MULTISCALE ASSESSMENT OF THE IMPACTS OF ROADS AND CUTOVERS ON CALVING SITE SELECTION IN WOODLAND CARIBOU

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ABSTRACT

Woodland caribou (*Rangifer tarandus caribou*) populations are declining worldwide, and predation is considered their most important limiting factor in North America. Caribou are known to reduce predation risk by spacing themselves away from predators and alternative prey. This strategy is now compromised by forestry activities that reduce the amount of suitable caribou habitat and trigger an increase in densities of alternative prey and predators. Our objective was to investigate the influence of predation risk and food availability on selection of a calving location by woodland caribou at three different spatial scales (from coarse to fine: annual home range, calving home range, and forest stand scales) in the boreal forest of Québec, Canada. Using GPS telemetry, we identified calving locations and assessed those using Resource Selection Functions. We determined habitat characteristics using digital ecoforest and topographic maps at the annual and calving home range scales, and with vegetation surveys at the forest stand scale. Caribou selected calving locations located at relatively high elevation and where road density was low, both at the annual and calving home range scales. Within the annual home range scale, they also selected calving locations where the proportion of young and old cutovers was lower than in random areas of similar size. At the forest stand scale, females calved away from roads and young cutovers, using stands where the basal area of black spruce and balsam fir trees was low. At this fine scale, females still selected calving locations located at a relatively high elevation and where the availability of food resources was lower than in random areas located within the same habitat type. The selection of a calving location was driven by predation risk from the largest to the finest spatial scale. Therefore, our results suggest that females may not be able to lower predation risk at larger scales, despite general avoidance of roads and cutovers. We recommend amalgamating all forestry activities within intensive management zones in order to spatially isolate large patches of suitable calving habitat from anthropogenic disturbances. If not possible, we recommend concentrating forestry activities in low-lying areas since caribou consistently selected for relatively high elevations at all scales.

Keywords: calving, cutovers, hierarchical habitat selection, Québec, woodland caribou.

1. Introduction

Caribou (*Rangifer tarandus*) populations are declining worldwide (Vors and Boyce, 2009; Festa-Bianchet et al., 2011) and the southern limit of their range has regressed northwards since the 19th century (McLoughlin et al., 2003; Vors et al., 2007). Causes of this decline include hunting and poaching (Bergerud, 1971), habitat alteration and loss (Nellemann and Cameron, 1996; Vors et al., 2007), cumulative impacts of anthropogenic activities (Johnson et al., 2005), and predation (Seip, 1991; Gustine et al., 2006). Predation is usually considered to be the most important proximal factor limiting caribou populations (McLoughlin et al., 2003; Festa-Bianchet et al., 2011) and its effects appear exacerbated by habitat alteration (Wittmer et al., 2007; Courbin et al., 2009).

Forest management that involves logging and the development of a dense forest road network intensifies predation pressure on caribou (James and Stuart-Smith, 2000; Vors et al., 2007). In addition to reducing the availability of preferred caribou winter habitat, i.e., old-growth coniferous forest (Mahoney and Virgl, 2003; Bowman et al., 2010), logging increases the proportion of early successional stands which are favourable to moose (*Alces alces;* Potvin et al., 2005) and thus triggers a numerical response in wolf (*Canis lupus*), the main predator of adult caribou (Seip, 1991; Gustine et al., 2006). Early successional stands are also favourable to black bear (*Ursus americanus*; Brodeur et al., 2008) which is recognized as an important predator of caribou calves (Mahoney and Virgl, 2003; Pinard et al., 2012). Caribou appear able to reduce predation risk by wolves, the predator with which it co-evolved, through spatial segregation (James et al., 2004) but their calves suffer from black bear predation in regions where there is a significant human footprint (Mahoney and Virgl, 2003; Pinard et al., 2012). Some authors have also suggested that wolf-avoidance strategies displayed by caribou could result in an increased exposure to predation risk by bear (Faille et al., 2010; Pinard et al., 2012; St-Laurent and Dussault, 2012). If true, the wolf avoidance strategy used by caribou is potentially maladaptive due to recent increases in bear density across caribou range.

