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Stairway to heaven or highway to hell? How characteristics of forest roads shape their use by large mammals in the boreal forest

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ABSTRACT

Decades of expansion of industrial resource extraction in boreal forests have resulted in the legacy of thousands of kilometers of linear features (seismic lines, forest roads) that have fragmented several wildlife habitats. The decommissioning of anthropogenic linear features and the restoration of suitable habitat are top priorities for the recovery of several species at risk, among which, the threatened populations of boreal caribou (*Rangifer tarandus caribou*). However, the decommissioning of linear features found in caribou range is expensive, and determining which characteristics make them more beneficial to caribou predators and competitors could assist in prioritizing those that may be most critical for boreal caribou habitat restoration. We thus aimed to determine how fine-scale forest road characteristics influence their use by gray wolf (*Canis lupus*), black bear (*Ursus americanus*), moose (*Alces americanus*) and caribou. We used camera traps and generalized linear mixed models to test the effect of road-scale characteristics on the use of forest roads by wolves, bears and moose while also considering larger-scale covariates. Wolves had a greater probability of using roads that were surrounded by wetlands and had a low lateral cover density. For bears, the intensity of use was lower on 20+ year-old roads when compared to 0–10-year-old roads, and higher on roads surrounded by coniferous stands. Moose intensity of use was higher on 11–20-year-old roads and lower on 30+ year-old roads, and decreased on roads surrounded by clearcuts and with a lower number of deciduous stems growing on them. We could not test for caribou use as we did not capture enough events. Nevertheless, by showing which forest roads are more used by caribou predators (wolves and bears) and its apparent competitor (moose), our study highlights the importance of considering both road-scale characteristics and the landscape context in which roads are built to prioritize the most detrimental roads to caribou conservation and guide efficient restoration efforts of its habitat.

1. Introduction

Biodiversity loss represents one of the greatest challenges of the Anthropocene era, and current extinction rates are now approaching those of past mass extinction events (Barnosky et al., 2011). Recent conservation efforts are still deemed insufficient to reverse the effects of the main drivers of biodiversity loss, namely anthropogenic habitat loss, overexploitation and invasive species, but also geological and climate change (Purvis et al., 2000). Ecosystems are increasingly impacted by anthropogenic disturbances, and some are even being pushed outside their natural range of variability (Cyr et al., 2009; Seidl et al., 2016). Therefore, the restoration of disturbed landscapes is essential to re-establish key functional or ecological conditions.

The boreal populations of woodland caribou (*Rangifer tarandus caribou*; hereafter caribou) are currently listed as Threatened under the Species at Risk Act in Canada, and most populations are currently declining (Environment Canada, 2011). During the past decades, several studies have shown that this decline is mainly driven by the expansion of anthropogenic disturbances encroaching on caribou habitat (e.g. Environment Canada, 2011; Festa-Bianchet et al., 2011). Among all anthropogenic disturbances, timber harvesting converts late-seral forest stands, known to be favorable to caribou, into early-seral stands preferred by alternative prey such as moose (*Alces americanus*) and white-tailed deer (*Odocoileus virginianus*) (Dawe et al., 2014; Mumma

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et al., 2021). The increased access to abundant, palatable, energy- and protein-rich foraging resources triggers an increase of alternative prey densities that, in turn, support larger gray wolf (*Canis lupus*; hereafter wolf) densities that can jeopardize caribou persistence via higher predation pressure through a complex trophic relationship called apparent competition (*sensu* Holt, 1977; see also DeCesare et al., 2010). Regenerating vegetation found in recent cutblocks is also profitable to black bears (*Ursus americanus*), as it provides plenty of high-quality food items that are otherwise scarce in the boreal forest (Mosnier et al., 2008). Although black bears feed mostly on plants (Raine and Kansas, 1990; Lesmerises et al., 2015), they are efficient opportunistic predators of ungulate calves (Murrow et al., 2009; Popp et al., 2018). Throughout Canada, black bears were identified as an important mortality agent for caribou calves (Pinard et al., 2012; Mumma et al., 2019a). Anthropogenic linear features such as seismic lines—narrow corridors built for energy exploration—and forest roads were shown to be selected by predators (Tigner et al., 2014; Dickie et al., 2017a), increasing their movement rate and travel speed (Dickie et al., 2017b), which results in higher encounter rates with prey, and, consequently, greater predation on caribou (Whittington et al., 2011; Leblond et al., 2013; Mumma et al., 2017). The combination of all these behavioral responses to a changing landscape following anthropogenic disturbances is currently the main hypothesis used to explain the decline of boreal caribou populations in Canada (Hervieux et al., 2013; Johnson et al., 2020).

The protection of remaining intact landscapes and the restoration of altered caribou habitat are top priorities for caribou conservation (Hervieux et al., 2013; Ray, 2014). Although disturbances are not solely restricted to linear features throughout the species' distribution range, the decommissioning of these structures in particular represents one of the key measures to implement. Compared to wildfires and cutblocks (Bartels et al., 2016), seismic lines (Brandt et al., 2013) and forest roads (Pasher et al., 2013) in Canada have relatively uneven and unsuccessful natural closure and vegetation regrowth (Lee and Boutin 2006; St-Pierre et al. 2021). Reclaiming these linear features and restoring a vegetation cover may speed up the return to a pre-disturbance forest state representative of suitable caribou habitat and unfavorable to predator movement (Johnson et al., 2019). Linear feature decommissioning can be either slow and passive, where the regeneration of vegetation on forest roads (St-Pierre et al., 2021) or seismic lines (Van Rensen et al., 2015; Finnegan et al., 2018a) is initiated by natural recolonization from adjacent shrubs and trees, or it can be active, which can involve road closure, soil decompaction and tree planting (Tattersall et al., 2020a; Lacerte et al. 2021). However, as active decommissioning of linear features can be costly (Schneider et al., 2010; Hebblewhite, 2017; Johnson et al., 2019), and because some linear features are leading to important infrastructures (e.g. touristic or recreational facilities), it can be considered as virtually impossible to reclaim all anthropogenic linear features in caribou range. Consequently, determining which characteristics of linear features make them more or less attractive to predators and alternative prey is essential to establish an order of priority and could guide managers tasked with caribou habitat restoration in choosing where to spend the limited financial resources first.

A growing number of studies described several aspects of the use of anthropogenic linear features by wolves, such as wolf-caribou encounters (Whittington et al., 2011; Mumma et al., 2017), linear feature selection by wolves (Dickie et al., 2017a; DeMars et al., 2018), and characteristics impeding wolves travel speed (Dickie et al., 2017b; Finnegan et al., 2018b). However, relatively few studies have described the use of linear features by black bears (but see Tigner et al., 2014; DeMars et al., 2018) and moose (but see Mumma et al., 2018; Dickie et al., 2020), and the studies that did, often focus on seismic lines in western Canada. A small number of studies focused on the use of forest roads (e.g.; Leblond et al., 2013; Muhly et al., 2019; Mumma et al., 2019b) with a rather limited classification of roads (e.g. unpaved/paved roads) using telemetry data and tools such as resource selection functions and step selection functions at a relatively large scale. While these results are useful for caribou conservation, they mostly provide information on animal's behavioral choices (i.e. how animals react to linear features) rather than information centered on individual linear features (i.e. why a specific linear feature is used more than another), which is important from the perspective of linear feature management (Keim et al., 2019). Camera-traps are tools increasingly used for a wide range of objectives such as determining the density of a species or evaluating the use of ecological resources by animals (Burton et al., 2015; Sollmann, 2018). A growing number of studies successfully use camera-traps to study boreal mammals and communities as well as the impact of anthropogenic disturbances on their distributions (e.g. Fisher and Burton, 2018; Wittische et al., 2021). More specifically, camera-traps are now progressively being used to study the impact of anthropogenic linear disturbances on large mammals (e.g. Keim et al., 2019; Tattersall et al., 2020a,b; Beirne et al., 2021) and offer an opportunity to study how fine-scale characteristics of linear features, and forest roads in particular, influence their use by large mammals.

