsimonious models using a 10-fold cross validation and Spearman’s rank correlation (mean $r_s$ reported; Boyce et al. 2002). We used 95% confidence intervals for selection coefficients to determine their statistical significance. We conducted spatial analyses of caribou and hunter locations and harvest sites with ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, CA, USA). We performed RSF analyses in SAS 9.3 (SAS Institute, Cary, NC, USA; GLIMMIX), and decay distance selection and model validation in R 3.0.3 (R Development Core Team; GLMER).

RESULTS
Models with the occurrence of hunters or caribou, or their co-occurrence, had no empirical support to explain the spatial distribution of caribou harvest. The relative probability of occurrence at harvest sites remained low for caribou ($\bar{x} = 0.23$) and hunters ($\bar{x} = 0.06$). Although these probabilities for caribou and hunters are not directly comparable because they are relative to different availabilities defined for each group, our results suggest that harvest occurred where caribou were more likely to occur than hunters. The top-ranked model explaining the spatial distribution of caribou harvest was the landscape characteristics model, and it had good predictive power ($r_s = 0.96$, range = 0.94–0.98; Table 2). Roads and camps had a strong positive effect on the probability of harvest (Table 3). Harvest probability was high near these infrastructures and decreased with increasing distance (decreasing decay distance; Fig. 2). A high proportion (83%) of harvest sites were located within 10 km of the nearest road, but caribou were 7 times more likely to be harvested a few meters from a road than at 10 km from it. In comparison, caribou harvest was 6 times more likely to occur at 1 km from an outfitter camp than at 10 km from it. Harvest sites were spread over a larger area around outfitter camps than they were relative to roads, with 82% of the harvests observed within 60 km of a camp. We did not detect any significant effect of buildings and power lines on the probability of harvest. Probability of harvest was higher on lakes than for any other land cover type, but closed forest with lichens also showed a relatively high probability of harvest. Harvest was less likely to occur in open or disturbed
areas without lichens. The probability of harvest increased with decreasing distance to the nearest road for closed forest with lichens but decreased for lakes near roads (Fig. 3A). Finally, harvest sites were more likely to occur in areas with low altitudinal range.

The best model explaining habitat selection by caribou (environment, topography, and human infrastructures model, $r = 0.77$, range = 0.53–0.96; Table 2) indicated that caribou strongly avoided roads during the hunting season (Table 3). Areas located near outfitter camps appeared to be selected by caribou, whereas other infrastructures had no effect on caribou selection. Caribou also selected conifer forest with lichens but avoided lakes. Selection for land cover types also varied with distance to the nearest road. Selection tended to decrease for open or disturbed areas without lichens and open areas with lichens with decreasing distance to roads. Selection for conifer forests with lichens and lakes tended to increase with decreasing distance to roads. The general tendency for all land cover types was a decrease in the probability of use by caribou with decreasing distance to the nearest road (Fig. 3B), because the effect size of roads was approximately 10 times larger than the effect sizes for the interactions with cover type (Table 3). Caribou avoided higher elevations, but altitudinal range did not affect habitat selection.

The best model explaining hunter habitat selection was the same than for caribou (environment, topography, and human infrastructures model, $r = 0.90$, range = 0.80–0.98; Table 2). Roads were strongly selected by hunters. Outfitter camps were also selected by hunters but to a lesser extent than roads, and other buildings were avoided (Table 3). All land cover types were used proportionally to their availability. The relative probability of use by hunters for closed forest with lichens and open or disturbed areas without lichens increased with decreasing distance to roads. The relative probability of use of open areas with lichens and lakes by hunters decreased with decreasing distance to roads. All land cover types showed a general decrease in relative probability of use by hunters as the distance to the nearest road increased (Fig. 3C), highlighting the large effect size of roads on the probability of use by hunters compared to land cover type. Finally, hunters avoided high elevations, but altitudinal range did not affect probability of use.

### Table 2. Competing models based on Akaike’s Information Criterion (AIC) used to assess the spatial distribution of probability ($p$) of caribou harvest (1997–2014) and use by caribou (1997–2015) and hunters (2013–2015) during the winter sport hunting season on the Rivière-aux-Feuilles herd, James Bay region, northern Québec, Canada.

