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Use of linear features by mammal predators and prey in managed boreal forests

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A R T I C L E I N F O

Mots-clés:
Prédateurs du caribou boréal
Perturbations anthropiques
Structures linéaires
Chemins forestiers
Utilisation de l'habitat
Caméras de surveillance
Couvert latéral
Aménagement forestier

Keywords:
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anthropogenic disturbances
linear features
forest road
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lateral cover
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A B S T R A C T

In managed boreal forests, logging operations maintain high levels of anthropogenic disturbance in the ecosystem. The establishment of permanent anthropogenic linear features such as logging roads in the landscape may be a major factor in the predator-prey system. Logging roads may potentially improve the numerical and functional response of predators. Using camera traps, our objective was to explain according to local and landscape factors how the number of uses by wolves, black bears, lynx and moose, varies along different natural and anthropogenic linear features during the snow-free season. In western Quebec (Canada), the managed forest south of Val-d'Or encloses an isolated caribou population facing extinction that requires active restoration of their habitat. In this site, we used stratified random selection of gravel forest roads (n = 33), winter forest roads (n = 28) and riparian areas (n = 19) to compare their characteristics and number of uses by the four species. For wolves, black bears, and lynx, positive differences in lateral cover between the surroundings and the linear feature mainly explained their number of uses. Number of uses by wolves and lynx were positively related to use by their respective prey species (moose and snowshoe hare). Gray wolf use was also positively affected by distance to a higher forest road class and negatively affected by distance to the nearest urban area. Gravel forest roads had the highest number of uses by all species, as they showed greater positive differences in lateral cover as compared to the surroundings area due to their limited vegetation growth and by frequent maintenance activities. We recommend that restoration efforts aimed at forest road closures should target roads with a high value of difference in lateral cover, which is particularly the case in most gravel roads. Lower lateral cover on these linear feature as compared to their surroundings area favors the movement of predators and alternative prey. Our results thus suggest that investing in gravel roads restoration can benefit conservation efforts in caribou habitat.

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R É S U M É

En forêt boréale aménagée du Québec, l'exploitation forestière maintient un niveau de perturbation anthropique trop élevé dans l'écosystème forestier entrainant le déclin des populations de caribou boréal. Étant en général une perturbation permanente, l'implantation de structures linéaires anthropiques, comme les chemins forestiers, est un facteur prépondérant du système prédateurs-proies. Les chemins forestiers améliorent la réponse numérique et fonctionnelle des prédateurs et des proies alternatives. Notre objectif était d'expliquer par des facteurs locaux et de paysages comment le nombre d'utilisations de l'habitat en période sans neige du loup, de l'ours noir, du lynx ainsi que du compétiteur apparent du caribou, l'orignal, varie sur différentes structures linéaires naturelles et anthropiques avec l'aide de caméras de surveillance. Dans l'ouest du Québec, au Canada, le site faunique du caribou, au sud de Val-d'Or, abrite une population isolée en voie d'extinction qui nécessite une

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restauration active de son habitat. Dans ce site, une sélection aléatoire stratifiée de chemins gravelés (n = 33) et de chemins d'hiver (n = 28) de classe inférieure ainsi que du milieu riverain (n = 19) a été faite pour comparer leurs caractéristiques ainsi que le nombre d'utilisations de ces espèces. Pour le loup, l'ours noir et le lynx, la différence du couvert latéral entre le milieu environnant et la structure linéaire expliquait principalement leur nombre d'utilisations par 100 jours. Cette utilisation par le loup et le lynx était positivement liée à l'utilisation par leurs proies respectives (orignal et lièvre d'Amérique). Le nombre d'utilisations du loup gris était affecté positivement par la distance à un chemin forestier de classe supérieure et négativement par la distance à la ville la plus près. Essentiellement, les chemins forestiers gravelés présentaient le nombre d'utilisations le plus élevé par toutes les espèces car ils présentaient des différences positives plus importantes dans la couverture latérale par rapport aux milieu environnant, en raison de la croissance limitée de la végétation et des activités d'entretien fréquentes. Nous recommandons que les efforts de restauration visant la fermeture des chemins forestiers ciblent ceux ayant une valeur élevée de différence de couvert latéral, ce qui est particulièrement le cas pour la plupart des chemins gravelés. Le faible couvert latéral sur ces structures linéaires par rapport à leur environnement favorise le déplacement des prédateurs et des proies alternatives. Nos résultats suggèrent que d'investir dans la restauration des chemins forestiers gravelés peut être bénéfique pour les efforts de conservation de l'habitat du caribou.

Introduction

The ongoing growth of the human population and the global economy is leading to considerable losses of biodiversity on the planet (Grooten and Almond, 2018). In general, this decline is primarily due to loss and fragmentation of habitats (Fahrig, 1997, 2003). Despite remaining relatively intact, boreal forest ecosystems are also being affected. In certain regions, exploitation of natural resources through industrial activities (forestry, hydroelectric generation, mineral and hydrocarbon extraction) may potentially contribute to a high level of anthropogenic disturbance, leading to concerns about jeopardizing biodiversity preservation (St-Laurent et al., 2009; Imbeau et al., 2015). These disturbances alter the composition, structure, and level of fragmentation of forests. Such changes may affect the density and spatial distribution of wildlife species, potentially affecting certain species with large home ranges that are associated with mature forests, such as woodland caribou (*Rangifer tarandus caribou*; Seip, 1992; Crête and Manseau, 1996; James et al., 2004; Bowman et al., 2010; Fisher and Burton, 2018; Lafontaine et al., 2019).

Anthropogenic disturbances associated with forest activity may be categorized as temporary or permanent on land. The duration of the impact on anthropogenic disturbance is more of a gradient. As observed with natural disturbances (e.g., fires, insect epidemics), forest harvesting can initiate a process of development and succession leading to more favourable conditions for caribou within an estimated time-frame of 40 years (Courtois et al., 2007; Environnement, 2011). Anthropogenic linear features such as forest roads, in contrast, may increase the rate of disturbance in caribou habitat over a longer temporal period. Although anthropogenic linear features often occupy a small portion of the land area, they can have a disproportionate effect on ecological processes (Trombulak and Frissell, 2000). Several studies in western Canada assert that the placement of anthropogenic linear features in the landscape, such as gravel forest roads and seismic lines, are overriding factors that alter predator-prey dynamics by favouring predators at the expense prey (Schneider, 2002; Whittington et al., 2005, 2011; DeMars and Boutin, 2018). When present in prey habitats, anthropogenic linear features induce an increase in functional and numerical responses from its predators. Functionally, anthropogenic linear features increase the hunting efficiency of predators. For instance, they promote spatial overlap of gray wolves (*Canis lupus*) and black bears (*Ursus americanus*) in prey refuge areas undisturbed or mature forest (McKenzie et al., 2012; DeMars and Boutin, 2018; Mumma et al., 2018) and facilitate movement by increasing their travel speed (Dickie et al., 2017, 2020) and, thus, their daily movement. Regarding the numerical response, it simply means a rise in the number of predators hunting within the prey habitat (McCutchen, 2007). Both responses can cause an increase in natural predation that changes the sensitive demographic balance that is traditionally known for caribou (Bergerud, 1974; Leclerc et al., 2012). The demographic effect of linear features on large wildlife is well known, especially from a species habitat restoration perspective, but it would be relevant to identify which anthropogenic linear features are most likely to favour species that are associated with his decline. To do so, the level of use must be identified across various natural and anthropogenic linear features in the managed forest landscape to target the factors that explain a decrease or an increase in their uses. Understanding these factors holds particular importance in the context of caribou habitat restoration.

Over the past decades, with the aid of camera traps, models have been developed that provide information on large mammal distributions and intensity of space use within their home ranges. Site occupancy models developed by MacKenzie et al. (2002) have emerged as invaluable assets for effective wildlife habitat management and conservation purposes. The intensity of use or counting model, on the other hand, informs whether a particular resource will be used more or less frequently over time (Keim et al., 2019). The outcome thus directly refers to the expected number of events in which the species uses a particular resource. The major distinction between occupancy and counting models is that the probability of occupancy may remain constant over time as intensity of use varies (Keim et al., 2011, 2019). Therefore, these models allow us to directly quantify the actual risk that is experienced by caribou using the space near a linear feature that is also frequented by predators and alternative preys.

Using local and landscape factors, our objective was to explain how the number of uses by woodland caribou predators, including gray wolves, black bears, and Canada lynx (*Lynx canadensis*), together with its alternative prey (moose; *Alces americanus*), varies along different natural and anthropogenic linear features during the snow-free season. Indeed, the number and distribution of black bears has increased on rejuvenating landscapes in Quebec, given the greater availability of its food resources (Mosnier et al., 2008), which raises predation on caribou calves (Latham et al., 2011a; Pinard et al., 2012; Leblond et al., 2016). Some studies in Labrador show that Canada lynx may also represent a significant predator of caribou calves when coyote and wolf are absent (Bergerud et al., 1983; Mahoney et al., 2016). This increase in predation, which in some areas had been linked to anthropogenic disturbance, has led to the designation of caribou as a threatened species in Canada since 2002 (Bergerud, 1974; Thomas and Gray, 2002; Festa-Bianchet et al., 2011; Leclerc et al., 2014). The literature reveals little information in North America on the level of use of winter forest roads and riparian areas by these species. Knowing the number of uses on gravel forest roads, winter forest roads and riparian areas during the snow-free season is relevant to forest management, because predation on calves is concentrated in the summer. This will help identify roads heavily used by species associated with calves predation and thus caribou decline. We hypothesized that gravel forest roads had a higher number of uses by large mammals than did winter roads and riparian areas. We assumed that the difference in lateral cover conditions between the surrounding area and the linear feature was more conducive to movement on gravel forest roads. Furthermore, we expected that prey use was more frequent, and the availability of edible plants for black bear and moose was also higher along gravel forest roads. Predicting the number of uses of these species based on ecological and anthropogenic covariates in a context of managed forest landscape is essential to guide woodland caribou habitat restoration initiatives (Ray, 2014; Muhly et al., 2019).

Materials and methods

Study area

The study area was located in western Quebec, within the administrative region of Abitibi-Témiscamingue. Logging is the main economic activity for this region. The forest ecosystem is mainly located in the northern part of the white birch-balsam fir bioclimatic domain (Saucier et al., 2009; MFFP, 2016). During the sampling periods in 2020 and 2021, the average temperatures were recorded at 15.7 ° C and 16.2 ° C and precipitation was 419 mm and 254 mm, respectively (Environment, 2022). The highest elevation in the study area was about 421 m, while the lowest point was 308 m above sea-level. The study area was located within Forest Management Unit (FMU) 08351 (MRN, 2020) and included the caribou wildlife site south of Val-d′Or (47°53'20''N, 77°39'15''W), which was designated in 2013–2018 covering about 2145 km^2 (MFFP, 2018; Fig. 1). This caribou wildlife site was delimited by historical and recent telemetry surveys of tagged Val-d'Or caribou individuals (MRN, 2013). For several years, a gray wolf depredation program has been conducted in the northeastern part of the caribou wildlife site. Construction of gravel and winter roads in the wildlife site was achieved between 2004 and 2008. The wildlife site was primarily composed of softwood species including black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus bankisiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.), together with white or paper birch (*Betula papyrifera* Marsh.). Mammals such as moose, gray wolf, black bear, lynx and snowshoe hare (*Lepus americanus*) were also present (Saucier et al., 2009).