Studying more precisely how fine-scale characteristics of roads influence their use by large mammals is needed as not all forest roads are the same: they can be located in different environments (e.g. successional forest stages) or have different intrinsic characteristics (e.g. varying compaction, St-Pierre et al., 2021) that can prevent vegetation regrowth and their resulting use by caribou predators and competitors. For example, forest roads with sparser regrowth could be more attractive to wolves as they facilitate movement (Dickie et al., 2017a), while roads with a well-established deciduous regrowth could provide food items for black bears and moose (Finnegan et al., 2018a, 2019) and consequently be used more by these species. Co-use by interacting species could also play a role in one's use of a road: linear features can be perceived as a predation risk by prey (Leclerc et al., 2014; Dickie et al., 2020), so roads increasingly used by predators could be less used by caribou and moose. As such, distinguishing how the intensity of use of forest roads varies in relation to varying fine-scale characteristics could help further identify which roads should be restored first, and therefore appears to be of paramount importance for caribou conservation.

In this study we aim at documenting the effect of different forest road fine-scale (i.e. road level) characteristics on the intensity of use by wolves, black bears, moose and caribou. We also test the effect of large-scale variables known to influence responses of large mammals to roads. We hypothesize that roads providing characteristics known to facilitate movements will be selected by wolves. Accordingly, we predict that the intensity of use of a road by wolves will be more important when the percentage of lateral cover is lower. Because black bears and moose are known to select for abundant forage, we hypothesize that they would both be attracted to forest roads offering easy access to food items. We predict that the intensity of use by these species will be greater on younger roads with a greater herbaceous cover for black bears, and more deciduous stems for moose. However, since moose could perceive roads used by wolves, its main predator, as risky, it could consequently balance forage accessibility with predation risk. If so, we predict that moose intensity of use will be negatively related to wolf use. Finally, as caribou are known to avoid linear features (Leclerc et al. 2012), where the probability of encountering a predator is higher (Whittington et al. 2011), and usually stay away from alternative prey (Peters et al., 2013), we expect that caribou intensity of use will be lower on roads frequented by other species.

2. Materials and methods

2.1. Study area

Our study area was divided into 3 different regions on the north shore of the St. Lawrence River in Québec, Canada (Fig. 1). The southernmost region encompasses the Laurentides Wildlife Reserve and the northern part of the Jacques-Cartier National Park (47.3–47.7°N, 71.0–71.5°W, 2,120 km^2; hereafter LWR) and is located in the range of

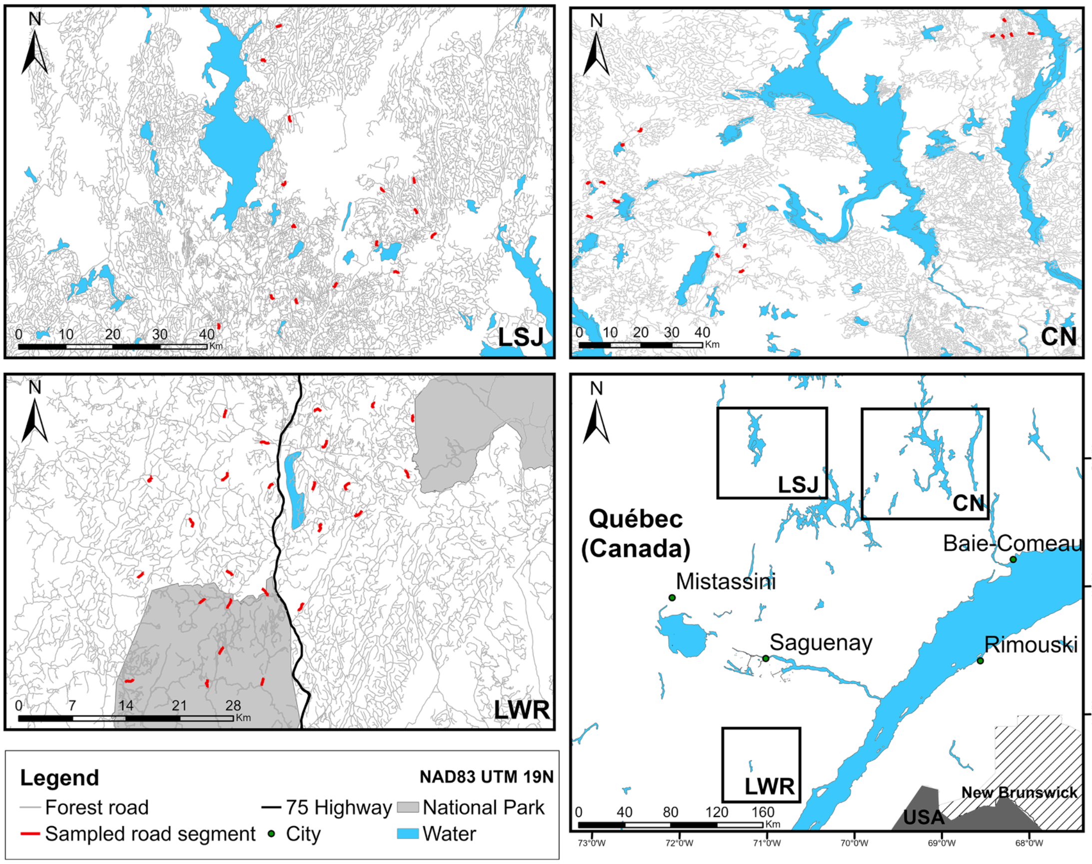

Fig. 1. Distribution of sampled forest road segments across three regions (LWR: Laurentides Wildlife Reserve, LSJ: Saguenay – Lac-St-Jean, CN: Côte-Nord) in boreal caribou range in Québec, Canada.

the Charlevoix caribou population. The second region is located in northern Saguenay-Lac-St-Jean, in the Portneuf and Piraube caribou population ranges (49.7–50.3°N, 70.6–71.2°W, 3,900 km^2; LSJ). Finally, the third region covers the northwestern part of the Côte-Nord and is part of the Manicouagan caribou population range (49.6–50.5°N, 68.6–69.9°W, 9,009 km^2; CN). These three regions encompass two boreal bioclimatic domains. The LWR region is comprised in the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain, the LSJ region is located at the limit of the balsam fir-white birch and black spruce (*Picea mariana*) – moss *Bryophyta* domain and the CN region is located in the black spruce – moss domain (Robitaille and Saucier, 1998). Mature stands in the LWR are mostly composed of coniferous trees such as balsam fir, black spruce, and white spruce (*Picea glauca*) found in pure stands or with boreal deciduous species, mainly white birch and trembling aspen (*Populus tremuloides*). LSJ is mostly dominated by black spruce combined with a mix of the above-mentioned species, with a feathermoss understory cover typical of the black spruce–moss domain (Robitaille and Saucier, 1998). Pure black spruce stands dominate the landscape in the CN region with an understory mainly composed of mosses and ericaceous shrubs. At time of data collection (2018–2020), all three regions were used for intensive commercial logging and comprised recent and regenerating clearcuts. While the mean elevation is high in the LWR region (853 m), both the LSJ and CN regions have a relatively low mean elevations (respectively 535 m and 495 m). LSJ and CN are located >100 km north of the nearest towns and are essentially uninhabited, and human presence in mainly due to resource extraction activities, whereas the LWR region is crossed by the 75 Highway and used for both commercial logging and recreational activities (hiking, fishing, camping). According to the Environment Canada (2011), total disturbance levels reach 80% in LSJ, 82% in the LWR and 32% in CN. In 2018, the overall road density reached 1.6 km/km^2, 1.4 km/km^2 and 1.0 km/km^2 in LSJ, LWR and CN, respectively.

The large mammal community is similar across the three regions: caribou and moose are the main large prey species while gray wolves and black bears are the main predators. Data on wolf, black bear and moose densities are scarce. No estimate of wolf density exists in Québec, while black bear density estimates vary and are estimated to be 0.24 bear/10 km^2 in LWR, 0.33–0.93 bear/10 km^2 in CN and 0.41–1.32 bear/10 km^2 in LSJ (Ministère des Forêts, de la Faune et des Parcs du Québec, hereafter MFFP, *unpublished data*). Moose density was estimated to be 0.21 moose/km^2 in the southern part of the LWR region (in the Jacques-Cartier provincial park) but are thought to be currently lower (MFFP, *unpublished data*). Moose density estimates based on hunting statistics vary between 0.10 and 0.20 moose/km^2 in LSJ and 0.05 to 0.24 moose/km^2 in CN (Ayotte and Chenel, 2019). The Charlevoix caribou population is a small population undergoing continuous declines with an estimate of 31 individuals in 2019 and approximately 23 individuals in 2020, which represents a density of 0.6 caribou/100 km^2 (Hins and Rochette, 2019, 2020). Caribou densities are 0.6 caribou/100 km^2 in the LSJ region (Plourde et al., 2020) and are estimated to range between 1.2 and 2.1 caribou/100 km^2 in the CN region (Heppell, 2020).