<table>
<thead>
<tr>
<th>Response</th>
<th>Hypotheses and models</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>AIC weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial distribution of caribou harvest (1997–2014)</td>
<td>Habitat characteristics</td>
<td>230,548.3</td>
<td>0.0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>$p(harvest) = \text{distance to road} + \text{distance to outfitter camp} + \text{distance to building} + \text{distance to power line} + \text{vegetation cover types} + \text{mean elevation} + \text{topographic variation}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Caribou occurrence</td>
<td>293,403.7</td>
<td>62,855.4</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(harvest) = p(occurrence) \text{ caribou}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hunter occurrence</td>
<td>432,991.3</td>
<td>202,443.0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(harvest) = p(occurrence) \text{ hunters}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Caribou-hunters' co-occurrence</td>
<td>446,506.3</td>
<td>215,958.0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(harvest) = p(\text{co-occurrence}) \text{ caribou-hunters}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribou habitat selection during the hunting season (1997–2015)</td>
<td>Environment, topography, and human infrastructures</td>
<td>83,606.8</td>
<td>0.0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>$p(\text{use}) = \text{distance to road} + \text{distance to outfitter camp} + \text{distance to building} + \text{distance to power line} + \text{vegetation cover types} + \text{mean elevation} + \text{topographic variation}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Environment, topography and probability of use by hunters</td>
<td>83,929.0</td>
<td>322.2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(\text{use}) = \text{vegetation cover types} + \text{mean elevation} + \text{topographic variation} + p(\text{occurrence}) \text{ hunters}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Environment and topography</td>
<td>85,164.9</td>
<td>1,558.1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(\text{use}) = \text{vegetation cover types} + \text{mean elevation} + \text{topographic variation}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>All infrastructures</td>
<td>87,504.3</td>
<td>3,897.5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(\text{use}) = \text{distance to road} + \text{distance to outfitter camp} + \text{distance to building} + \text{distance to power line}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hunting infrastructures</td>
<td>87,572.7</td>
<td>3,965.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(\text{use}) = \text{distance to road} + \text{distance to outfitter camp}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Roads</td>
<td>87,574.6</td>
<td>3,967.8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(\text{use}) = \text{distance to road}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Probability of use by hunters</td>
<td>88,138.5</td>
<td>4,531.7</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$p(\text{use}) = p(\text{occurrence}) \text{ hunters}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hunters' habitat selection (2013–2015) (same as for caribou)</td>
<td>Environment, topography, and human infrastructures</td>
<td>117,516.4</td>
<td>0.0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>All infrastructures</td>
<td>137,419.8</td>
<td>19,903.4</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Roads</td>
<td>152,965.8</td>
<td>35,449.4</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Hunting infrastructures</td>
<td>165,167.3</td>
<td>47,650.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Environment and topography</td>
<td>271,983.4</td>
<td>0.0</td>
<td>1</td>
</tr>
</tbody>
</table>
The increasing threat of human disturbances in northern ecosystems and potentially cumulative effects on wildlife, it is important to understand how different disturbances may influence habitat selection and survival. Only a few studies have tried to identify the factors associated with increased vulnerability to hunting (Lebel et al. 2012, Roever et al. 2013, Norum et al. 2015). We addressed these issues by studying caribou vulnerability to sport hunting over a 17-year period, taking into account caribou and hunter behaviors and landscape characteristics.

**Caribou Vulnerability to Sport Hunting**

Caribou mortalities resulting from sport hunting were mainly associated with landscape characteristics and not related to the habitat selection patterns of hunters and caribou. This is contrary to previous studies where vulnerability of game species depended on the behavior of hunters or game (Broseth and Pedersen 2000, Nielsen et al. 2004, Lone et al. 2015). Although harvest sites were found in areas where caribou were more likely to occur than hunters, their relative probability of occurrence was low in these areas. Caribou were more vulnerable in areas accessible to hunters (i.e., near roads) or in areas offering good visibility to detect and aim at caribou (i.e., lakes and smoother terrain). These areas were, for most cases, avoided or not selected by caribou or hunters. This discrepancy between caribou harvest and habitat selection by caribou and hunters suggests that harvest may be an opportunistic event facilitated by landscape attributes, such as visibility and accessibility. Discrepancy between habitats used and harvest sites was also reported for elephant (*Loxodonta africana*; Roever et al. 2013) and woodland caribou (James and Stuart-Smith 2000), where mortality occurred in areas with low probability of use by elephants or caribou. In our study, outfitter camps were the exception, where high probability of caribou-hunter co-occurrence also corresponded to high caribou vulnerability.