Linear feature selection

In Quebec, the construction, upgrading, repair and maintenance of forest roads on public forest land is based on the "user pays" principle (MFFP, 2022). The forest industry is therefore the main contractor of the anthropogenic linear features in the forest landscape with about 476721 km of forest roads established in 2020 (MFFP, 2021). These forest roads are legislated in Quebec by the Sustainable Forest Management Regulation and must be authorized by the regional forestry minister (MFFP, 2020). All forest roads are classified according to functional classes. High class gravel forest roads (Quebec functional classes 1 and 2) represented a small percentage of all forest roads combined (13082 km). These classes of forest roads, with a width of more than 8 m, were designed to have an almost permanent life span because they have multiple uses. The economic and social importance of these higher gravel forest road classes rendered their dismantling a considerable constraint. Narrow gravel forest roads (Quebec functional classes 3 and 4) and winter forest roads that were built near logging areas represented about half of those established in Quebec with 165875 km and 67703 km, respectively (MFFP, 2021). Such narrow forest roads were more suitable in terms of being dismantled for restoration purpose by the regional minister of forest in boreal caribou habitat. Therefore, this study has focused on these two types of anthropogenic linear features. Class 3 and 4 gravel forest roads have an estimated life span of 10–15 years and are dedicated to the transportation of wood, predominantly during the summer period. Gravel

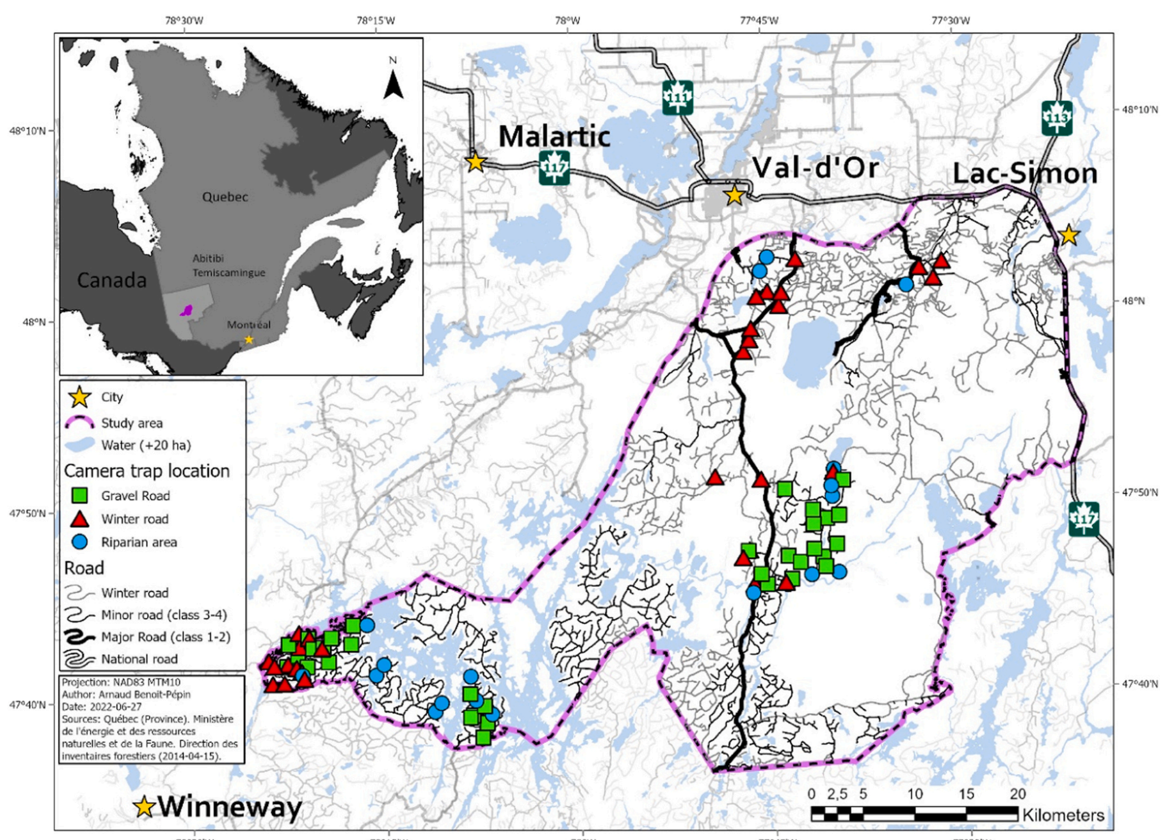

Fig. 1. Location of 33 gravel forest roads, 30 winter forest roads, and 19 riparian areas that were surveyed by camera traps during summer 2020 and 2021 in the caribou wildlife site south of Val d′Or, western Quebec, Canada.

forest roads were established and regulated using compacted aggregate and drainage system (culvert). For example, their sub-grade consists of natural gravel, mineral soil, organic soil and wood debris and has a medium to high degree of compaction, which allows the roads to perform better while preventing degradation from occurring quickly. Winter roads did not meet these standards; their construction is based upon a shorter-term planning horizon without aggregates and has a lower degree of compaction. Gravel forest roads are considered a long-lasting disturbance in the forest landscape (Girardin et al., 2022). Winter forest roads, in contrast, are used to transport wood when frozen ground conditions are established during the winter period. Low regulatory standards for such roads imply a status of temporary disturbances (MRN, 2013; MFFP, 2018, 2020). In addition to winter and gravel forest roads, we also studied a natural linear feature that is used by large wildlife, the riparian area. This natural edge constrains and concentrates movement and provides an important habitat for many prey species (Newton et al., 2017; Dickie et al., 2020).

Selection of linear features was performed with the help of a geographic information system (ArcGIS Pro 2.60, ESRI, Redlands, CA). Geographic data for forest roads in the study area were provided by the Quebec Ministry of Energy and Natural Resources. In this same area, we also received the locations of gravel and winter forest roads from the Ministry of Forests, Wildlife and Parks (MFFP). These roads were scheduled for dismantling in 2022 for the purpose of habitat restoration in the caribou wildlife site. To select the riparian areas, we excluded shorelines of water bodies less than 20 ha in surface area, since small water bodies were less likely to impede animal movements (Newton et al., 2017). The entire wildlife site was covered with a grid of points (fishnet function withing ARCGIS), each spaced 150 m apart from the others, to consider small sections of roads at the end of forest road network. On the 466 km of gravel roads, 1497 km of winter roads and 1361 km of riparian areas in study area, we selected points within in 20-metre buffer zone (407 points on gravel roads, 1151 on winter roads and 1106 on riparian areas). This 20-m zone corresponded influence area of a logging road affecting the vegetation (Zhou et al., 2020) and represented the minimum width of residual forest that left around water bodies after a cut as a protective measure. Thus, this area represented a connectivity space that can be used as a travel corridor by wildlife. To study how large mammals use linear features in a highly disturbed habitat, we applied four spatial constraints before randomly drawing the final sample. The first constraint excluded all points located more than 500 m from a drivable forest road. This distance was chosen to facilitate accessibility of sampled sites. The second constraint was to prioritize the points on roads that were scheduled for deconstruction due to their rarity and to assure long-term study. We applied a 3-km radius zone around these roads for sampling efficiency because some points on forest roads that will not be dismantled were located too far away from dismantled roads. The points that were located within the area delimited by these radii allowed us to identify those with a potential for being randomly drawn for the purpose of our study. To distribute our sample spatially, the third constraint separated the study area into two sub-areas according to the degree of recent use by Val-d′Or caribou and the intensity level of recent depredation (MRN, 2013). Thus, the sample was the result of a stratified random selection according to five groups of linear features: gravel forest roads with and without scheduled dismantling; winter forest roads with and without scheduled dismantling; and riparian areas. Lastly, a minimum distance of 1 km between each observation point was established to promote the independence of sites within the same group. We formed clusters that located in the two sectors, i.e., 44 observation points in the northeastern depredation sector used during the calving and breeding periods (1698 km^2) and 38 points in the southwestern sector without depredation in winter habitat (447 km^2). This process resulted in a distribution of sites where we selected 33 observation points on gravel forest roads, 30 on winter forest roads and 19 on riparian areas (Fig. 1). Within the drivable forest road area, we sampled 7.8% of points on the 466 km of gravel roads, 11.5% of points on the 613 km of winter roads and 5.2% on the 445 km of shorelines.

Camera-trap installation

This survey required the use of 87 camera traps for the 82 linear features studied (30 model #119876CN, Trophy Cam HD Brown; 40 model #119776, Trophy Cam Aggressor brown, Bushnell, Overland Park, Kansa, USA; 7 model #119875, Trophy Cam Camo; 5 model #119977, Core DS, no glow trail camera, Bushnell). Some cameras had to be replaced, which led to the purchase of newer models to complete the tracking of linear features (5 model #119837, Trophy Cam E3). We avoided the snow season, since the presence of snow cover and the absence of deciduous foliage could strongly modify the movement patterns of the species studied on linear features. We removed our cameras before the hunting season to avoid theft and considerable data loss. Sampling was conducted from 9 June to 6 October (93 days) in 2020, and from 14 May to 17 September (135 days) in 2021. Cameras were programmed to capture 3 photos per event to facilitate identification, with a 5-second capture interval between each event. We positioned the cameras about 50 cm above ground level and aimed them as far north as possible for best image clarity with a 30-degree angle to the forest roads or to the estimated location on the riparian area to capture moving animals. For the riparian area, we used Rovero and Zimmermann (2016) as a guide for determining the most likely wildlife passage near the shoreline around a 0–20 m radius of the pre-selected station. We were forced to modify the environment by cutting branches in the camera fields-of-view to avoid false triggers. The average camera detection radius on gravel roads, winter roads and riparian areas was 9.4 m, 7.8 m and 8.3 m, respectively. Photo and memory card retrieval were done about every 24–30 days. We used Wild ID software (Rovero and Zimmermann, 2016; Team Network, 2017) to annotate images in preparation for analysis.

Linear feature characteristics

Local variables

The vegetation sampling was conducted by the same observer between June 14 and September 20, 2021. To quantify lateral cover, the method of Collins and Becker (2001) was adapted to increase the accuracy and efficiency of measurements. Given the variable fields-of-view of the study species, lateral cover was measured at 50 cm, 100 cm and 150 cm above the ground surface. For each sampling unit (Fig. 2), we had two distinct micro-habitats (surrounding area and the linear feature) that were characterized by their own composition and plant cover. We arranged two 100 m^2 (5.64 m radius) plots per micro-habitat. The plots in the surrounding area excluded vegetation within 10 m of the forest road right-of-way to avoid edge effects (Zhou et al., 2020). On the linear feature, plots were located on both sides of the camera at a distance of 10 m to avoid vegetation that was disturbed during camera placement. Each plot had 20 observation points that were systematically distributed around its periphery, i.e., at an angle of 18° between each observation point. For each point, the observer, with the help of a pole, positioned the detector device to capture the rotary self-levelling laser signal (Bosch GRL900–20HVK). Percentage lateral cover was calculated by counting the number of times the rotary laser signal was obstructed, divided by the total number of observation points in the plot. For each plot, we thus obtained three values of the lateral cover according to three measured heights. The mean for each height (50 cm, 100 cm and 150 cm) was calculated for each environment. Average lateral cover value of each height of the linear feature was subtracted from the surrounding area to obtain the difference in lateral cover between the two micro-habitats. Possible values for differences in lateral cover between the surroundings area and the linear feature were between −100% and 100% for each linear feature sampled. A positive value means that the linear feature was less obstructed than the surrounding area, while a

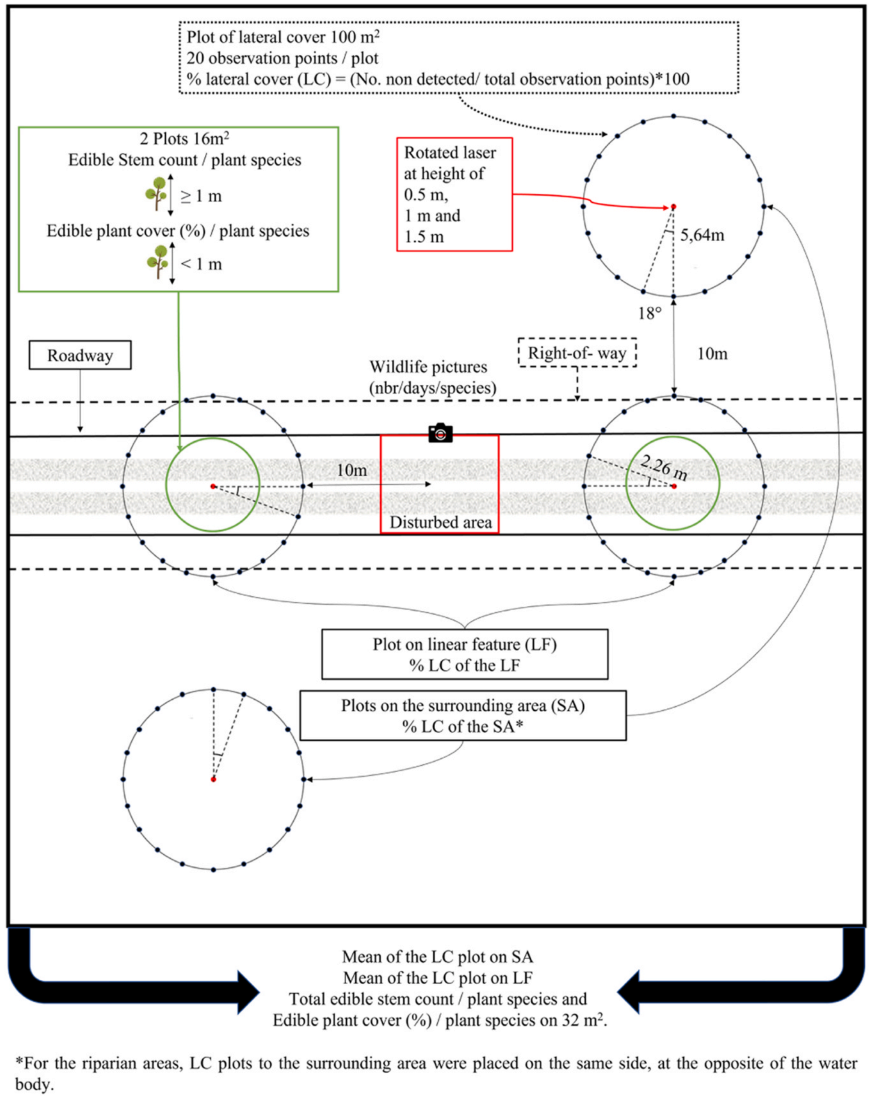

Fig. 2. Visual representation of each vegetation measurement in a single linear feature sampling in summer 2020 and 2021 in the caribou wildlife site south of Val-d'Or, Québec.

value of 0 means that there was no difference between the surrounding area and the linear feature; a negative value means that the linear feature was more obstructed than the surrounding area.