2.2. Sampling design and data collection

We selected 56 1-km forest (unpaved) road segments (excluding winter roads) following a three-step selection process and using 1:20,000 Routard numerical maps published by the MFFP. All forest roads were first sorted by their time since construction (hereafter age) into five categories: 0–10, 11–20, 21–30, 31–40 and 40+ years old (0 year old representing roads built the same year the selection process

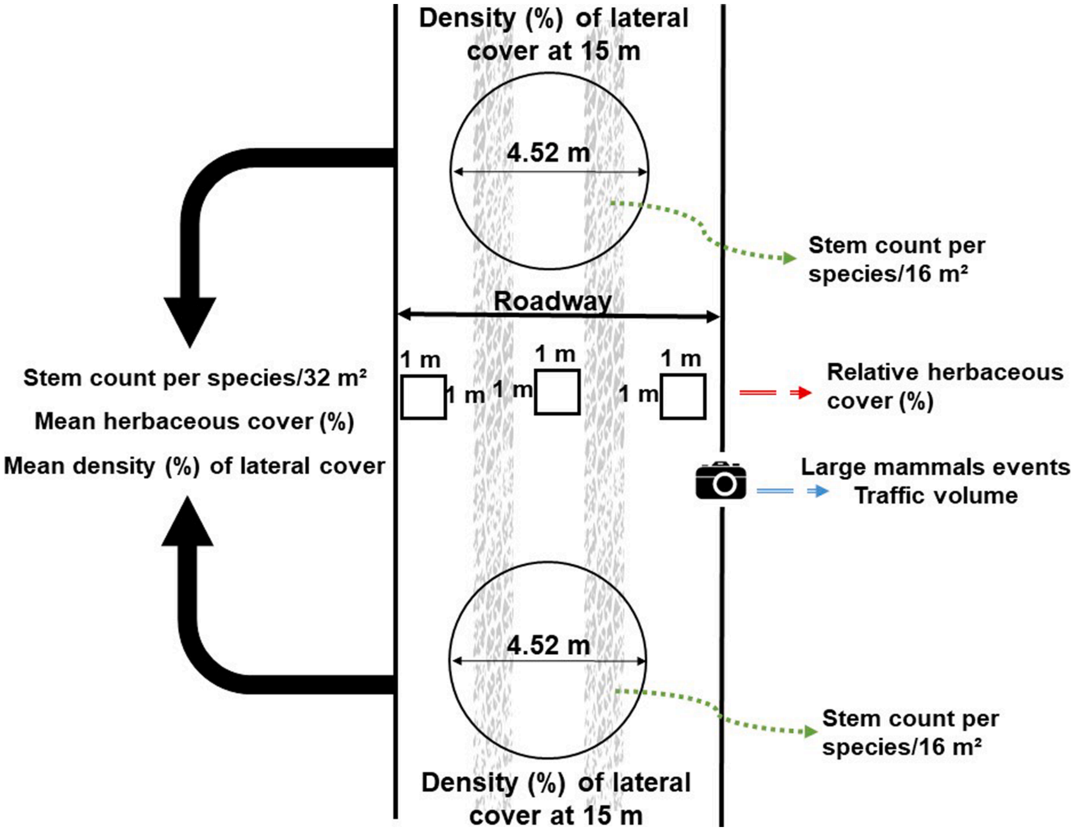

Fig. 2. Visual representation of each measurement taken at a camera station (4 per road segment) on forest roads in boreal caribou range in Québec, Canada.

took place, i.e. 2018). A subset of roads was then selected based on their accessibility (i.e. relative proximity to passable road networks). Although we did not conduct road decommissioning and habitat restoration in our project, we selected roads that could potentially be reclaimed for caribou habitat restoration, i.e. roads that were no longer used for timber harvesting or to access recreational, touristic, or industrial facilities. We believe this decision increased the representativeness of our road segments when compared to roads targeted for habitat restoration, as well as the inference of our results. These last two criteria were assessed by photointerpretation or following an aerial survey conducted by the MFFP. We ended with 7 road segments that could be accessed by vehicle, 25 by ATV (max distance traveled = 10 km) and 24 on foot (max distance traveled = 1 km). The mean distance between two road segments was 5.46 ± 2.36 (SD) km with a minimum distance of 1.56 km (see Appendix A, Table A1, for a complete distribution of road segments per age per region).

On each 1-km road segment, we established 4 stations separated by 250 m. In each station, we installed a motion-activated camera (Moultrie model A-30i; 220 in total) facing the roadway diagonally (to maximise the distance traveled by an animal in front of a camera) and ensured that any movement occurring from one side of the road to the other could activate the sensor. We also installed two motion-activated cameras (110 in total) at random locations 300 m away from each road segment (hereafter adjacent forest camera); their data were later used to estimate local densities (see section 2.3.1). Although adjacent forest cameras were 300 m away from a sampled road segment, they were not necessarily located 300 m away from other (unsampled) roads because of the high road density, which could reach up to 4.6 km/km^2, making equidistant placement of forest cameras too constraining. We fixed each camera at a height at which all target species would be detected (~1–1.4 m). Each camera (roadside and adjacent forest) was set at a 3-photo burst per detection mode with a 15 sec interval between detections. At each adjacent forest camera, we measured the detection zone to later derive the detection angle necessary to estimate densities (Appendix B). Cameras were active from early June to mid-September during three consecutive summers (2018, 2019 and 2020).

In 2019, we measured different covariates at each camera station to include them in our statistical analyses as independent variables. At each roadside camera station, we counted the number of stems with a measurable diameter at breast height (>0 cm at 1.3-m height above ground level; hereafter DBH) per species in two 16-m^2 circular plots and summed them to get a number of stems per 32 m^2 (see details in St-Pierre et al., 2021). We also determined the relative percentage of cover of herbaceous vegetation in three 1-m^2 quadrats (one on each side and one in the middle of the roadway; Fig. 2) and calculated the mean coverage for the entire camera station. Finally, we estimated the density (percentage) of lateral cover at a 15-m distance from the center in both directions parallel to the road using a 30 cm × 2 m vegetation profile board (*sensu* Nudds, 1977 as used by St-Laurent et al., 2008) and calculated the mean density of lateral cover for the camera station. The density of lateral cover corresponds to the percentage of the profile board that cannot be seen due to vegetation by an observer located at 15 m (e.g. a 90% density of lateral cover means that 90% of the profile board was hidden behind vegetation). Larger-scale covariates were later calculated using the coordinate of each camera station and a geographical information system (see Section 2.3.2).

2.3. Data preparation

2.3.1. Camera trapping data

We used the Timelapse2 software (Greenberg, 2016) to classify each photo taken by the cameras. An event was noted whenever a caribou, moose, wolf or black bear activated a camera. If multiple individuals of the same species triggered a camera at the same time, we considered that the number of events equaled the number of individuals observed (following Keim et al., 2019). For example, if two moose individuals were caught in the same picture, the number of events was considered to be two. To avoid the potential bias of counting the same individual twice in two photos, we considered any animal photographed in a 30-min time-lapse to be the same (Rovero and Zimmermann, 2016; as used by Tattersall et al., 2020a, 2020b). This gave us the number of events per species for each camera placed along a road segment. We also noted the number of photos of ATVs and vehicles and summed their count to get a proxy of traffic volume for each camera station. We noted the number of days during which each camera was active to account for the difference in sampling effort between cameras.