Hunt occurrence was not a good predictor of caribou vulnerability even though vulnerability was mainly influenced by the proximity to hunting infrastructures (e.g., roads, camps). Access to hunting areas via roads and camps influences habitat selection by hunters and harvest distribution (Foster et al. 1997, Broseth and Pedersen 2000, Diefenbach et al. 2005, Lebel et al. 2012). Other studies reported that most hunters concentrate search effort within 500 m of roads or within a few kilometers of a camp (Broseth and Pedersen 2000, Diefenbach et al. 2005, Lebel et al. 2012). High hunting pressure near camps can lead to higher probability of harvest (Broseth and Pedersen 2000). We found that proximity to hunting infrastructures influenced caribou vulnerability. High concentration of hunters made proximity to roads and camps risky for caribou. Caribou, however, strongly avoided roads during the hunting season,

![Image](https://example.com/image.png)

**Figure 2.** Probability of harvest for caribou of the Rivière-aux-Feuilles herd in relation to the distance to the nearest road or outfitter camp during the winter sport hunting seasons of 1997–2015, James Bay region, northern Québec, Canada.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Harvest sites</th>
<th>Caribou</th>
<th>Hunters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to road (decay)</td>
<td>β</td>
<td>Lower CI</td>
<td>Upper CI</td>
</tr>
<tr>
<td>Distance to outfitter (decay)</td>
<td>4.38</td>
<td>3.70</td>
<td>4.79</td>
</tr>
<tr>
<td>Distance to building (decay)</td>
<td>0.86</td>
<td>-0.06</td>
<td>1.78</td>
</tr>
<tr>
<td>Distance to power line (decay)</td>
<td>-0.56</td>
<td>-1.22</td>
<td>0.11</td>
</tr>
<tr>
<td>Conifer forests with lichens (%)</td>
<td>0.12</td>
<td>0.03</td>
<td>0.21</td>
</tr>
<tr>
<td>Open or disturbed areas without lichen (%)</td>
<td>-0.10</td>
<td>-0.21</td>
<td>-0.01</td>
</tr>
<tr>
<td>Open areas with lichen (%)</td>
<td>-0.03</td>
<td>-0.14</td>
<td>0.09</td>
</tr>
<tr>
<td>Lakes (%)</td>
<td>0.22</td>
<td>0.17</td>
<td>0.27</td>
</tr>
<tr>
<td>Mean elevation (m)</td>
<td>0.17</td>
<td>-0.01</td>
<td>0.35</td>
</tr>
<tr>
<td>Altitudinal range (m)</td>
<td>-0.25</td>
<td>-0.34</td>
<td>-0.15</td>
</tr>
<tr>
<td>Conifer forests with lichens × distance to road</td>
<td>-0.01</td>
<td>-0.15</td>
<td>0.14</td>
</tr>
<tr>
<td>Open areas with lichen × distance to road</td>
<td>-0.07</td>
<td>-0.15</td>
<td>0.14</td>
</tr>
<tr>
<td>Lakes × distance to road</td>
<td>-0.42</td>
<td>-0.54</td>
<td>0.30</td>
</tr>
</tbody>
</table>
suggesting that they adopted a tactic to minimize harvest risk. Animals avoid roads because they perceive a risk of predation associated with them (Fahrig and Rytwinski 2009) and road avoidance may depends on disturbance intensity; roads with high levels of human activity are more avoided by wildlife than those with low levels (Polfus et al. 2011, Leblond et al. 2013, Lesmerises et al. 2013). This is particularly true when roads are associated with greater predation risk resulting from intensive use by hunters (Kilgo et al. 1998, Benhaiem et al. 2008, Bonnot et al. 2013). Surprisingly, we found that the increase in human predation risk at the onset of the hunting season did not lead caribou to increase their avoidance of roads (Supplemental Appendix A). This suggests that the risk-avoidance tactic adopted by caribou of the RAF herd may be triggered by human activity in general, not only sport hunters.

Contrary to expectations, caribou appeared to select for proximity to camps. In reality, caribou did not actively select for proximity to camps, but camp locations were selected based on their proximity to caribou traditional grounds. Outfitter camps are not randomly located on the landscape and their development is linked to past local caribou abundance during winter. Many outfitter camps are located near the end of the traditional migration route of the RAF herd, where the probability of use by caribou is high (M. Le Corre, Université Laval, unpublished data). As reported for reindeer in Norway (Dahle et al. 2008), caribou may be more tolerant to human infrastructures (e.g., camps) when they use traditional areas. Stationary disturbances may also represent a more predictable risk than moving vehicles on roads, the later being more disturbing for wildlife (Neumann et al. 2013).

We found no relationship between proximity to power lines and buildings and caribou vulnerability to hunting. We were unable to verify whether power lines were selected by hunters, as reported by Nellman et al. (2001), because of their low availability for surveyed hunters. Using firearms under power lines in other areas of our study site was strictly prohibited, which may have contributed to lower caribou vulnerability near power lines. Other buildings in the hunting zone are mostly hydroelectric infrastructures or are associated with the town of Radisson, in the vicinity of which hunting is prohibited for safety reasons. Accordingly, hunters strongly avoided buildings whereas caribou did not, as if they could perceive a lower risk associated with the proximity to these infrastructures.