To test the effect of food quantity on linear features for bear and moose, we sampled two circular plots with a radius of 2.26 m (16 m^2) on the linear feature, within the lateral cover plots at a distance of 10 m from the camera location (St-Pierre et al., 2021; Fig. 2). This plots size was particularly justified on gravel roads. Our initial observations revealed a particularly uneven distribution of vegetation. Most of it was found on the edges, and our interpretation was that the use of 1 m^2 plots in the center of the road surface would have underestimated the amount of food < 1 m on the gravel roads (type 1 error). A count of the number of stems (≥1 m height) and an assessment of the percentage of plant cover (< 1 m) were made in this plot to quantify biomass substitute. We then counted and summed the total number of edible stems (Table A3) for bear and moose, as well as the average edible plant cover (Table A2) in both plots (32 m^2). For predators, habitat use may be strongly associated with the habitat use of their prey species (Fuller et al., 2003; Keim et al., 2011). The possible effect of respective prey number of uses on predators was a potentially favourable factor that affects their number of uses on the linear feature. The preys that were considered were snowshoe hare for Canada lynx, American beaver (Castor canadensis) and moose for gray wolf and black bear. From the prey events that were captured by the cameras, we then extracted the events of prey use on each of the linear features. For these same linear features, we also extracted the events of human activity to test whether human use causes species avoidance on the linear feature (Oberosler et al., 2017). Because the number of uses of a species depends upon the sampling effort of the cameras, we then divided the obtained events of each prey and human activity by the camera sampling effort (days) on each linear feature. The result gave a rate of use for snowshoe hare, beaver, moose and humans that was used for the analysis.

Landscape variables

Using ArcGIS Pro and MRNF data (5th Eco-forestry inventory of Southern Quebec), we extracted landscape variables that we assumed would be important for explaining mammal distribution (Table 1). On different radii (250 m, 500 m, 750 m and 1000 m) around each camera trap, we calculated the density of all forest road classes (km/km^2), and the percentage of the area of forests that were less than 20-years-old (harvested or not) compared to the total land area. In the case of lynx, the percentage of dense cover stands (cover density greater than 50%) was considered over the total productive area. Last, the distance to a higher-class forest gravel road (class 1 and 2) and the distance to nearest

Table 1
Variables and hypotheses related to gray wolf, Canada lynx, black bear, and moose that could explain the number of uses on linear features (gravel forest and winter roads, and riparian areas) in the caribou wildlife site south of Val-d′Or, Québec. The expected response for each species was represented by (+) for positive effect, (-) for a negative effect, (+/-) for varying effects and (NA) for non applicable covariate for that species.

Group variables	Variables	Short form	Species-specific effect	Hypothesis
Local	Difference in lateral cover between the surrounding area and the linear feature (%) at 50 cm for predator and 150 cm for moose	DifLateralCover	(+) Wolf (+) Lynx (+) Black bear (+) Moose	The difference in lateral cover between the surrounding area and the linear feature could reflect the number of uses. Number of uses increases with increasing difference in lateral cover (Abrahms et al., 2016).
	Count of edible stems (≥ 1 m) Edible plants (< 1 m) cover (%)	EdibleStems EdiblePlantCover	(NA) Wolf (NA) Lynx (+)Black bear (+) Moose	Availability of most digestible plants affect displacement patterns for Black bear (Mosnier et al., 2008). Moose preferentially forage in high productivity scrubland-early successional forests (Dussault et al., 2005; Crum et al., 2017).
	Rate of human use (count/sampling effort)	Human	(-) Wolf (-) Lynx (-) Black bear (-) Moose	For all species, local human activity can cause avoidance of linear features and their adjacent zones (Oberosler et al., 2017).
	Rate of prey use (count/sampling effort)	Prey (Moose, Beaver, Snowshoe hare)	(+) Wolf (+) Lynx (+)Black bear (NA) Moose	Predators such as wolf and lynx are positively related to prey density (Fuller, 1989; Fuller et al., 2003; Keim et al., 2011; King et al., 2020).
Landscape	Percentage of dense cover stands (more than 50% cover) in 1000 m radius	Densecoverstand	(NA) Wolf (+) Lynx (NA) Black bear (NA) Moose	Dense to closed-canopy stands are important components of lynx habitat in northern boreal forests (Poole et al., 1996).
	Percentage of regeneration stands (20 years) in 250 m radius	Regenaration-Stands	(+) Wolf (NA) Lynx (+) Black bear (+) Moose	Wolf selects regenerating stands based on its prey habitat preference (i.e., moose) (Houle et al., 2010). Black bear and moose select regenerating stands for forage opportunities (Brodeur et al., 2008; Mosnier et al., 2008).
	Density (km / km^2) of forest roads (all classes) in 250 m radius for *Alces* and 1000 m radius for wolf, black bear, and lynx	DensityRoad	(+/-) Wolf (+/-) Lynx (+/-) Black bear (-) Moose	Density of anthropogenic linear features can negatively affect lynx and wolf occupancy (Mech et al., 1988; Mladenoff et al., 1995; Marrotte et al., 2020) or positively improve movement and hunting (Thurber et al., 1994; Whittington et al., 2005; Fisher et Burton, 2018; Dickie et al., 2020). Bears use anthropogenic linear features to facilitate movement (Dickie et al., 2020) or perceive this type of landscape as a risk due to high level of human disturbance (Gould et al., 2019). Moose tend to avoid anthropogenic linear features (Laurian et al., 2008; Grosman et al., 2011; Beyer et al., 2013; Thomas, 2018).
	Distance (km) to a higher forest road class	NearRoad	(+/-) Wolf (-) Lynx (+) Black bear (-) Moose	Distance to a higher forest road class (1 and 2) has a positive spatial effect by promoting movement for wolf (McKenzie et al., 2012; St-Laurent and Gosselin, 2020). However, in regions with high levels of human activity, wolves tend to avoid anthropogenic disturbances (Lesmerises et al., 2012). Higher forest road classes may negatively affect lynx due to habitat loss, fragmentation and mortality risks (Bayne et al., 2008; Walpole et al., 2012). Black bears have a high tolerance of human activity, especially since anthropogenic linear features are often correlated with availability of high-quality food (Ladle et al., 2018). Disturbed areas with high human activity can be attractive to moose because these represent a refuge habitat from its predator (Rempel et al., 1997; Muhly et al., 2019).
	Distance (km) to nearest urban area	NearUrbanArea	(-) Wolf (-) Lynx (-) Black bear (+/-) Moose	The spatial urban area has an effect on density and space use of large mammal wildlife species (Berger, 2007; Bayne et al., 2008; Mcdonald et al., 2009; Muhly et al., 2011; Olsson et al., 2011).

urban area was calculated for each camera trap position.

Statistical analyses

Local and landscape characteristics of linear features

We compared local and landscape variables by linear feature type that did not differ between years (excluding species interaction variables). For this analysis, 32 gravel forest roads, 27 winter forest roads, and 19 riparian areas were selected. We used two-factor ANOVA according to the several heights (50 cm, 100 cm, 150 cm) of the difference in lateral cover, and the different radii (250 m, 500 m, 750 m, 1000 m) of the percentage of dense cover stand, percentage of regeneration stand and the density of forest road. For the variables quantifying food available on the linear feature for black bear and moose (count of edible stems $\geq$ 1 m and cover of edible plants $<$ 1 m) and the two distance variables (distance to higher forest road class and distance to nearest urban area), we used one-way ANOVA. For all of these ANOVA tests, Bonferroni adjustment ($P < 0.05/10 = 0.005$) for subsequent means comparison was applied. Only the lateral cover difference variable met normality and homoscedasticity assumptions; therefore, transformation was not required. The remaining variables required square-root transformation. Tukey's tests were performed for each variable to find whether the means differed between the three types of linear features.

Number of use models

Due to the long sampling duration (120 and 127 days/year), the large number of cameras deployed per year (76 and 66 cameras/year) and the study of common and highly detectable species, intensity models were more appropriate than occupancy models. In fact, the use of occupancy models for such a dataset proved useless since the probability of species occupancy on three type of linear feature was very high ($p = \sim 1$). The large number of detections for each species per habitat therefore justified the application of intensity models.

Prior to analysis, we removed linear feature samples with dysfunctional camera traps (loss by theft, destruction by bears, leaf movements) from the dataset (Hamel et al., 2013). We selected only those that performed the full tracking of linear features. In 2020 and 2021, respectively, we removed from the dataset 6 and 11 camera traps on gravel forest roads, 7 and 3 cameras on winter roads as well as 3 and 2 cameras on riparian areas. Note that data on the same linear feature, but collected in different years, were processed independently.

To determine the number of uses, calculations were based upon the number of use events, corrected by the number of days of monitoring at each site with a camera (offset). To avoid multiple events of the same individual passing and returning to the detection field of the camera traps on the same station, we specified a time interval of 10 minutes as a criterion for independence between 2 events of the same species at the same site (Keim et al., 2019). We used generalized linear mixed-effects model (GLMM) with Poisson distribution to calculate the number of uses of a species for the entire snow-free period. To do this, use-events for each species were employed as a response variable. This type of model then considered site variables that are specific to each species, and random variables that could affect the number of uses of gray wolves, black bears, Canada lynx and moose. To do so, all numerical variables were standardized prior to analysis. First, for fixed effects, we included the factor *year* in all models to control its effect. Second, for some fixed effect variables, a variable reduction filter was necessarily applied due to the presence of correlations among some variables. This was the case for the different measurements of lateral cover at 50 cm, 100 cm, and 150 cm above the ground surface, and for calculations of the density of forest roads (DR), the percentage of dense cover forest (DS) and the percentage of regenerating forest (RS) along different radii (250 m, 500 m, 750 m, 1000 m) extending from camera trap locations. We employed the Akaike Information Criterion (AIC; (Burnham and Anderson, 2002), for model comparisons for each previous variable that was taken at different scales allowed for the selection of the most parsimonious one for each species (Leblond et al., 2011). The fixed-effect variables that were selected for further analysis are presented in Table 1. The graphic tool developed by Schloerke et al. (2018) for fixed-effect variables found a strong correlation in lynx between distances to a higher forest road class and the percentage of dense forest cover ($r > 0.6$). To overcome this problem, we retained only the most parsimonious one between these two variables (Leblond et al., 2011), selecting the percentage of dense forest cover. Note that for the moose model, the distance to nearest urban area could not be included because it led to estimation problems. For random effects, we included the database ID of the linear feature as a random effect in each model to account for the effect caused by the two repeated annual measurements on the linear features.