Lele et al. (2013) pointed out the confusion in the use of different terms and concepts (e.g. occupancy, use, selection, choice) in habitat and resource selection studies and the need to define clearly what is being measured, and in which specific unit and during which specific time period. A large number of studies already showed the selection/avoidance of roads by large mammals at a broader scale using telemetry data (i.e. Leblond et al., 2013; Muhly et al., 2019; Mumma et al., 2019b) while focusing on behavioural responses described at the individual level. However, land managers have to adjust decommissioning practices at the road-segment level, which shows the importance of identifying the local and regional factors explaining variation in the use of roads (at the road-segment level) by mammals. Moreover, identifying determinants of variation in the use of a given landscape attribute by wildlife can take different forms. Here, we defined the “intensity of use” as the number of events per species (i.e. frequency of use) of a camera station on a road (specific unit) during a data collection season (time period). From a management perspective, the number of times a particular road segment is used by a species (i.e. intensity of use) during a certain period of time could be more informative than the simple probability that it is used at least once (i.e. probability of selection, probability of use) during the same period of time (Keim et al., 2011, 2019; Lele et al., 2013). Despite the potential limitations related to this approach (e.g. false absence, when the animal is found in the sampling unit but not detected) that are partially accounted for by using occupancy modeling (MacKenzie et al., 2002; Sollmann, 2018; but see Kays et al., 2021), we deemed it to be sufficiently robust to meet our objective. Consequently, we used the intensity of use per species as the response variable in our generalized linear mixed modeling (GLMM) framework (Sollmann, 2018; as done by Tattersall et al., 2020a).

Some authors have suggested that false absence can occur when the sampled area is quite small in comparison to the entire study area (Rovero and Zimmermann, 2016; Sollmann, 2018). In our case, we considered that the potential bias in detection rate (i.e. % of false absences) was low considering that we deployed 4 automated cameras (separated by 250 m) on each of the 56 road segments (i.e. our independent sampling unit) and ensured that each camera could detect any large mammal moving on the 6–8 m wide roads by manually removing vegetation in the camera detection zone and passing in front of the camera at different speeds and distance to trigger the sensor. Consequently, we were confident that if an animal was not detected on a road, it was obviously not using it. A companion study (Gagnon-Labrosse, Lesmerises, Pettigrew and St-Laurent, *unpublished data*) also tested the detection rate of multiple camera-trap models (including the one used in this study) at different camera heights, animal speeds and distances from the camera using domestic species of different sizes. Preliminary results suggested that the camera model we used did not miss any animal passages at an 8-m distance and only missed 3.3% of events at a distance of 15 m (which is at least twice as wide as our forest roads). Moreover, several recently published studies successfully described animal activity using the raw or transformed number of events as a proxy (Heim et al., 2017; Keim et al., 2019; Tattersall et al., 2020a, 2020b). Finally, we used the number of events detected by each adjacent forest camera and the mean number of individuals per event to derive an approximate regional density of each species per region per year. We used the Random Encounter Model (Rowcliffe et al., 2008) which uses the area of the detection zone of a camera (i.e. radius, angle) and an animal’s average travel speed to convert the photographic rate (i.e. the number of pictures per unit time) into a density estimate (see Pettigrew et al. 2021). We estimated black bear and moose travel speeds using GPS telemetry data used in previous studies in the LWR and LSJ regions (Leblond et al., 2010; Massé et al., 2014). We could not estimate local densities for wolves and caribou due to the low number of animals photographed on adjacent forest cameras.

2.3.2. *GIS data*

To account for the potential effect of the roads’ surrounding environment on their use by large mammals, we used the 1: 20000 digital forest cover maps published by the MFFP and characterized the landscape around each camera station. These maps are derived from aerial photographs, were updated in 2016, and have a spatial resolution of 4 ha for forest stands and 2 ha for non-productive areas (e.g. lakes). We categorized the landscape into four land cover types: recent cutovers (0–20 years post-logging), wetlands (marsh, bog, fen), mixed and deciduous stands (20+ years old; hereafter mixed), and coniferous stands (20+ years old). We defined the landscape as the habitat immediately available to animals or susceptible to influence the behavior of animals (following Leblond et al., 2015). We calculated the proportion of each land cover type in buffers of different radii (250, 500, 750, 1000 m) centered on the camera station. We also calculated road density in these buffers. We could not test for the potential effect of land cover type at a larger scale (e.g. 5 or 10-km radii) considering that cameras were placed every 250 m on each road segment. Using buffers with a radius>1 km would have resulted in having similar percentages of the different land cover types since the buffers of adjacent cameras would be overlapping too much, causing pseudo-replication problems and decreasing our statistical power. We used this multiscale approach to account for the variation in scale of selection by animals and to minimize the bias induced by choosing an arbitrary and potentially inappropriate scale (following Leblond et al., 2011). The four selected radii are commonly used in studies conducted on the same species in similar environment using telemetry data and were originally based on animal movement rates (Leblond et al., 2011,2013; Dussault et al., 2012; Lesmerises et al., 2012). Finally, for each camera station, we extracted the slope, the distance to the closest permanent water body, longitude and latitude.

2.4. *Statistical analyses*

According to our hypotheses, we built a model with road-scale variables describing ease of movement for wolves, another model including vegetation variables associated with forage availability for black bears and moose, and a co-use model for each species (see Appendix A; Tables A2–A4 for description of variables, and Tables A5–A7 for composition of candidate models). The combinations of variables included in each model vary and are described below for each species. We also built models for each species at a larger scale using anthropogenic footprint and surrounding habitat covariates that have already been shown to influence selection of linear features by large mammals (Latham et al., 2011a, 2011b; Mumma et al., 2019b). Covariates included in the anthropogenic footprint model were road density and the proportion of 0–20-year-old clearcuts in the surroundings of a camera. Habitat covariates were the proportion of mixed stands, coniferous stands, wetlands and the distance to the nearest permanent water body. We then tested each model and their combinations (total of 15 models, see Appendix A; Tables A5–A7) and selected the most parsimonious one using the AIC$_c$ (Burnham and Anderson, 2001). We used the buffer radius that best explained the observed variation using the AIC$_c$ (as used by Lesmerises et al., 2018) to calculate the proportion of each covariate (0–20-year-old clearcuts, wetlands, mixed stands, and coniferous stands) as well as road density. The assumptions of our statistical models were verified using the visual tools comprised in the DHARMa package (Hartig, 2020). Because we captured too few pictures of caribou during the three years of survey, we could not build models to test our hypotheses for this species, but consider that results obtained from models built for bears, wolves and moose can inform caribou conservation.

Due to our zero-inflated dataset for wolves, we could not test for the intensity of use and thus recoded event counts into binary (0/1) data to test the effect of covariates on the probability of use in a mixed logistic regression (library lme4; Bates et al., 2015), where the probability of use is defined as the use of a camera station at least once during the data collection season. The first candidate model contained variables linked to ease of movement: road age, slope, and density (%) of lateral cover. Co-use model covariates included traffic volume (log-scale) and use by moose and black bears. We assessed model fit using a leave-one-out cross-validation, the area under the ROC curve (AUC) and by comparing the model to the null model.

We modeled the intensity of use by black bears using a mixed negative binomial regression (package glmmTMB; Brooks et al., 2017). The covariates used in the forage accessibility model were road age, slope, density of lateral cover (%), and mean cover of herbaceous species (%). Co-use model covariates included traffic volume (log-scale) and use by moose and wolves. We also used a mixed negative binomial regression to describe the effect of different covariates on the intensity of use by moose. Forage accessibility covariates included road age, slope, density of lateral cover (%) and forage availability (the summed abundances of trembling aspen, white birch and willow stems at each camera station). We included a quadratic term to better describe variation in forage availability (following the observed distribution of residuals). Co-use covariates were traffic volume (log-scale) and use by wolves and black bears. We compared the model to the null model and calculated the marginal R^2 for both moose and black bear models.

To account for the spatial autocorrelation that often occurs at different scales in natural systems, we used a principal coordinate of neighboring matrix (PCNM; Borcard and Legendre, 2002) analysis. The only significant PCNM was the one at the largest scale and was thus included into each candidate model to account for its confounding effect (see St-Laurent et al., 2008 for an example). For moose and black bear, we included in all models the regional density of each species, respectively. Finally, the effort (i.e. the number of days a camera was active) was included as a fixed effect in the logistic regressions for wolves and as an offset in the negative binomial models for black bears and moose. We also included road ID-year as a random factor in each model to account for pseudoreplication problems. There was no overparameterization in our models: the most complex candidate model had 21 independent variables and was tested on a dataset based on 652 cameras distributed on 165 independent road segments. All model converged and analyses were conducted using R 4.0.3 (R core team, 2019).