Vulnerability of game species is known to be higher in open or fragmented areas, where visibility and detectability by hunters are good (Swenson 1982, Foster et al. 1997, Lebel et al. 2012, Norum et al. 2015). Caribou were more vulnerable on lakes than in any other land cover types, even though lakes were avoided by caribou and not selected by hunters. Surprisingly, harvest was less likely in other open cover types than on lakes and these areas were not avoided by caribou. This contradicts results reported for other game species, where animals avoided open areas during hunting seasons (Kilgo et al. 1998, Tolon et al. 2009, Lone et al. 2015). The large buffer areas we used around used caribou locations allowed us to identify landscape characteristics influencing caribou habitat selection at the regional scale, but other variables could be in play at finer scales. For example, we may have underestimated avoidance of small open areas (e.g., peatlands).

We also expected caribou vulnerability would be higher in open areas in proximity to roads because visibility and accessibility can increase harvest (Lebel et al. 2012). Avoidance of open areas by hunted ungulates, however, can be exacerbated in proximity to roads (Bonnot et al. 2013). Surprisingly, we found caribou were more vulnerable in areas with high lateral cover (i.e., closed forest with lichens) near roads than far from them. Caribou avoided lakes near roads less frequently than lakes farther from roads, possibly selecting for escape habitat near risky areas such as roads (Ferguson and Elkie 2005). Perhaps this behavior would increase harvest because both lakes and roads were identified as risky habitat for caribou. The use of lakes near roads by caribou, however, did not increase

![Figure 3. Resource selection functions (RSFs) showing the relative probability of harvest (A) and relative probability of use by caribou (B) and hunters (C) of land cover types as a function of the distance to the nearest road during the caribou winter sport hunting seasons of 1997–2015 on the Rivière-aux-Feuilles herd, James Bay region, northern Québec, Canada. Only land cover types for which the interactions with distance to road were significant are shown.](image-url)
their vulnerability when compared to lakes farther from roads, suggesting that this did not translate into higher risk of mortality. It also suggests that the openness of habitat near roads may not influence caribou vulnerability as initially expected. Proximity to roads had a much larger effect on caribou vulnerability than land cover type, leading to relatively low variability in harvest probability for different land cover types near roads (Proffitt et al. 2013).

High elevations and flat terrain can favor detectability of game species (Swenson 1982, Little et al. 2014). Our findings suggested that caribou were more vulnerable in less rugged areas. This effect did not appear to be linked to caribou and hunter habitat selection. Even if hunters do not actively search for topographic characteristics that facilitate detectability and harvest, it appears they take advantage of it when they opportunistically encounter caribou in these conditions.

Caribou of the RAF herd avoided risky areas such as roads and lakes. Although this behavior is well adapted for avoiding human predators, it may not be efficient for avoiding natural predators. Hunting may alter prey ability to respond to natural predation risk, especially when the landscapes of fear created by human and natural predators differ (Proffitt et al. 2009, Norum et al. 2015). Whereas caribou may use lakes in winter to reduce predation by wolves (Ferguson and Elkie 2005), this may increase their vulnerability to hunting. By contrasting the landscapes of fear and vulnerability created by human hunters and natural predators, it may be possible to determine whether safe habitat selection during hunting seasons could lead to suboptimal habitat selection in regard to natural predation. Our multi-species approach, that is applicable to multi-prey, multi-predator systems, could be used for this purpose.

We used only 2 years of survey data to evaluate habitat selection of hunters. Our sample of hunters for these years may not have represented the range of hunting tactics and behaviors of hunters. Our discussions with outfitters, however, did not suggest this was likely. We are relatively confident that the 87 hunters we surveyed at 2 different outfitter camps over 2 years were sufficient to obtain a representative sample of hunting techniques and to describe the general pattern of habitat selection by hunters.

**MANAGEMENT IMPLICATIONS**

Access to hunting areas, via roads and outfitter camps, and visibility were the main factors influencing caribou vulnerability to sport hunting. Managers could use this information to manipulate hunting success according to population estimates and harvest quota by establishing minimal distance to roads and camps within which hunting would be prohibited. Similarly, prohibiting hunting on certain lakes could efficiently reduce hunting success. Roads increased human access into these remote areas and facilitated harvest of the RAF herd. Further development in northern ecosystems could expand the area available to hunters and further increase vulnerability of Arctic species to hunting. We recommend future studies on cumulative impacts to consider roads as a human disturbance that may cause avoidance and as a potential source of mortality due to the increase in accessibility for hunters (James and Stuart-Smith 2000, Tromblak and Frissell 2000).

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**LITERATURE CITED**


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