Since the effects of some local and landscape variables were strongly influenced by the type of linear features, separating the number of use models into groups for all species was more appropriate. This meant that the first group of models considered only the local and landscape variables in the fixed effects, which considers the biological aspects of the species. The effect of linear feature type was excluded from the averaging of the first group so that the model would predict local and landscape variables only. The second group and third group of models were relevant from a management perspective. The second group was used to predict and compare the number of uses and types of linear features. Therefore, we included only the type of linear features (gravel forest roads, winter forest roads and riparian areas) as fixed effects. Last, for each species, a third group of models compared the best models of the first two groups to determine whether the type of linear feature is sufficient to identify restoration priorities.

We used R package *lme4* (version 1.1–29) to construct the models (Bates et al., 2011). For the first group, we generated a global model and models with a single fixed-effect variable, for each species and their respective variables. The second group considered only the linear feature type as the fixed effect, while the third group compared the best models by species from the first two groups. All groups of models were compared to a null model. The goodness-of-fit of the global model for each group was performed following Mazerolle (2020). This test showed for the first group of models that the global lynx model fitted the observed data (c-hat = 0.99). However, we detected a slight under-dispersion for the wolf, bear and moose global models (c-hat < 1). For the global species models, the prediction resulted of 1000 simulations with 95% prediction interval shows good representation of the data (Fig. A1). The pseudo-R-square for Generalized Mixed-Effect models was then calculated for all models in comparison to their null models. For each species, we used model selection and multi-model inference based upon AIC; Burnham and Anderson, 2002), applying the *AICcmodavg* package (Mazerolle, 2020) to the first and second groups of models. With the *Shrinkage* estimator function, we assessed the presence or absence of effects for local and landscape variables under all models. Prediction of the number of uses on the snow-free season was calculated with the *modavgPred* function of (Mazerolle, 2020).

To determine whether there was spatial bias in the use data for the four species of interest, we performed neighbourhood analysis per year with the geographic coordinate locations of the camera traps (Bivand et al., 2013). To build the neighbourhood list, the function *Graph-based spatial weights* was used with the Gabriel graph method. To add spatial dependence in the generalized mixed-effect models, we used the *fitme* function of the package *spam* (Rousset, 2023). Moran's test was performed only for the complete model of each species, showing that the location of the camera traps was not correlated respectively with the number of uses of wolves (P-value 2020–2021 = 0.89 – 0.92), lynx (P-value 2020–2021 = 0.28 – 0.68), or moose (P-value 2020–2021 = 0.70 – 0.43). Therefore, in the presence of only one incidence of spatial bias for black bear (P-value 2020–2021 = 0.01 – 0.39) in 2020 that was related to camera trap locations in the study area, we did not include spatial location of the camera trap in the further analysis of number of use models.

All statistical analyses were performed in R version 4.0.2 (R Core Team, 2020). For all statistical analyses, we considered the results to be significant at a threshold value of $P = 0.05$.

Results

Characteristics of local and landscape variables of linear feature

Local variables

The summary results of the difference in lateral cover showed a mean discrepancy in paired samples of 16% for the surrounding area and 14% for the linear feature. We attributed this difference to the variability of the vegetation community, which determined the difference in lateral cover among sampling units. This small difference in lateral cover between the plots on roads and those in forests suggested that the plant community was relatively homogeneous.

The difference in lateral cover (Fig. 3, Table A4) showed significant difference in linear feature type (F-value = 26.806; $D_f = 2$; $P < 0.001$) among level of heights of lateral cover measured (F-value = 3.967; $D_f = 4$; $P = 0.004$). The difference in lateral cover between gravel forest roads and the two other linear features was larger at 50 cm and decreased as height increased. At 50 cm, 100 cm and 150 cm above the ground, we obtained respective differences of 38%, 18% and 8% between gravel forest roads and winter forest roads. Between gravel forest roads and riparian areas, the difference was 35%, 18% and 11%, respectively. The interaction indicates that the difference in lateral cover on the inside *vs.* outside of gravel roads differed by height stratum, but this pattern was not apparently present for the other two linear features (Fig. 3). The difference in lateral cover was consistent between winter forest roads and riparian areas, regardless of height. These two linear features were very close to 0%, signifying the absence of cover differences between the surrounding area and the linear feature. On gravel forest roads, especially at 50 cm and 100 cm above the ground, the mean difference was 36% and 22%, respectively. Lateral cover was significantly lower on gravel forest roads compared to the surrounding areas.

Regarding the two variables representing the food that was available to black bear and moose, only the proportion of edible plant cover (plants < 1 m) for black bear (F-value =16.97; $D_f = 2$; $P < 0.001$) was different among the three types of linear features. For bear, there was respectively 17% and 18% less edible plant cover on gravel forest roads than on winter forest roads and riparian areas (Table A4).

Landscape variables

The landscape variables around the camera trap locations are presented in Fig. 4 and Table A5 according to the type of linear features. The proportion of regenerating stands (20-year age class) differed between the three types of linear features (*F*-value = 35.32; $D_f = 2$; $P < 0.001$). On average, 16% and 13% less regenerating stands were found around winter forest roads than around gravel forest roads and riparian areas respectively (Fig. 4F). For the proportion of dense cover stands, this variable differed between types of linear features (*F*-value = 12.9; $D_f = 2$; $P < 0.001$) with subsequent comparisons differentiating winter forest roads from the two other linear features (Fig. 4G). On average, we observed more dense cover stands around winter forest roads than around gravel forest roads (13% less) and riparian areas (16% less). Forest road density (km / km^2) differed according to the type of linear features (*F*-value = 81.1; $D_f = 2$; $P < 0.001$) and among the different radii that were measured (*F*-value = 12.4; $D_f = 3$; $P < 0.001$). Furthermore, interaction existed between the type of linear feature and radii that were selected (*F*-value = 13.28; $D_f = 4$; $P < 0.001$), resulting in a negative relationship for gravel and winter forest roads, whereas the relationship was positive for riparian areas. At 250 m and 500 m from the camera locations, the difference in density was greatest between riparian areas and the two other linear features. At these radii, on average, the density of forest roads was lower around riparian areas compared to winter forest roads (2.84 km/km^2 *versus* 1.45 km/km^2 higher, respectively) and gravel forest roads (2.36 km/km^2 and 0.8 km/km^2 higher, respectively). At an average of 750 m, the distinction was only present between winter forest roads and the riparian areas. At this distance, the density of all forest road classes around the camera trap locations on winter forest roads was higher than for riparian areas (0.97 km/km^2 less) and around gravel forest roads (0.33 km/km^2 less). At a radius of 1000 m, no difference was observed between the three types of linear features. Overall, only by type of linear feature, the density of forest roads was 2.76 km/km^2 on winter forest roads, 2.12 km/km^2 on gravel forest roads and 1.2 km/km^2 around riparian areas (Fig. 4H). For the distance to a higher forest road class, this variable differed among the three types of linear features (*F*-value = 17.76; $D_f = 2$; $P < 0.001$). We obtained average distances to the camera traps that were respectively 6.38 km, 4.93 km and 1.75 km for riparian areas, gravel forest roads and winter forest roads (Fig. 4I).

Number of uses

For 5589 sampling days in 2020 and 7906 days in 2021, the cameras detected 21 mammal species on all linear features combined. Those that were most common were, in descending order of total detections, snowshoe hare, red fox, human, Canada lynx, red squirrel, moose, American beaver, black bear and gray wolf (Table A1). For all species of interest and models, results of model selection and the marginal and conditional R-square values for the three groups of models are presented in Tables 2, 3 and 4.

The first group of models considered the local and landscape variables for each species, the effect of year and a random effect of the identifier of the linear features (Table 2, Table A6). At the level of local variables, we observed a positive effect of the difference in lateral cover between the surrounding area and the linear feature with respect to the number of uses by all predators during the snow-free season (Table 5, Fig. 5). Note that the measured height of the most parsimonious lateral cover difference was 50 cm for predators and 150 cm for moose. The number of uses by gray wolf and Canada lynx was positively associated with the number of uses by their prey species (Table 5, Fig. 6A, Fig. 6B). The number of human activity variables did not influence the number of uses of any of the species that were investigated. No effect was found on the two variables quantifying food quantity on linear features for black bear or moose. For landscape variables, the number of Canada lynx uses seemed to increase marginally as the percentage of dense cover stands increases near the linear feature (Table 5, Fig. 6C). We found no evidence that the percentage of regenerating stands within 250 m affected the number of uses for wolf, bear and moose (Table 5). None of the four species responded to the forest road density within a radius of 1000 m (Table 5). Furthermore, we observed that distance to a higher forest road class (Table 5, Fig. 6D) and distance to the nearest urban area (Table 5, Fig. 6E) respectively had positive and negative effects on the number of uses for gray wolf.

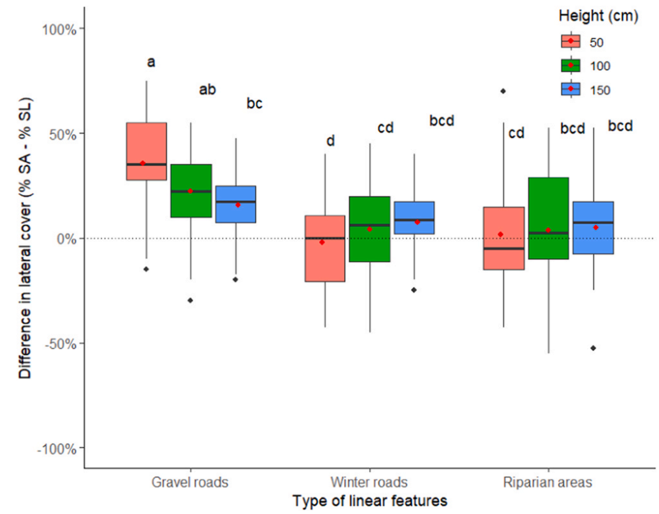

Fig. 3. Distribution of differences in lateral cover between the surrounding area (SA) and the linear feature (LF) measured at 50 cm (red boxplots), 100 cm (green boxplots) and 150 cm (blue boxplots) above the ground for 33 gravel forest roads, 29 winter forest roads, and 18 riparian areas in western Quebec, Canada. Mean values are red dots on the box-and-whisker plots. The dotted horizontal line represents the absence of difference (zero difference) between the SA and LF. Positive values mean that the LF has lower cover than the SA, while negative values mean that the LF has greater cover than the SA. The comparisons were conducted with two-way ANOVA without transformation. Letters indicate significant differences between linear features and their respective heights, with a > b > c > d (pairwise Tukey tests).

The results of the second group of models considering only the fixed effects of linear feature type and year, together with the random effect of linear feature (Table 3), are presented in Fig. 7. For each species, number of uses over a period of 100 days during snow-free season was always significantly higher on gravel roads than on the two other linear features (winter roads and riparian areas). Mean predictions of the number of wolves uses on gravel forest roads were 2.1 and almost no use respectively on the two other linear features (0.3 on winter roads and 0.2 on riparian areas). For black bears, there were 3.1 uses on gravel roads, 1.1 on winter roads and 1.7 on the riparian areas. For Canada lynx, its use was 8.5 on gravel roads, 1.9 on winter roads and 1.7 on riparian areas. No significant difference was evident between winter roads and riparian areas for predators, except for black bear, where a slightly higher number of uses were observed for riparian areas. For moose, the number of uses differed among types of linear features, with a value for riparian areas that was lower than that for the two other types. There were 4.4 uses by moose uses on gravel roads, 2.7 uses on winter roads and only 1 use on riparian areas.