3. Results

The total sampling effort over the three consecutive summers was 58,035 camera-days for cameras placed alongside a road segment (mean of 92 days per camera per year) and 29,656 camera-days for adjacent forest cameras (mean of 90 days per camera per year). The most photographed species (on roads: R; adjacent forest: AF) was moose (R: 3614 events; AF: 277) followed by black bear (R: 1866; AF: 115), wolf (R:

Table 1

Most parsimonious mixed regression models explaining wolf probability of use and black bear and moose intensity of use of forest roads during the three consecutive summers of 2018–2020 in boreal caribou range, Québec, Canada. Covariates are presented with their coefficient (**β**) and bootstrapped 95% confidence interval (95 % CI). Significant covariates (95 %CI not overlapping zero) are highlighted in bold. The 0–10-year-old category was used as reference category for the age covariate. PCNM: vector of principal coordinates of neighbour matrices controlling for spatial autocorrelation. The effort was used as a fixed effect in the wolf model and as an offset for black bear and moose. $N = 652$.

	Wolf (mixed logistic)		Black bear (mixed negative binomial)		Moose (mixed negative binomial)	
Covariates	β	95% CI [Lower: Upper]	β	95% CI| [Lower: Upper]	β	95% CI [Lower: Upper]
Intercept	−0.17	[-2.09: 1.29]	**−3.30**	**[-3.57: −3.02]**	**−2.69**	**[-2.91: −2.44]**
Age15	0.20	[-1.96: 2.21]	0.05	[-0.19: 0.37]	**0.27**	**[0.06: 0.51]**
Age25	0.46	[-0.92: 2.68]	**−0.41**	**[-0.73: −0.17]**	0.12	[-0.20: 0.35]
Age35	0.30	[-1.63: 2.94]	**−0.85**	**[-1.19: −0.44]**	**−0.74**	**[-1.06: −0.40]**
Age45	−0.35	[-1.99: 2.24]	**−1.40**	**[-1.82: −0.98]**	**−1.26**	**[-1.72: −0.95]**
Lateral cover	**−0.64**	**[-1.04: −0.27]**	−0.08	[-0.19: 0.02]	−0.05	[-0.14: 0.07]
Slope	−0.12	[-0.40: 0.10]	−0.01	[-0.07: 0.09]	−0.004	[-0.08: 0.06]
Log(Traffic + 1)	**0.42**	**[0.10: 1.18]**	**−0.16**	**[-0.33: −0.06]**	0.003	[-0.100: 0.110]
Herbaceous cover			0.01	[-0.12: 0.08]		
Log(forage + 1)					**0.27**	**[0.11: 0.56]**
Log(forage + 1)^2					**−0.20**	**[-0.44: −0.02]**
Wolf use			**0.17**	**[0.09: 0.28]**	**0.09**	**[0.03: 0.16]**
Black bear use	**0.37**	**[0.08: 0.71]**			0.03	[-0.03: 0.11]
Moose use	**0.43**	**[0.07: 0.82]**	0.06	[-0.03: 0.17]		
Mixed	0.23^{a}	[-0.16: 0.77]	0.02^{b}	[-0.08: 0.13]		
Coniferous	0.05^{a}	[-0.42: 0.72]	**0.20**$^{\mathbf{b}}$	**[0.02: 0.38]**		
Wetlands	**0.53**$^{\mathbf{a}}$	**[0.17: 0.92]**	−0.07^{b}	[-0.17: 0.00]		
Distance to water	−0.001	[-0.35: 0.45]	−0.01	[-0.09: 0.11]		
Road density					−0.04^{b}	[-0.12: 0.04]
0–20 Clearcuts					**−0.17**$^{\mathbf{b}}$	**[-0.30: −0.04]**
Effort	**0.33**	**[0.01: 0.75]**				
Local density			−0.08	[-0.19: 0.01]	**0.18**	**[0.07: 0.27]**
PCNM	**−0.63**	**[-1.07: −0.04]**	**−0.45**	**[-0.56: −0.34]**	**0.32**	**[0.19: 0.42]**

a: Calculated in a 500-m radius buffer.

b: Calculated in a 250-m radius buffer.

1125; AF: 6) and caribou (R: 36; AF: 9) (Appendix A Table A8).

The probability of use of roads by wolves was best explained by model 12 (road-scale + habitat) although models 1, 3 and 8 received comparable support ($AIC_c < 2$; Appendix A Table A5). As model 12 includes all the covariates used in models 1, 3 and 8, we only retained model 12 for further interpretation (Table 1). The probability of using a road was lower when the density of lateral cover was high and when the road was surrounded by a lower proportion of wetlands (in a 500-m radius), but higher when traffic volume and use by black bears and moose were high (Table 1). Finally, a greater sampling effort increased the probability of photographing at least one wolf, and the PCNM was significant. The model was significantly different from the null model ($P < 0.001$), had an area under the ROC curve of 0.955, a mean leave-one-out cross-validation accuracy of 0.78 and a R^2 of 0.20.

The top-ranking models explaining black bears intensity of use were model 3 (road-scale) and model 12 (road-scale + habitat; $AIC_c < 2$; Appendix A, Table A6). We only interpret the result of model 12 (Table 1) because model 3 is nested in model 12. Black bear intensity of use was lower on roads in the 21–30, 31–40 and 40+ year-old categories compared to roads aged 0–10 years, and lower when traffic volume was high and when a road was surrounded by a lower proportion of coniferous stands (in a 250-m radius). Black bear intensity of use and wolves use were also positively correlated. The PCNM was also significant. The model was different from the null model ($p < 0.001$) and had a marginal R^2 of 0.26.

Moose intensity of use was best explained by model 11, which included road-scale and anthropogenic footprint covariates, and by model 7 (forage availability + anthropogenic footprint; $AIC_c < 2$; Appendix A Table A7), which is nested in model 11; we thus only interpret model 11 (Table 1). Moose used more 11–20-year-old roads and less 31–40 and 40+ year-old roads compared to the 0–10-year-old category. We found a quadratic relationship between moose intensity of use and forage availability; the intensity of use was greater when forage availability increased until a threshold above which an increase in forage availability had no further effect on the intensity of use by moose. We also noted that moose intensity of use of a road was positively linked with wolf use, and positively influenced by a lower proportion of 0–20-year-old cutblocks surrounding the road (in a 250-m radius) and by a higher moose density. The PCNM was also significant. This model was different from the null model ($p < 0.001$), and the marginal effects explained 31% of the variation (R^2 of 0.31).

4. Discussion

We showed that fine-scale characteristics of forest roads, which are typically not considered when studying the use of roads by large mammals, appeared to play an important role in explaining the use of road segments by wolves, black bears and moose. Large-scale variables that contextualized roads in their environment also contributed to the top-ranking models, suggesting that both intrinsic characteristics of linear features and the immediate environment in which they are built are predictors of their use by large mammals. However, testing the influence of some variables failed for caribou, as the number of caribou photos taken by our automated cameras was insufficient to conduct statistical analyses explaining the variation in caribou use of forest roads. Such a low number of events could be explained by the low density of caribou in our 3 study areas, but could also suggest that caribou in our study areas are avoiding forest roads regardless of the state of vegetation regrowth. This result would be consistent with the widely demonstrated avoidance of linear features by caribou (Leblond et al., 2011; Dussault et al., 2012; Mumma et al., 2019b). Nevertheless, we considered that the findings we obtained regarding the determinants of predators and alternative prey use of different types of roads could inform caribou conservation and guide managers in choosing forest roads that should be decommissioned first in other caribou ranges where such measures are warranted.