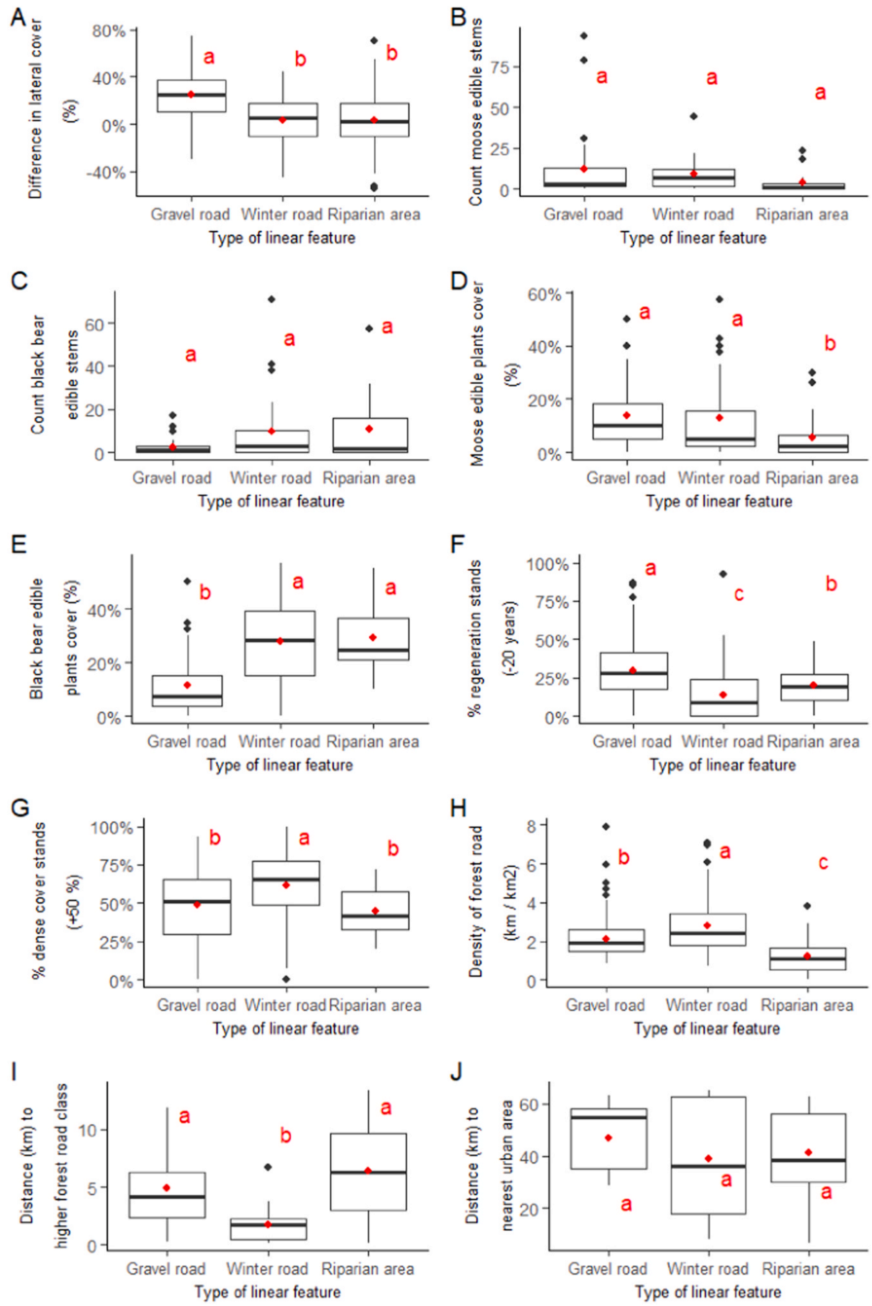

Fig. 4. Distribution of local and landscape variables for 33 gravel forest roads, 29 winter forest roads and 18 riparian areas in western Quebec, Canada. The comparisons were conducted using one-way ANOVA for all variables with square-root-transformation. Mean values are red dots on the boxplots. Red letters indicate significant differences between linear features, with a > b > c > d (Tukey tests).

The third group of models that compared the two best models of the first two groups of models are presented in Table 4. For moose, the model with the type of linear feature only in the fixed effects was more parsimonious than the global model considering all local landscape variables. For black bears, the model with the difference in lateral cover in the fixed effects was a little more parsimonious than the one considering the effect of linear feature type. For both carnivores, their respective global models were much more parsimonious than the ones considering only the type of linear feature.

Discussion

We investigated how local and landscape variables affect the use of linear features by gray wolves, black bears, and Canada lynx. Our findings revealed that their use was primarily explained by local variables. Specifically, our results supported the hypothesis of a positive effect of important local explanatory variables, including the difference in lateral cover between the surrounding area and the linear feature for these predators, as well as the presence of prey species for gray wolves (moose) and Canada lynx (snowshoe hare). Contrary to what we expected, we did not find evidence to support the hypothesis that the rate of human activity leads to linear feature avoidance by all species. Furthermore, while we expected a favourable effect of the quantity of food on linear features upon the number of uses by black bears and moose, our results did not show any evidence of such effect, preventing us from confirming this hypothesis.

Table 2
Model selection based on the Akaike Information Criterion (AIC) explaining the number of uses of linear features (gravel forest roads, winter forest roads and riparian areas) according to linear feature characteristics (first group of models) by gray wolf, black bear, Canada lynx and moose in the caribou wildlife site south of Val-d′Or, western Québec, Canada, in 2020 and 2021. The models for each species were compared to a null model. Only the two best models of each species are represented with respective Akaike weights (ω_i), log likelihood (LL), the number of estimated parameters (K), the marginal (R^2M) and conditional R-square (R^2C).

Models	LL	K	AIC	ΔAIC	ω_i	R^2M	R^2C
Gray wolf ~							
DifLateralCover50cm + Human + Moose + Beaver + RegenerationStands250m + DenstyRoad1000m + NearRoad+ NearUrbanArea + Year + (1|LinearFeatureID)	-224.70	11	473.59	0.00	0.97	0.51	0.94
DifLateralCover50cm + Year + (1|LinearFeatureID)	-236.19	4	480.69	7.09	0.03	0.33	0.94
Null + Year + (1|LinearFeatureID)	-249.14	3	504.47	30.87	0.00	0.009	0.94
Black bear ~							
DifLateralCover50cm + Year + (1|LinearFeatureID)	-275.60	4	559.51	0.00	0.77	0.16	0.45
DifLateralCover50cm + EdibleStems + EdiblePlantsCover + Human + Moose + Beaver + RegenerationStandS250m + DensityRoad1000m + NearRoad + NearUrbanArea + Year + (1|LinearFeatureID)	-266.48	13	562.04	2.53	0.22	0.26	0.45
Null + Year + (1|LinearFeatureID)	-285.61	3	577.41	17.90	0.00	0.03	0.47
Canada lynx ~							
DifLateralCover50cm + Human + SnowshoeHare + DenseCoverStands1000m + DensityRoad1000m + NearUrbanArea + Year + (1|LinearFeatureID)	-355.65	9	730.78	0.00	0.99	0.40	0.75
DifLateralCover50cm + Year + (1|LinearFeatureID)	-365.86	4	740.04	9.26	0.01	0.32	0.76
Null + Year + (1|LinearFeatureID)	-383.33	3	772.85	42.08	0.00	0.0004	0.78
Moose ~							
DifLateralCover150cm + EdibleStems + EdiblePlantsCover + Human + RegenerationStands250m + DensityRoads250m + NearRoad + Year + (1|LinearFeatureID)	-303.12	10	628.06	0.00	0.47	0.15	0.50
DifLateralCover150cm + Year + (1|LinearFeatureID)	-310.76	4	629.84	1.77	0.19	0.06	0.47
Null + Year + (1|LinearFeatureID)	-314.19	4	636.69	8.62	0.01	0.00005	0.47

Table 3
Model selection based on the Akaike Information Criterion (AIC) explaining the number of uses of linear features (gravel forest roads, winter forest roads and riparian areas) according to type of linear features (second group of models) by gray wolf, black bear, Canada lynx and moose in the caribou wildlife site south of Val-d′Or, western Quebec, Canada in 2020 and 2021. The models for each species were compared to a null model. All models are represented with respective Akaike weights (ωi), log likelihood (LL), the number of estimated parameters (K), the marginal (R^2M) and conditional (R^2C) R-square.

Models	LL	K	AIC	ΔAIC	ω_i	R^2M	R^2C
Gray wolf ~							
TypeLinearFeature + Year + (1| LinearFeatureID)	-236.82	5	484.11	0.00	1.00	0.32	0.94
Null + Year + (1| LinearFeatureID)	-249.14		504.47	20.36	0.00	0.001	0.002
Black bear ~							
TypeLinearFeature + Year + (1| LinearFeatureID)	-274.66	5	559.79	0.00	1.00	0.17	0.45
Null + Year + (1| LinearFeatureID)	-285.61	3	577.41	17.61	0.00	0.0001	0.0003
Canada lynx ~							
TypeLinearFeature + Year + (1| LinearFeatureID)	-369.84	5	750.16	0.00	1.00	0.25	0.77
Null + Year + (1| LinearFeatureID)	-383.33	3	772.85	22.7	0.00	0.004	0.01
Moose ~							
TypeLinearFeature + Year + (1| LineraFeatureID)	-303.08	5	616.64	0.00	1.00	0.17	0.49
Null + Year + (1| LinearFeatureID)	-314.23	3	634.65	18.01	0.00	0.0005	0.002

Local and landscape explanatory variables

Regarding the explanatory variables which were common to the three predators, our results showed that the number of uses during the snow-free season on linear features increased positively with the difference in the lateral cover between the surrounding area and the linear feature. While the type of linear feature possibly introduced a confounding effect, our results suggest that positive values of this variable, indicating less dense vegetation cover and lower energy costs on the linear feature, were associated to increased use by gray wolves, black bears, and Canada lynx. Linear features with these conditions therefore canalize predator paths, ultimately favouring their movements in the habitat and potentially contribute increased hunting opportunities (Abrahms et al., 2016; Dickie et al., 2017; Latham et al., 2011b). Furthermore, gray wolves and Canada lynx exhibited distinct patterns in their use of linear features based on lateral cover differences. Canada lynx, with its ambush hunting behaviour, seemed to use linear features as soon as the difference in lateral cover was positive (> 0%; Maletzke et al., 2008). In contrast, wolves that are known to travel long distances in packs to hunt prey and maintain their territory (Mech and Boitani, 2010), showed a tendency to use linear features with strongly positive values (towards 75%) of lateral cover difference. It is also noteworthy that the higher number of uses of Canada lynx compared to wolf was probably related to its higher population density in the study area (Royle et Dorazio., 2008).

Unlike gray wolves and Canada lynx, black bears, an opportunistic and omnivorous species (Basille et al., 2011), exhibited a greater variability in their use of linear features based on the difference in lateral cover. Given that this species has a largely plant-based diet, this variability may be attributed to a less pronounced selection of its environment compared to grey wolves and Canada lynx (Latham et al., 2011a). Bears may spend less time than these two carnivores on linear features that are suitable for travel. It is suggested that black bears use, to a lesser extent, linear features with a high lateral cover difference as an efficient means of moving to their food plots rather than foraging on them (Mosnier et al., 2008). This was supported in our study by the lack of a positive effect between the amount of food available and the bear number of uses in linear features. Another interesting fact was that the three predators seemed to favor linear features with a difference in lateral cover at 50 cm above the ground surface, where vegetation is sparse, for increased efficiency in movement and vision for hunting.

Finally, the number of uses of the respective prey species of wolf (moose) and Canada lynx (snowshoe hare) on linear features, was a dominant factor explaining the number of uses of their predator, consistent with our hypotheses. In line with prior research, our results indicate that predators select resources based on the presence of their

Table 4
Model selection based on the Akaike Information Criterion (AIC) of the two best models (third group of models) explaining the number of uses of linear features (gravel forest roads, winter forest roads and riparian areas) by gray wolf, black bear, Canada lynx and moose in the caribou wildlife site south of Val-d'Or, western Quebec, Canada in 2020 and 2021. The models for each species were compared to a null model. All models are represented with respective Akaike weights (ωi), log likelihood (LL), the number of estimated parameters (K), the marginal (R^2M) and conditional R-square (R^2C).

Models	LL	K	AIC	ΔAIC	ω_i	R^2M	R^2C
Gray wolf ~							
DifLateralCover50cm + Human + Moose + Beaver + RegenerationStands250m + DenstyRoad1000m + NearRoad+ NearUrbanArea + Year + (1|LinearFeatureID)	-224.70	11	473.59	0.00	0.99	0.51	0.94
TypeLinearFeature + Year + (1| LinearFeatureID)	-236.82	5	484.11	0.00	1.00	0.32	0.94
Null + Year + (1| LinearFeatureID)	-249.14	3	504.47	20.36	0.00	0.001	0.002
Black bear ~							
DifLateralCover50cm + Year + (1|LinearFeatureID)	-275.60	4	559.51	0.00	0.54	0.17	0.45
TypeLinearFeature + Year + (1| LinearFeatureID)	-274.66	5	559.79	0.29	1.00	0.17	0.45
Null + Year + (1| LinearFeatureID)	-285.61	3	577.41	17.90	0.00	0.0001	0.0003
Canada lynx ~							
DifLateralCover50cm + Human + SnowshoeHare + DenseCoverStands1000m + DensityRoad1000m + NearUrbanArea + Year + (1|LinearFeatureID)	-355.65	9	730.78	0.00	1.00	0.40	0.75
TypeLinearFeature + Year + (1| LinearFeatureID)	-369.84	5	750.16	19.38	0.00	0.25	0.77
Null + Year + (1| LinearFeatureID)	-383.33	3	772.85	42.08	0.00	0.004	0.01
Moose ~							
TypeLinearFeature + Year + (1| LineraFeatureID)	-303.08	5	616.64	0.00	1.00	0.17	0.49
DifLateralCover150cm + EdibleStems + EdiblePlantsCover + Human + RegenerationStands250m + DensityRoads250m+ NearRoad + Year + (1|LinearFeatureID)	-303.12	10	628.06	11.42	0	0.15	0.49
Null + Year + (1| LinearFeatureID)	-314.23	3	634.65	18.01	0	0.0005	0.002

preferred prey species rather than the quality of the prey species habitat (Keim et al. 2011; Fuller et al. 2003). Furthermore, the avoidance of higher forest road classes (1 and 2) was only observed for wolves, in line with Lesmerises et al. (2013). The presence of a relative high level of vehicle traffic on such large linear features was likely associated with a high risk of mortality. Surprisingly, the assumption that proximity to urban areas negatively affects large mammals was not supported. On the contrary, gray wolf activity was slightly higher near urban areas. It is difficult to interpret this result with such a small effect or with no effect for the other three species. Indeed, Lesmerises et al. (2013) demonstrated the wolf aversion to human disturbance when human activity is high. Our study area encompassed the Caribou Val-d'Or Biodiversity Reserve, which covers an area of 434.2 km^2, and is located less than 20 km southeast of the urban area of Val-d'Or, perhaps a factor that can mitigates the impact of Val-d'Or urban community on wolves. Also, located 5 km east of Val-d'Or, a landfill serves as a potential food source that could probably contribute to the observed result.

Type of linear feature

Comparing the number of uses by mammal predators and prey across different types of linear features is highly relevant for forest management. Our results supported the hypothesis that there was no significant distinction in predators use between winter roads and riparian areas, and that the number of uses on gravel roads for all species were significantly higher compared to the other two linear features. Thus, it appeared that wolves, bears, lynx and moose can differentiated gravel roads from the other two linear features. However, this was probably affected by the relationship between varying levels of lateral cover and the type of linear features mentioned earlier. These values tended to be

Table 5
Shrinkage version of model-averaged estimates explaining the number of uses during the snow-free season according to the characteristics (first group of models) of linear features (gravel forest roads, winter forest roads and riparian areas) by gray wolf, black bear, Canada lynx and moose in the caribou wildlife site south of Val-d'Or, western Québec, Canada, in 2020 and 2021. Estimates, unconditional standard error, and unconditional confidence interval of fixed-effect explanatory variables on the number of uses (λ) are presented, together with their 95% confidence intervals. All candidate models were used to estimate the effects of each parameter.

Parameters **Gray wolf**	Estimate	SE	Lower limit	Upper limit	Parameters **Canada Lynx**	Estimate	SE	Lower limit	Upper limit
DifLateralCover50cm	0.85	0.2	0.46	1.25	DifLateralCover50cm	0.78	0.12	0.55	1.02
Human	0.03	0.01	-0.16	0.22	Human	0.01	0.05	-0.09	0.11
Moose	0.29	0.13	0.04	0.54	SnowshoeHare	0.17	0.05	0.06	0.27
Beaver	0.04	0.11	-0.17	0.26	DenseCoverStands1000m	0.25	0.13	0.00	0.51
RegenarationStands250m	0.24	0.21	-0.17	0.65	DensityRoad1000m	-0.18	0.13	-0.43	0.07
DensityRoad1000m	0.17	0.22	-0.26	0.60	NearUrbanArea	-0.14	0.13	-0.39	0.11
NearRoad	0.54	0.23	0.09	0.98					
NearUrbanArea	-0.60	0.23	-1.06	-0.15					
Black bear					**Moose**				
DifLateralCover50cm	0.39	0.11	0.17	0.61	DifLateralCover150cm	0.18	0.17	-0.15	0.51
EdibleStems	-0.04	0.09	-0.21	0.14	EdibleStems	0.01	0.08	-0.14	0.16
EdiblePlantCover	-0.02	0.06	-0.14	0.09	EdiblePlantsCover	0.09	0.21	-0.14	0.31
Human	-0.03	0.07	-0.16	0.11	Human	-0.15	0.17	-0.47	0.18
Moose	0.02	0.05	-0.08	0.11	RegenerationStands250m	0.15	0.16	-0.16	0.45
Beaver	0.01	0.04	-0.06	0.09	DensityRoad250m	0.08	0.13	-0.18	0.35
RegenerationStands250m	0.01	0.05	-0.09	0.12	NearRoad	-0.02	0.10	-0.22	0.17
DensityRoad1000m	-0.01	0.05	-0.11	0.09					
NearRoad	0.05	0.10	-0.15	0.25					
NearUrbanArea	-0.01	0.05	-0.11	0.09					

frequently higher on gravel forest roads than on the two other linear features. Therefore, while predator number of uses was higher on gravel roads, this could be attributed the lower lateral cover on these forest roads ass compared to the surrounding areas rather than a clear preference for this type of linear feature. To summarize, our findings suggest that the level of predator use may be linked with the specific characteristics of gravel roads on one hand, and winter roads grouped with riparian areas on the other, highlighting the complexity of predator behavior in these habitats.

In addition to the lateral cover observed on gravel road, it also appeared that the use of prey (moose for wolf, and snowshoe hares for Canada lynx) is more pronounced on this linear feature compared to winter roads and riparian areas. The presence of these two important explanatory local variables on gravel roads largely explained the strong difference in the number of uses of the three predators (especially Canada lynx) compared to the two other linear features. Given that they are a persistent disturbance in the landscape, gravel roads lack vegetation cover on the road surface, making it challenging for plants to colonize and persist in this compacted soil (St-Pierre et al., 2021) where maintenance activities are carried out on a regular basis. Gravel roads, with fewer barriers to animal movement, represented an efficient and sustainable corridor in both space and time for large mammals.

Winter roads, in contrast, had similar values of difference in lateral cover with respect to riparian areas, with values close to 0 indicating little difference between the linear feature and its surrounding area. Indeed, this aligns well with lower predator numbers of uses compared to gravel roads, but similar levels to riparian areas. This result is probably explained by the fact that winter roads were generally heavily revegetated. Indeed, the lack of land-shaping on winter roads allowed vegetation to quickly recolonize after its construction (Girardin et al., 2022; Braham et al., 2023). After a few years, the lateral cover on winter roads may closely resembled that of surrounding forest, making it less conducive for movement within the landscape. It should be noted that our selection of winter roads were less connected lower-class logging roads (3 and 4) than higher forest road classes (1 and 2) in our study area, potentially explaining the reduced use of winter roads by wolves.

While the patterns of predator use were similar in riparian areas and winter roads, riparian areas exhibited a lower number of uses for moose. Possibly, the small differences in lateral cover between the surrounding area, may explain the low number of uses by carnivores. While several studies have highlighted the riparian area as frequently used by predators during the summer season (Latham, 2009; Mech and Boitani, 2010; Latham et al., 2011b; Kittle et al., 2017), our findings align with those of Newton et al. (2017), indicating that gray wolves tend to select forest roads over natural linear features in a compensatory manner. Similarly, Dickie et al. (2020) observed for wolves and bears, as did Terwilliger and Moen (2012) for lynx, that these three predators responded less to natural linear features in the presence of anthropogenic linear features in the landscape. Our study supported these observations, as we found that gravel roads offered better conditions in terms of lateral cover compared to the other two linear features. Habitat use by these species seemed to shift towards gravel roads within the forest landscape, rather than natural linear features, such as riparian area surrounding large water bodies, during the snow-free season.

To facilitate management while upholding restoration and conservation goals, predicting the number of uses for each species with only the specific type of linear features proved to be extremely relevant. Yet, the comparison of the best model (biological factors versus type of linear

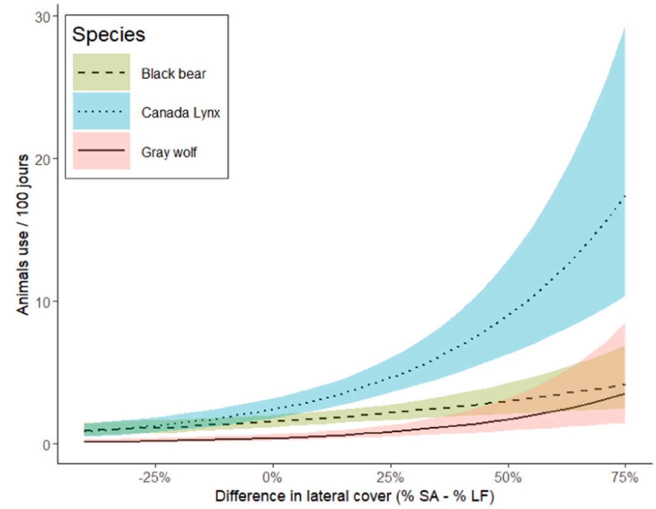

Fig. 5. Model-averaged predicted number of uses over a period of 100 days during snow-free season of a linear feature by gray wolf, black bear, Canada lynx and moose based on the sequence of observed values of the difference in lateral cover between the surrounding area (SA) and the linear feature (LF), and the average value of all other variables. Data that were collected from 27 to 22 gravel forest roads, 24–27 winter forest roads and 16–17 riparian areas in 2020–2021, respectively, were sampled in the caribou wildlife site south of Val-d'Or, western Quebec, Canada. Colour shading denotes 95% prediction intervals about the estimates for predators.

feature) revealed that relying on the type of linear features was adequate only for identifying priorities in forest road restoration for moose, and potentially for black bear. On the other hand, for gray wolves, black bears and Canada lynx, the biological models incorporating local and landscape variables were more representative of their use during the snow-free season and can eventually offer a more precise identifications of roads that promote the functional response of these three boreal predators.

Our study presented some limitations. Firstly, we focused on predicting the number of uses while holding all other factors constant. We had therefore selected common variables within the linear features that under investigation. Thus, some explanatory variables specific to anthropogenic linear features were not included in our model, given our interest in studying riparian areas. For studying exclusively anthropogenic linear features, it would be relevant to analyze the variables proposed by Braham et al. (2023), such as width and years-post construction. Furthermore, we were restricted to habitats highly impacted by forestry activities, particularly those heavily disturbed by gravel roads due to spatial constraints. Regarding to vegetation sampling, a larger number of small, well-distributed plots on the road surface to quantify the amount of plant < 1 m would have minimized misinterpretations of plant structure. Also, adding a third replicate per micro-habitat to quantify differences in lateral cover of linear features would have allowed us a more precise identification of biologically relevant cover differences. The methodology associated with the use of camera traps may have influenced our results in some extent, in favouring the detection of species that use linear features as movement corridors. However, the wolf was the most difficult species to detect, due to its movement speed and wariness (Burton et al., 2015).