4.1. *Fine-scale characteristics of roads shape their use by large mammals*

According to our predictions, wolves were more likely to use forest roads that facilitate movement: the probability of use of a road was higher when the density of lateral cover was low. This finding is consistent with studies conducted in western Canada on other types of linear features where wolves selected features with sparser vegetation and moved faster when using them (Dickie et al., 2017a, 2017b; Finnegan et al., 2018b). We also showed that roads with a higher traffic volume had a greater probability of use by wolves, a result that could also support our ease of movement hypothesis. A higher traffic volume could maintain roadways cleared of vegetation, facilitating predator movement and thus being more attractive for wolves. Indeed, we previously demonstrated in the same study area that whenever a road was used once by humans during summer, there was never a growing stem in the middle of it (St-Pierre et al., 2021), and other studies have also demonstrated that the use of linear features by vehicles can damage regrowth and prevent its establishment (Pigeon et al., 2016; Hornseth et al., 2018). Linear features used by humans were also shown to positively influence wolf use (Tattersall et al., 2020a).

We found no effect of the percentage of herbaceous cover on the use of roads by black bears, but found an effect of road age, thus partially supporting our increased forage accessibility hypothesis. The intensity of use of roads by black bears significantly decreased with road age compared to the levels of use of 0–10-year-old roads. We interpret this result as the slow replacement of early seral vegetation selected by black bears by less palatable or accessible plant species as roads age. Indeed, previous studies showed that roadways, roadsides (Bastille-Rousseau et al., 2011; Lesmerises et al., 2015) and other linear features (Finnegan et al., 2018a, 2019; MacDonald et al., 2020) are often colonized by early-seral vegetation such as forbs, graminoids and shrub species that are selected by black bears (Latham et al., 2011a; Tigner et al., 2014). Contrary to wolves, the use of roads by black bears was negatively influenced by traffic volume. This could be explained by the suppression of vegetation on roadways linked to the passage of vehicles that would compact the soil and break young stems (Pigeon et al., 2016; Hornseth et al., 2018; St-Pierre et al., 2021), but it could also be explained by the disturbance associated with humans and vehicles (ATVs), as black bears can avoid human activity (Zeller et al., 2019).

The intensity of road use by moose was explained by road age but in a nonlinear way, with a higher intensity of use of 11–20-year-old roads compared to younger (0–10 years old) and older (30+ years old) road segments. This suggests that food accessibility could play a role in explaining variation in the intensity of use of road segments by moose, which is supported by the positive effect of the number of deciduous stems (forage availability covariate) on moose intensity of use that we also found. Moose are known to be associated with and benefit from regenerating disturbances where forage is abundant (Rempel et al., 1997; Fisher and Wilkinson, 2005). The higher use of 11–20-year-old roads compared to younger roads and the subsequent decrease in use of older roads appears supported by the transition between different stages of vegetation regeneration. Mumma et al. (2021) showed that moose tended to select 9–24-year-old cutblocks while avoiding 1–8-year-old and older (25–40 years old) cutblocks. In Québec, Potvin et al. (2005) showed that 10-year-old clearcuts offered better habitat conditions (browse availability, regeneration height, and lateral cover) for moose than immediately after harvest, which also aligns with our explanation. As forest roads are built for timber extraction and are consequently mostly the same age as the surrounding clearcuts, it could be argued that moose favored 11–20-year-old roads not because of the road itself, but due to the presence of 11–20-year-old cuts nearby. Although we included the proportion of 0–20-year-old clearcuts in our models as a covariate to control for its effect, we were not able to break down the clearcut age category into more precise subcategories (e.g. 0–10, 11–20) because of statistical constraints (i.e. skewed repartition between both categories). Nevertheless, our results confirm the concerns raised regarding the potential attractiveness of deciduous regrowth on linear features to moose (Finnegan et al., 2018a; MacDonald et al., 2020; St-Pierre et al., 2021).

We noted that the intensity of use of one species of large mammals was influenced by the use made by others, as we found positive correlations between wolf and black bear use in both the wolf and bear models, and between wolves and moose in the moose and wolf models. Tattersall et al. (2020b) have previously reported empirical evidence of co-occurrence between wolves and bears on seismic lines (at the daily scale), while other studies suggested that wolves used roads to increase their probability of encounter with prey (i.e. moose and caribou; Latham et al., 2011b; Whittington et al., 2011; Dickie et al., 2020). However, some caution is needed when interpreting these results; we evaluated co-use of a road segment during an entire summer (early June to mid-September), i.e. at a temporal scale that prevents from inferring the predator hunting (and prey avoidance) strategies. While wolves and moose were both using road segments at the scale of an entire summer, we consider that moose could have avoided roads recently used by wolves at a finer temporal scale (temporal niche partitioning, *sensu* Frey et al., 2017; Latombe et al., 2014). Positive interactions could also have been a result of a shared use of roads with similar characteristics rather than species responding to each other (Tattersall et al., 2020b; Beirne et al., 2021). Our results suggest that wolves, black bears and moose sometimes use forest roads with similar characteristics, meaning that road reclamation targeting one species could potentially influence the use and distribution of other sympatric mammals.

4.2. Large mammals respond to the landscape context surrounding forest roads

The probability of use of a road by wolves increased when the proportion of wetlands (peatlands, marsh) in the surrounding area was higher, which can potentially be explained by poor regrowth on these roads and the resulting easier travel opportunities they provided throughout wetlands. In a companion study conducted on the same road segments, we showed that roads surrounded by a higher proportion of wetlands had a sparser lateral cover (i.e. a lower density of stems; St-Pierre et al. 2021). With our automated cameras, we showed that the probability of use of a road by wolves was higher when the density of lateral cover was low. Our result thus suggests that these poorly regenerated roads further facilitate wolf movements in wetlands and are thus more likely to be used by them. Considering the selection of wetlands by caribou (James et al., 2004; Leblond et al., 2011), we believe that these roads could increase the probability of encounter between wolves and caribou. Seismic lines located in lowlands were also shown to support poor regrowth in western Canada (Van Rensen et al., 2015; Finnegan et al., 2019), and wolves were shown to select linear features in peatlands (Mumma et al., 2019b). Such findings are of great concern considering that peatlands are often used as a spatial refuge for caribou, and the presence of roads in these habitats could increase wolf access to these refuges (DeMars et al., 2018). Consequently, we consider that roads with no regrowth located in wetlands should be prioritized for active restoration.

The use of forest roads by black bears was modulated by the composition of the surrounding environment; we showed that it was positively influenced by the surrounding proportion of coniferous stands, although a 95% confidence interval close to 0 (i.e. 0.02) suggests a weak effect. This result could be due to the feeding behavior of female black bears with cubs and their relative selection of coniferous stands. In their study, Lesmerises and St-Laurent (2017) showed that females with cubs selected old coniferous stands—which are considered to be of low food value—to avoid predation on cubs by big males who are more present in food-rich habitat such as clearcuts. Lesmerises et al. (2015) also showed that secondary roads provide important food sources (i.e. poplar and grasses) for female black bears with yearling cubs. In our case, females with cubs present in coniferous stands could have thus been using roads to forage, explaining higher use of roads surrounded by coniferous stands by black bears. We however point out that we did not consider sex in this study and that our interpretation should be considered with caution.

We showed that a higher proportion of clearcuts surrounding a road reduced the use of roads by moose. When forage is abundant near a forest road, the potential benefit of food accessibility on the road is reduced, and moose could consequently borrow roads less and spend more time foraging in adjacent cuts. Indeed, moose are known to exhibit lower movement rates in food-rich areas (Dussault et al., 2005) and to select regenerating cutblocks where food availability is high (Dussault et al., 2006; Mumma et al., 2021), which supports our results. Also, the selection of roads by wolves (Dickie et al., 2017a), the main predator of moose, could also discourage moose from using roads to facilitate their movements.

5. Implications for caribou habitat restoration

Ray (2014) argued that vegetation on linear features will need to be both functionally and structurally restored for the restoration of caribou habitat to have higher probabilities of being effective. Our study supports this conclusion, as we showed that both components need to be considered. While the functional role of roads (ease of movement) had an effect on wolf use, the structure and composition of regrowth positively influenced its use by black bears and moose. Our results thus seem important to support the adjustment of caribou habitat restoration strategies to the specific drivers of caribou decline operating in a given study area. For example, predation on caribou calves by black bears might be a more important limiting factor in some populations (i.e. Charlevoix; Leclerc et al. 2014), making the decommissioning of young road segments with forage suitable to black bears a priority in these populations. Inversely, in populations where predation by wolves is the main driver of decline (i.e. Chinchaga, Johnson et al., 2019), road decommissioning efforts should prioritize roads with a lower percentage of lateral cover and surrounded by wetlands with no respect to road age.

Overall, our results will help to identify which road characteristics best explain the use by caribou predators and consequently assist in prioritizing road segments to be selected for reclamation and habitat restoration efforts in order to contribute to caribou conservation. Nevertheless, we recognize that decommissioning only a small subset of roads in a range to restore suitable habitat will be insufficient to reverse the decline of a caribou population and will need to be combined with others conservation strategies (e.g. protected areas, maternity penning, predator control; Johnson et al., 2019; Serrouya et al., 2020). Finally, monitoring the success of restoration has already been conducted in the first years following restoration (Tattersall et al., 2020a; Dickie et al., 2021; Lacerte et al., 2021); however, doing so over a longer time period will further improve our comprehension and ability to effectively restore caribou habitat.

CRediT authorship contribution statement

Fabien St-Pierre: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Pierre Drapeau:** Writing – review & editing, Supervision. **Martin-Hugues St-Laurent:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition, Validation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Description of covariates and list of candidate models for each species, sampled road distribution and events

Table A1
Breakdown of sampled forest road segments into age categories (no. of years since construction) and regions (CN: Côte-Nord, LSJ: Saguenay-Lac-St-Jean, LWR: Laurentides Wildlife Reserve) across boreal caribou range in Québec, Canada.

Region	Age category					
	0–10	11–20	21–30	31–40	40+	Total
CN	2	4	4	0	5	15
LSJ	1	1	3	7	3	15
LWR	3	2	6	6	9	26
Total	6	7	13	13	17	56

Table A2
Covariates used in the mixed logistic regression models used to explain variations in the probability of use of forest roads by wolves across boreal caribou range in Québec, Canada.

Covariate	Description	Type and range
Ease of travel		
Age category	Time since road construction	Categorical with 5 levels: 0–10 (Age5), 11–20 (Age15), 21–30 (Age25), 31–40 (Age35), 40+ (Age45) years old.
% of lateral cover	Mean percentage of lateral cover at 15 m in both direction parallel to the road	Continuous positive [0: 100]
Slope	Slope at each camera station	Continuous positive [0.00: 19.21]
Co-use		
Log(Traffic volume + 1)	Number of human events/effort on a log-scale	Continuous positive [0.00: 1.35]
Moose use	Number of moose events/effort	Continuous positive [0.00: 0.38]
Black bear use	Number of black bears events/effort	Continuous positive [0.00: 0.27]
Anthropogenic footprint		
% of 0–20 Clearcuts	Proportion of 0–20-year-old clearcuts (%) in a buffer of 500-m radius	Continuous [0: 97.14]
Road density	Road density in a 500-m radius buffer (km/km^2)	Continuous [0: 5.10]
Habitat		
% of coniferous stands	Proportion of > 20-year-old coniferous stands (%) in a buffer of 500-m radius	Continuous [0.00: 99.99]
% of mixed stands	Proportion of > 20-year-old deciduous stands (%) in a buffer of 500-m radius	Continuous [0.00: 63.48]
% of wetlands	Proportion of wetlands (%) in a buffer of 500-m radius	Continuous [0: 14.83]
Distance to water	Distance to the nearest permanent water body (m)	Continuous [4.79: 1126.66]
All model		
Effort	Days during which the camera was active	Continuous [10.02: 120.03]
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.04: 0.04]
(1|RoadID-Year)	Random effect at the road-year level	Categorical with 165 levels

Table A3
List of covariates used in the mixed negative binomial regression models used to explain variations in the intensity of use of forest roads by black bears across boreal caribou range in Québec, Canada.

Covariate	Description	Type and range
Food accessibility		
Age category	Time since road construction	Categorical with 5 levels: 0–10 (Age5), 11–20 (Age15), 21–30 (Age25), 31–40 (Age35), 40+ (Age45) years old.
% of lateral cover	Mean percentage of lateral cover at 15 m in both direction parallel to the road	Continuous positive [0: 100]
Slope	Slope at each camera station	Continuous positive [0.00: 19.21]
Herbaceous cover	Relative mean herbaceous cover (%)	Continuous positive [0.00: 90.00]
Co-use		
Log(Trafficvolume + 1)	Number of human events/effort on a log-scale	Continuous positive [0.00: 1.35]
Moose use	Number of moose events/effort	Continuous positive [0.00: 0.38]
Wolf use	Number of wolf events/effort	Continuous positive [0.00: 0.25]
Anthropogenic footprint		
% of 0–20 Clearcuts	% of 0–20-year-old clearcuts in a buffer of 250-m radius	Continuous [0: 99.99]
Road density	Road density in a 250-m radius buffer (km/km^2)	Continuous [0: 8.03]
Habitat		
% of coniferous stands	% of >20-year-old coniferous stands in a buffer of 250-m radius	Continuous [0.00: 99.99]
% of mixed stands	% of >20-year-old deciduous stands in a buffer of 250-m radius	Continuous [0.00: 85.73]
% of wetlands	% of wetlands in a buffer of 250-m radius	Continuous [0: 23.96]
Distance to water	Distance to the nearest permanent water body (m)	Continuous [4.79: 1126.66]
All model		
Effort	Days during which the camera was active.	Offset [10.02: 120.03]
Regional density	Estimated density of black bears per region per year (bear/km^2)	Continuous [0.02: 0.09]
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.04: 0.04]
(1|RoadID-Year)	Random effect at the road-year level	Categorical with 165 levels

Table A4
Covariates used in the mixed negative binomial regression models used to explain variations in the intensity of use of forest roads by moose across boreal caribou range in Québec, Canada.

Covariate	Description	Type and range
Food accessibility		
Age category	Time since road construction	Categorical with 5 levels: 0–10 (Age5), 11–20 (Age15), 21–30 (Age25), 31–40 (Age35), 40+ (Age45) years old.
% of lateral cover	Mean percentage of lateral cover at 15 m in both direction parallel to the road	Continuous positive [0: 100]
Slope	Slope at each camera station	Continuous positive [0.00:19.21]
Forage availability	Sum of white birch, willows and trembling aspen stems in a 32 m^2 surface	Discrete positive [0: 57]
Co-use		
Log(Traffic volume + 1)	Number of human events/effort on a log-scale	Continuous positive [0.00: 1.35]
Black bear use	Number of black bear events/effort	Continuous positive [0.00: 0.27]
Wolf use	Number of wolf events/effort	Continuous positive [0.00: 0.25]
Anthropogenic footprint		
% of 0–20 Clearcuts	Proportion of 0–20-year-old clearcuts (%) in a buffer of 250-m radius	Continuous [0: 99.99]
Road density	Road density in a 250-m radius buffer (km/km^2)	Continuous [0: 8.03]
Habitat		
% of coniferous stands	% of > 20-year-old coniferous stands in a buffer of 250-m radius	Continuous [0.00: 99.99]
% of mixed stands	% of > 20-year-old deciduous stands in a buffer of 250-m radius	Continuous [0.00: 85.73]
% of wetlands	% of wetlands in a buffer of 250-m radius	Continuous [0: 23.96]
Distance to water	Distance to the nearest permanent water body (m)	Continuous [4.79: 1126.66]
All model		
Effort	Days during which the camera was active.	Offset [10.02: 120.03]
Regional density	Estimated density of moose per region per year (moose/km^2)	Continuous [0.20: 0.94]
PCNM	Principal coordinates of neighbour matrices	Continuous [-0.04: 0.04]
(1|RoadID-Year)	Random effect at the road-year level	Categorical with 165 levels

Table A5
List of candidate models for the mixed logistic regressions used to model the probability of use of forest roads by wolves in boreal caribou range in Québec, Canada during three consecutive summers in 2018–2020. Covariates composing each model, their log-likelihood (LL), ΔAIC_c and AIC_c weight (ω) are shown. The effort and a PCNM as fixed effects and a random effect at the road-year level were also included in each model.