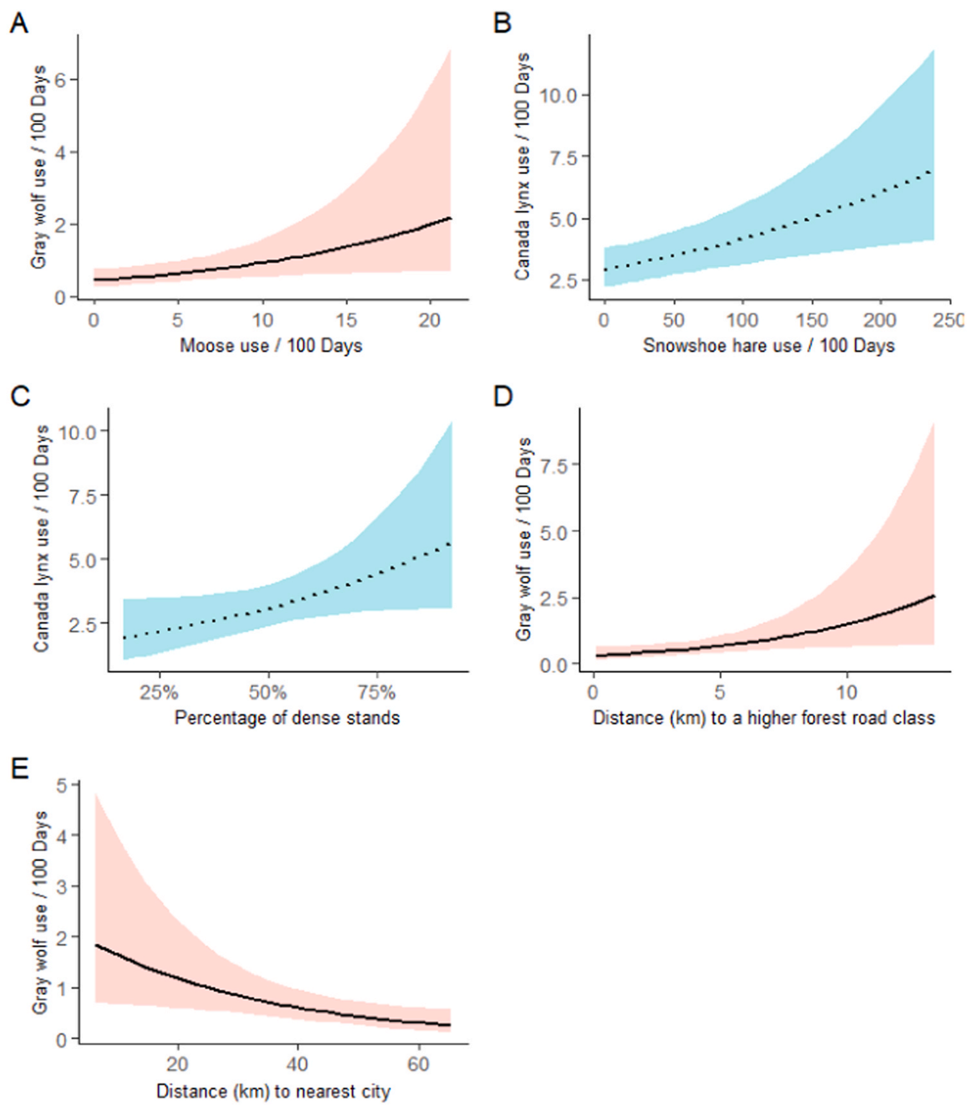

Fig. 6. Model-averaged predicted number of uses over a period of 100 days during snow-free season by gray wolf (solid line) and Canada lynx (dotted line) based upon the sequence of observed values of moose use (panel A), snowshoe hare use (panel B), percentage of dense stands (% 50 – 100%) in 1000 m radius (panel C), distance (km) to a higher forest road class (panel D) and the distance (km) to nearest urban area (panel E) and the average value of all other variables. Data that were collected from 27 to 22 gravel forest roads, 24–27 winter forest roads and 16–17 riparian areas in 2020–2021, respectively, were sampled in the caribou wildlife site south of Val-d'Or, western Quebec, Canada. Colour shading denotes the 95% prediction interval around estimates for gray wolf and Canada lynx.

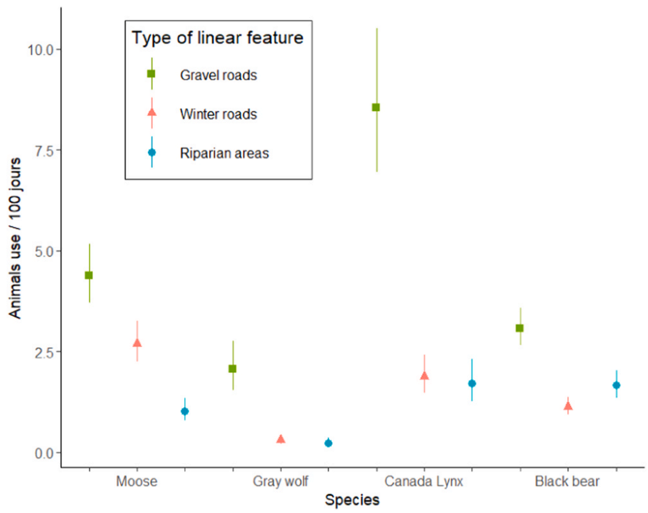

Fig. 7. Model-averaged predicted number of uses over a period of 100 days during the snow-free season by caribou predators (gray wolf, black bear and Canada lynx) and the apparent competitor (moose). Data that were collected on 27–22 gravel forest roads, 24–27 winter forest roads and 16–17 riparian areas in 2020–2021, respectively, were sampled in the caribou wildlife site south of Val-d'Or, western Quebec, Canada. Error bars denote 95% confidence intervals about the estimates.

Conclusions

Our findings are of paramount importance in managed areas to understand how the causes of the decline of boreal caribou can be linked to an increase in predation by wolves and bears associated with forest roads in managed boreal forests. Gray wolf and Canada lynx were influenced by the presence of their prey species and were slightly affected by landscape variables, but difference in lateral cover was an extremely informative variable in the context of forest management. This is particularly important, as these data enabled us to predict the number of predators uses more accurately than if we only used the linear feature type as information. Future investigations could use this data in relation to very high-resolution remote sensing to potentially extract this vegetation structure on a larger scale and more rapidly. Reducing the number of linear features with low lateral cover relative to the surrounding area, especially gravel forest roads, could reduce the ability of predators to locate and move through caribou habitat. This reduction could potentially reduce the likelihood of co-occurrence, which should help reduce the risk of predation on caribou. Forest road planning process thus needs to be improved to favour less gravel forest road density and prone restoration activities. Closing or re-vegetating gravel roads with an effective short-term treatment (Lacerte et al., 2021) can potentially decrease gray wolf, black bear, Canada lynx and moose use on this type of anthropogenic linear feature. Long-term research of restoration activities (closures, barriers, and revegetation) on gravel and winter roads is required to estimate effectiveness of these treatments and to see whether changes in the functional response of predators emerge in such restored habitats.

Declaration of Competing Interest

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

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CRediT authorship contribution statement

Arnaud Benoit-Pépin: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Mariano Javier Feldman:** Writing – review & editing, Validation, Methodology, Investigation. **Louis Imbeau:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Osvaldo Valeria:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

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.

Data Availability

Data will be made available on request.

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Appendix

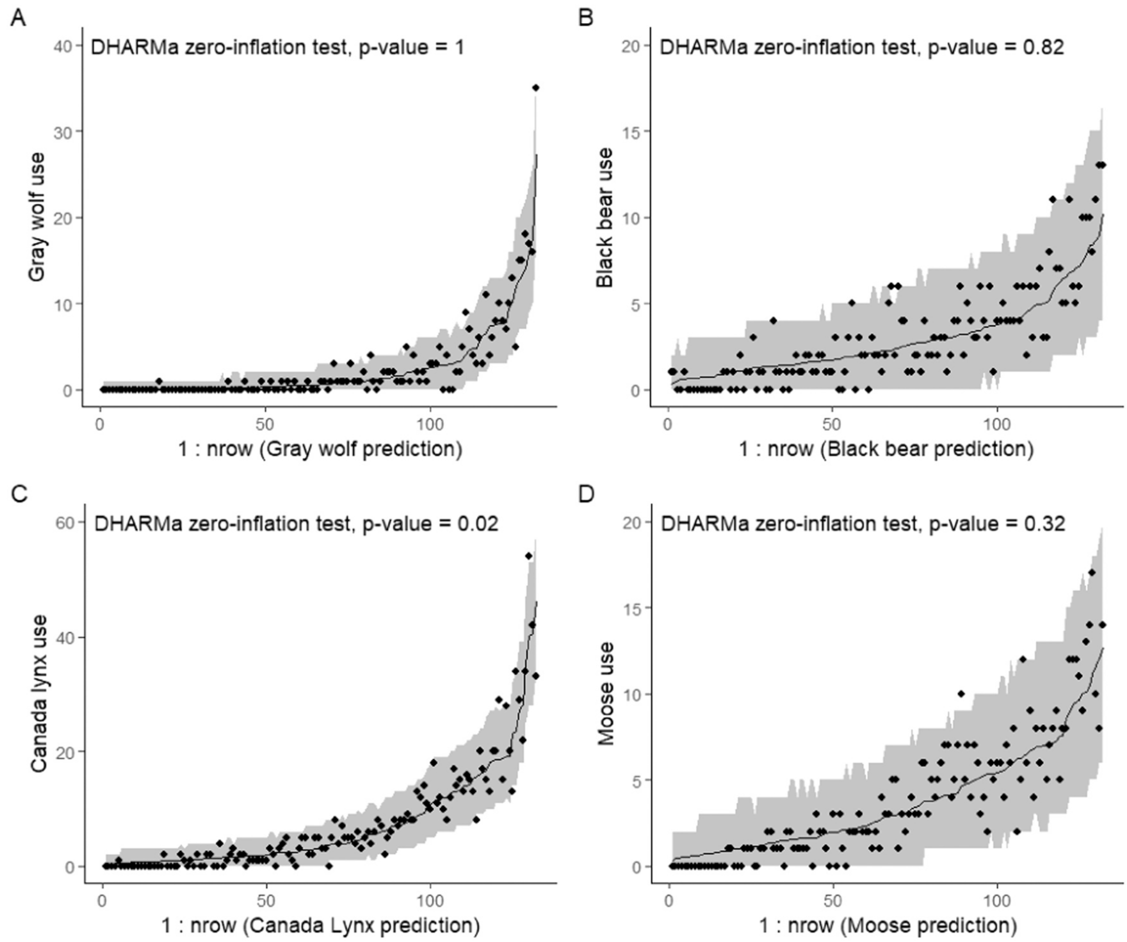

Figure A1. Simulation (1000) of global models for gray wolf, black bear, Canada lynx and moose, using a generalized linear mixed-effect model with a Poisson distribution. Data were ordered according to their predicted values and were collected from 27 to 22 gravel forest roads, 24–27 winter forest roads and 16–17 riparian areas in 2020–2021, respectively, which were sampled in the caribou wildlife site south of Val-d'Or, western Quebec, Canada. Shading denotes 95% prediction intervals for each observation in the dataset. The DHARMa zero-inflation test (Hartig, 2017) compares the observed number of zeros with the zeros that were expected from simulations (a value < 1 means that the observed data have fewer zeros than would be expected).

Table A1
Mammal detections observed during the snow-free season in 2020–2021 on 27–22 camera traps on gravel forest roads, 24–27 on winter forest roads, and 16–17 on riparian areas, respectively, which were sampled in the caribou wildlife site south of Val-d′Or, western Québec, Canada. Mammals in boldface represent those that were used for the statistical analyses.

Species	2020			2021		
	Gravel roads	Winter roads	Riparian areas	Gravel roads	Winter roads	Riparian areas
Snowshoe hare (*Lepus americanus*)	901	727	313	777	765	419
Red fox (*Vulpes vulpes*)	1056	6	2	287	9	7
Human (*Homo sapiens*)	570	112	4	470	109	19
Canada Lynx (*Lynx canadensis*)	292	69	60	324	143	56
American red squirrel (*Tamiasciurus hudsonicus*)	145	31	59	59	222	291
Moose (*Alces americanus*)	136	57	21	129	123	35
Beaver (*Castor canadensis*)	3	22	33	21	220	113
Black bear (*Ursus americanus*)	83	23	30	127	72	58
Gray wolf (*Canis lupus*)	102	12	18	129	46	10
Eastern chipmunk (*Tamias striatus*)	107	2	20	19	0	22
Porcupine (*Erethizon dorsatum*)	27	0	0	22	4	0
Northern flying squirrel (*Glaucomys sabrinus*)	0	0	12	0	2	38
Striped skunk (*Mephitis mephitis*)	2	5	1	21	16	5
American marten (*Martes americana*)	3	0	2	1	1	5
Coyote (*Canis latrans*)	4	0	0	2	2	0
Fisher (*Martes pennanti*)	3	3	2	0	0	0
North American river otter (*Lontra canadensis*)	0	0	0	0	6	0
Muskrat (*Ondatra zibethicus*)	0	0	0	1	4	0
Groundhog (*Marmota monax*)	2	0	0	2	0	0
Long-tailed weasel (*Mustela frenata*)	1	0	2	0	0	1
Raccoon (*Procyon lotor*)	1	0	0	0	1	0

Table A2
List of summer edible plants (< 1 m) for moose and black bear that were found on linear features. Data were collected on 33 gravel forest roads, 29 winter forest roads and 18 riparian areas in the caribou wildlife site south of Val-d'Or, western Quebec, Canada, in 2021. For each mammal species, the sum of plant cover with values of 1 in each linear feature represented edible plant cover (EPR) variables

Plant species	Edible for	
	Moose	Black bear
Red maple (*Acer rubrum*)	1	0
Mountain maple (*Acer spicatum*)	1	0
American green alder (*Alnus alnobetula*)	1	0
Wild sarsaparilla (*Aralia nudicaulis*)	0	1
Paper or white birch (*Betula papyrifera*)	1	0
Leatherleaf (*Chamaedaphne calyculata*)	1	0
Yellow clintonia (*Clintonia borealis*)	0	1
Bunchberry (*Cornus canadensis*)	1	1
Red-osier dogwood (*Cornus sericea*)	0	1
Woody debris	0	1
Horsetail (*Equisetum* sp.)	1	1
Wild strawberry (*Fragaria virginiana*)	0	1
Mountain holly (*Ilex mucronata*)	0	1
Twinflower (*Linnaea borealis*)	1	0
Lycopod (*Lycopodium* sp.)	1	0
Grass (*Poaceae sp.*)	1	1
Trembling aspen (*Populus tremuloides*)	1	1
Pin cherry (*Prunus pensylvanica*)	1	1
Skunk currant (*Ribes glandulosum*)	1	1
Rose (*Rosa* sp.)	1	0
Red raspberry (*Rubus idaeus*)	1	1
Dwarf raspberry (*Rubus pubescens*)	1	1
Willow (*Salix* sp.)	1	0
Canada goldenrod (*Solidago canadensis*)	1	0
American mountain-ash (*Sorbus americana*)	1	1
Rose twisted stalk (*Streptopus lanceolatus*)	1	0
Early lowbush blueberry (*Vaccinium angustifolium*)	0	1
Small cranberry (*Vaccinium oxycoccos*)	0	1
Wild raisin (*Viburnum nudum*)	0	1

Table A3
List of summer edible plants (≥ 1 m) for moose and black bear that were found on linear features. Data were collected on 33 gravel forest roads, 29 winter forest roads and 18 riparian areas in the caribou wildlife site south of Val-d'Or, western Quebec, Canada, in 2021. For each mammal species, the sum of plant counts with value of 1 in each linear feature represented counts of edible stems (ES) variables.

Plant species	Edible for	
	Moose	Black bear
Red maple (*Acer rubrum*)	1	0
Mountain maple (*Acer spicatum*)	1	0
American green alder (*Alnus alnobetula*)	1	0
Serviceberry (*Amélanchier* sp.)	1	1
Paper or white birch (*Betula papyrifera*)	1	0
Red-osier dogwood (*Cornus sericea*)	0	1
Beaked hazelnut (*Corylus cornuta*)	1	1
Mountain holly (*Ilex mucronata*)	0	1
Trembling aspen (*Populus tremuloides*)	1	1
Balsam poplar (*Populus balsamifera*)	1	1
Pin cherry (*Prunus pensylvanica*)	1	1
Willow (*Salix* sp.)	1	0
American mountain-ash (*Sorbus americana*)	1	1
Wild raisin (*Viburnum nudum*)	0	1

Table A4
Distribution of local variables depending on the type of the linear feature. Camera traps are located on 33 gravel forest roads, 29 winter forest roads and 18 riparian areas in the caribou wildlife site south of Val-d'Or, western Quebec, Canada. Comparisons were conducted following one-way Anova for all variables, except for the difference in lateral cover between the surrounding area and the linear feature, which was analysed with two-way ANOVA. Results of Tukey tests are presented with letters.

Type of linear feature	DLC[a] at			ES[b] for		EPR[c] for	
	50 cm	100 cm	150 cm	Black bear	Moose	Black bear	Moose
Gravel road[a]	36 ± 25^{a}	22 ± 21^{ab}	16 ± 16^{bc}	2 ± 4^{a}	12 ± 21^{a}	11 ± 12^{b}	14 ± 12^{a}
Winter road[b]	-2 ± 22^{d}	4 ± 23^{cd}	8 ± 15^{bcd}	10 ± 16^{a}	9 ± 10^{a}	28 ± 16^{a}	13 ± 15^{a}
Riparian area[b]	1 ± 28^{cd}	4 ± 28^{bcd}	5 ± 23^{bcd}	11 ± 15^{a}	4 ± 6^{a}	29 ± 14^{a}	6 ± 9^{b}

[a] Difference in lateral cover between the surrounding area and the linear feature (%)
[b] Count of edible stems (≥ 1 m)
[c] Edible plant (< 1 m) cover (%)

Table A5
Distribution of landscape parameters depending upon the type of linear feature on different radii around camera-trap locations. Camera traps are located on 33 gravel roads, 29 winter roads and 18 riparian areas in the caribou wildlife site south of Val-d'Or area, western Quebec, Canada. The comparisons were conducted with two-way ANOVA for all variables, except for distance to higher forest road class and distance to nearest urban area, which were analysed with a one-way ANOVA. The results of Tukey tests are presented as letters.

Landscape variables	Type of linear feature	Radius			
		250 m	500 m	750 m	1000 m
Proportion of regenerating stands (10 years)	Gravel road[a]	39 ± 26[a]	29 ± 18[ab]	26 ± 14[ab]	25± 12[ab]
	Winter Road[c]	15 ± 23[c]	14 ± 16[c]	13 ± 12[c]	12 ± 11[c]
	Riparian area[b]	16 ± 15[bc]	21 ± 12[abc]	21 ± 12[abc]	22 ± 12[abc]
Proportion of dense cover stands (50%-100% cover)	Gravel road[b]	48 ± 27[a]	49 ± 22[a]	49 ± 19[a]	48 ± 17[a]
	Winter Road[a]	64 ± 30[a]	60 ± 21[a]	61 ± 18[a]	61 ± 16[a]
	Riparian area[b]	44 ± 12[a]	44 ± 14[a]	46 ± 16[a]	47 ± 15[a]
Density of forest roads (km /km^2)	Gravel road[b]	3.21 ± 1.25[ab]	2.06 ± 0.77[cde]	1.67 ± 0.52[def]	1.55 ± 0.36[def]
	Winter Road[a]	3.96 ± 1.86[a]	2.71 ± 1.18[bc]	2.31 ± 0.77[bcd]	2.07 ± 0.63[cde]
	Riparian area[c]	0.85 ± 1.11 [g]	1.26 ± 0.76 [f]	1.34 ± 0.72[ef]	1.35 ± 0.59[ef]
Distance (km) to higher forest road class	Gravel road	4.93 ± 3.16[a]			
	Winter Road	1.75 ± 1.53[b]			
	Riparian area	6.38 ± 3.89[a]			
Distance (km) to nearest urban area	Gravel road	46.8 ± 12.7[a]			
	Winter Road	41.2 ± 17.6[a]			
	Riparian area	39.0 ± 22.1[a]			

Table A6
Model selection based on the Akaike Information Criterion (AIC) explaining the number of uses of linear features (gravel forest roads, winter forest roads and riparian areas) according to linear feature characteristics (first group model) by gray wolf, black bear, Canada lynx and moose in the caribou wildlife site south of Val-d'Or, western Québec, Canada, in 2020 and 2021. The models for each species were compared to a null model. All models of each species are represented with respective Akaike weights (ω_i), log likelihood (LL), the number of estimated parameters (K), the marginal (R^2M) and conditional (R^2C) R-square.

Models	LL	K	AIC	ΔAIC	ω_i
Gray wolf ~					
DifLateralCover50cm + Human + Moose + Beaver + RegenerationStands250m + DensItyRoad1000m + NearRoad+ NearUrbanArea + Year + (1|LinearFeatureID)	-224.70	10	473.59	0.00	0.97
DifLateralCover50cm + Year + (1|LinearFeatureID)	-236.19	4	480.69	7.09	0.03
Moose + Year + (1|LinearFeatureID)	-242.79	4	493.89	20.30	0.00
RegenerationStands250m + Year + (1|LinearFeatureID)	-244.59	4	497.49	23.90	0.00
NearRoad + Year + (1|LinearFeatureID)	-245.76	4	499.84	26.24	0.00
DenstyRoad1000m + Year + (1|LinearFeatureID)	-247.57	4	503.46	29.86	0.00
Null + Year + (1|LinearFeatureID)	-249.14	3	504.47	30.87	0.00
Beaver + Year + (1|LinearFeatureID)	-248.54	4	505.39	31.80	0.00
NearUrbanArea + Year + (1|LinearFeatureID)	-248.69	4	505.69	32.09	0.00
Human + Year + (1|LinearFeatureID)	-249.05	4	506.41	32.82	0.00
Black bear ~					
DifLateralCover50cm + Year + (1|LinearFeatureID)	-275.60	4	559.51	0.00	0.77
DifLateralCover50cm + EdibleStems + EdiblePlantsCover + Human + Moose + Beaver + RegenerationStandS250m + DensityRoad1000m + NearRoad + NearUrbanArea + Year + (1|LinearFeatureID)	-266.48	13	562.04	2.53	0.22
NearRoad + Year + (1|LinearFeatureID)	-280.26	4	568.84	9.34	0.01
EdibleStems + Year + (1|LinearFeatureID)	-281.15	4	570.62	11.12	0.00
RegenerationStand250m + Year + (1|LinearFeatureID)	-281.94	4	572.19	12.68	0.00
DensityRoad1000m + Year + (1|LinearFeatureID)	-282.43	4	573.17	13.66	0.00
EdiblePlantsCover + Year + (1|LinearFeatureID)	-282.48	4	573.27	13.76	0.00
Moose + Year + (1|LinearFeatureID)	-283.49	4	575.29	15.78	0.00
Null + Year + (1|LinearFeatureID)	-285.61	3	577.41	17.90	0.00
NearUrbanArea + Year + (1|LinearFeatureID)	-285.21	4	578.74	19.23	0.00
Human + Year + (1|LinearFeatureID)	-285.58	4	579.47	19.96	0.00
Beaver + Year + (1|LinearFeatureID)	-285.59	4	579.49	19.99	0.00
Canada lynx ~					
DifLateralCover50cm + Human + SnowshoeHare + DenseCoverStands1000m + DensityRoad1000m + NearUrbanArea + Year + (1| LinearFeatureID)	-355.65	9	730.78	0.00	0.99
DifLateralCover50cm + Year + (1|LinearFeatureID)	-365.86	4	740.04	9.26	0.01
SnowshoeHare + Year + (1|LinearFeatureID)	-378.59	4	765.50	34.72	0.00
DensityRoad1000m + Year + (1|LinearFeatureID)	-380.82	4	769.96	39.19	0.00
DenseCoverStands1000m + Year + (1|LinearFeatureID)	-381.81	4	771.94	41.16	0.00
Null + Year + (1|LinearFeatureID)	-383.33	3	772.85	42.08	0.00
NearUrbanArea + Year + (1|LinearFeatureID)	-382.92	4	774.16	43.38	0.00
Human + Year + (1|LinearFeatureID)	-383.00	4	774.32	43.54	0.00
Moose ~					
DifLateralCover150cm + EdibleStems + EdiblePlantsCover + Human + RegenerationStands250m + DensityRoads250m + NearRoad + Year + (1|LinearFeatureID)	-303.12	10	628.06	0.00	0.47
DifLateralCover150cm + Year + (1|LinearFeatureID)	-310.76	4	629.84	1.77	0.19
RegenerationStad250m + Year + (1|LinearFeatureID)	-311.10	4	630.52	2.46	0.14
DensityRoads250m + Year + (1|LinearFeatureID)	-311.62	4	631.55	3.49	0.08
EdiblePlantsCover + Year + (1|LinearFeatureID)	-312.06	4	632.44	4.38	0.05

(*continued on next page*)

Table A6 (*continued*)

Models	LL	K	AIC	ΔAIC	ω_i
Human + Year + (1|LinearFeatureID)	-312.27	4	632.86	4.80	0.04
Null + Year + (1|LinearFeatureID)	-314.23	3	634.65	6.59	0.02
EdibleStems + Year + (1|LinearFeatureID)	-314.15	4	636.61	8.54	0.01
NearRoad + Year + (1|LinearFeatureID)	-314.19	4	636.69	8.62	0.01

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