Model	Explanatory covariates	LL	k	ΔAIC_c	ω
1 – Ease of travel	Age category + Slope + % of lateral cover	−349.69	10	0.83	0.16
2 – Co-use	log(Traffic volume + 1) + Moose use + Bear use	−356.11	7	7.51	0.00
3 – Road-scale	Model 1 + Model 2	−346.29	13	0.25	0.22
4 – Anthropogenic footprint	% of clear cuts + Road density	−362.89	6	19.01	0.00
5 – Habitat	% of mixed stands + % of coniferous stands + % wetlands + Distance_to_water	−356.77	8	10.87	0.00
6 – Surrounding environment-scale	Model 4 + Model 5	−356.52	9	12.43	0.00
7 – Ease of travel + Anthropogenic footprint	Model 1 + Model 4	−349.46	12	4.51	0.02
8 – Ease of travel + Habitat	Model 1 + Model 5	−345.96	14	1.69	0.10
9 – Co-use + Anth_Foot	Model 2 + Model 4	−356.08	9	11.54	0.00
10 – Co-use + Habitat	Model 2 + Model 5	−349.70	11	2.93	0.05
11 – Road-scale + Anth_Foot	Model 3 + Model 4	−345.95	15	3.77	0.04
12 – Road-scale + Habitat	Model 3 + Model 5	−341.96	17	0.00	0.25
13 – Environment-scale + Ease of travel	Model 6 + Model 1	−345.99	15	3.83	0.04
14 – Environment-scale + Co-use	Model 6 + Model 2	−349.62	12	4.83	0.03
15 – Full model	Model 3 + Model 6	−342.02	18	2.24	0.08

Table A6
List of candidate models for the mixed negative binomial regressions used to model the intensity of use of forest roads by black bears in boreal caribou range in Québec, Canada during three consecutive summers in 2018–2020. Covariates composing each model, their log-likelihood (LL), ΔAIC_c and AIC_c weight (**ω**) are shown. The effort as an offset, a PCNM and black bear density as a fixed effect and a random effect at the road-year level were also included in each model.

Model	Explanatory covariates	LL	k	ΔAIC_c	ω
1 – Forage accessibility	Age category + Slope + % of lateral cover + Mean herbaceous cover	−1266.87	12	9.72	0.00
2 – Co-use	log(Traffic volume + 1) + Moose use + Wolf use	−1276.41	8	20.54	0.00
3 – Road-scale	Model 1 + Model 2	−1258.87	15	0.0	0.64
4 – Anthropogenic footprint	% of clear cuts + Road density	−1279.40	7	24.48	0.00
5 – Habitat	% of mixed stands + % of coniferous stands + % wetlands + Distance_to_water	−1281.51	9	32.79	0.00
6 – Surrounding environment-scale	Model 4 + Model 5	−1278.37	10	28.59	0.00
7 – Forage + Anthropogenic footprint	Model 1 + Model 4	−1266.67	14	13.51	0.00
8 – Forage + Habitat	Model 1 + Model 5	−1264.02	16	12.40	0.00
9 – Co-use + Anth_Foot	Model 2 + Model 4	−1270.12	10	12.08	0.00
10 – Co-use + Habitat	Model 2 + Model 5	−1271.93	12	19.85	0.00
11 – Road-scale + Anth_Foot	Model 3 + Model 4	−1258.79	17	4.05	0.08
12 – Road-scale + Habitat	Model 3 + Model 5	−1255.59	19	1.88	0.24
13 – Environment-scale + Forage	Model 6 + Model 1	−1264.92	17	16.30	0.00
14 – Environment-scale + Co-use	Model 6 + Model 2	−1268.77	13	15.61	0.00
15 – Full model	Model 3 + Model 6	−1256.76	20	6.35	0.03

Table A7
List of candidate models for the mixed negative binomial regressions used to model the intensity of use of forest roads by moose in boreal caribou range in Québec, Canada during three consecutive summers in 2018–2020. The covariates included in each model, their log-likelihood (LL), ΔAIC_c and AIC_c weight (**ω**) are shown. The effort as an offset, a PCNM and moose density as a fixed effect as well as a random effect at the road-year level were also included in each model.

Model	Explanatory covariates	LL	k	ΔAIC_c	ω
1 – Forage accessibility	Age category + Slope + % of lateral cover + log(Forage availability + 1)^2	−1627.13	13	6.18	0.02
2 – Co-use	log(Traffic volume + 1) + Black bear use + Wolf use	−1658.15	8	66.13	0.00
3 – Road-scale	Model 1 + Model 2	−1622.82	16	3.85	0.07
4 – Anthropogenic footprint	% of clear cuts + Road density	−1665.16	7	70.09	0.00
5 – Habitat	% of mixed stands + % of coniferous stands + % wetlands + Distance_to_water	−1665.35	9	74.33	0.00
6 – Surrounding environment-scale	Model 4 + Model 5	−1662.60	10	70.90	0.00
7 – Forage + Anthropogenic footprint	Model 1 + Model 4	−1622.77	15	1.64	0.21
8 – Forage + Habitat	Model 1 + Model 5	−1623.37	17	7.05	0.01
9 – Co-use + Anth_Foot	Model 2 + Model 4	−1657.65	10	61.00	0.00
10 – Co-use + Habitat	Model 2 + Model 5	−1658.15	12	66.13	0.00
11 – Road-scale + Anth_Foot	Model 3 + Model 4	−1618.79	18	0.00	0.47
12 – Road-scale + Habitat	Model 3 + Model 5	−1619.40	20	5.48	0.03
13 – Environment-scale + Forage	Model 6 + Model 1	−1620.96	18	4.34	0.05
14 – Environment-scale + Co-use	Model 6 + Model 2	−1655.16	13	62.24	0.00
15 – Full model	Model 3 + Model 6	−1616.87	21	2.55	0.13

Table A8
Raw and standardized (per 10,000 camera-days) number of events (i.e. number of photographed animals) captured by cameras placed on forest roads and in adjacent forest during three consecutive summers of 2018–2020 in boreal caribou range in Québec, Canada.

Species	Raw events on roads	Raw events in adjacent forest	Events on roads per 10,000	Events in forest per 10,000
Moose	3614	277	622	93
Black bear	1866	115	321	38
Grey wolf	1125	6	194	2
Caribou	36	9	6	3

Appendix B. Method used to calculate the area of the detection zone of each adjacent forest camera

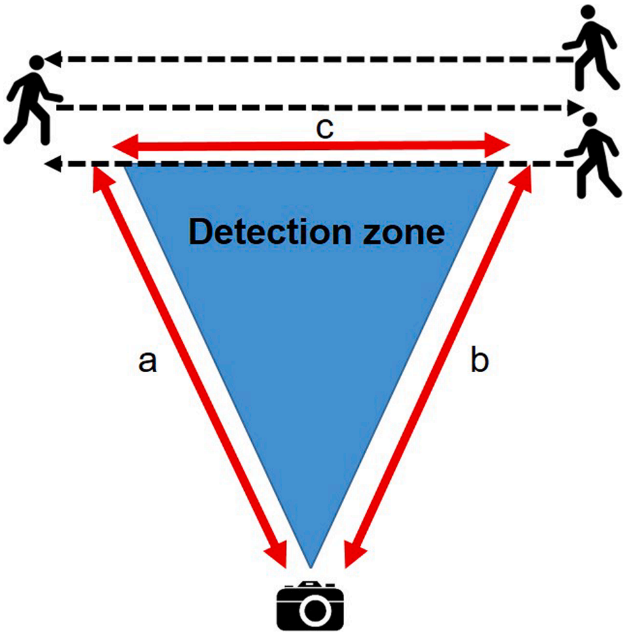

Fig. B1. Visual representation of the method used to determine the area of the detection zone. A series of passages were made starting further away and gradually closer to the camera until it detected movement. We then noted the length of each sides (letter a, b and c) of the detection zone to later derivate the detection angle and area.

We made a series of passages in front of each adjacent forest camera to determine the length of the sides of the detection zone. The first passage was done further away from the camera, where we knew it would not detect any movement, and each subsequent passage was done gradually closer to the camera until we were certain the camera detected it. We then measured the length of each side: a (distance from the camera to the leftmost detected movement), b (distance from the camera to the rightmost detected movement) and c (distance between leftmost detection and rightmost detection). We used these measurements to calculate the detection zone and the detection angle (angle ab).

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