Habitat selection is a hierarchical process (Johnson, 1980) through which an animal aims to reduce the influence of limiting factors depending on their relative importance, and the most important limiting factors likely drive selection patterns at larger spatial scales (Rettie and Messier, 2000; Dussault et al., 2005). During the calving period, female caribou select habitats that minimize predation risk, such as old-growth coniferous forests (Lantin et al., 2003; Mahoney and Virgl, 2003), open lichen woodlands and peatlands (McLoughlin et al., 2005; Hins et al., 2009), and areas located at high elevation or in rugged terrain (Nellemann and Cameron, 1996; Pinard et al., 2012). Females avoid cutovers and other regenerating areas (Hins et al., 2009), as well as cabins and roads (Vistnes and Nellemann, 2001; Carr et al., 2011; Pinard et al., 2012). Such anthropogenic features are known to be associated with higher predator occurrences (Whittington et al., 2011), which results in higher predation risk (James and Stuart-Smith, 2000).

There have been few descriptions of calving site selection at a fine spatial scale, and available studies yielded variable conclusions. For example, Carr et al. (2007) found that female caribou were seeking a high density of mature trees, as well as thick vegetation ground cover; Pinard et al. (2012) did not find any selection of concealment cover, but showed avoidance of black spruce stands with a high basal area. Nevertheless, both studies found that female caribou were selecting calving sites located at a high elevation relative to surrounding areas. Both wolves and moose are known to use low elevations and slopes as travel routes (Bergerud et al., 1984; Seip, 1991; Dussault et al., 2007; Leblond et al., 2010; Tremblay-Gendron, 2012; Lesmerises et al., 2012). Thus, high elevation can be used as a suitable strategy to maintain separation from wolves and moose as well as to detect an oncoming predator and escape more efficiently (Chekchak et al., 1998; Carr et al., 2007). It is possible that the selection of high elevations at larger spatial scales decreases predation risk sufficiently so that caribou may switch selection pattern toward the second most important limiting factor at a finer scale, food. Food can also be a limiting factor guiding the selection of calving sites because energy requirements are high during the last stages of gestation (McEwan and Whitehead, 1972) and during lactation (Chan-McLoed et al., 1994). The abundance of terrestrial lichens, forbs, and grasses, sources of food for lactating females (Bergerud and Nolan, 1970; Bergerud, 1972), was shown to be important for calving site selection (Lantin et al., 2003; Carr et al., 2007). We believe that a tradeoff between caribou food acquisition and predation risk could explain regional disparities in calving site selection at a fine spatial scale (Gustine et al., 2006; Panzacchi et al., 2010).

Our objective was to assess calving site selection of woodland caribou (*R. t. caribou*; hereafter referred as caribou) at multiple spatial scales. We investigated the joint influence of elevation and forestry activities on calving site selection by caribou, two variables frequently reported to reduce and increase predation risk, respectively (Landers et al., 1979; Bergerud et al., 1984). Assuming that predation by wolves is likely perceived by caribou as their main limiting factor, we hypothesized that female caribou will select, at larger spatial scales, calving sites located at high elevation and away from roads, where predation risk by wolves have been shown to be lower (Bergerud et al., 1984; James and Stuart-Smith, 2000; McPhee et al., 2012). We also predicted that, at finer spatial scale, female caribou will select habitat types allowing them to find suitable food resources, the second most important limiting factor. Because caribou diet in spring is diversified (Bergerud and Nolan, 1970; Bergerud, 1972) and that energy requirements are high during the last stages of gestation (McEwan and Whitehead, 1972) and during lactation (Chan-McLoed et al., 1994), we expected calving sites to support relatively high availabilities of forbs, grasses, and lichens. Further, we examined the potential trade-off between predation risk and food availability by parturient caribou (Barten et al., 2001; Gustine et al., 2006). Considering that caribou are known to reduce predation risk (Rettie and Messier, 2000), we expected them to seek food resources away from cutovers, especially at lower altitude were predators were shown to thrive in our study area (Tremblay-Gendron, 2012; Lesmerises et al., 2012).

2. Study area

The study area (27,168 km^2) was located 125 km north of Saguenay (Québec, Canada; 48°28’-50°59’ N, 69°59’-72°15’ W). The northern part of the study area is characteristic of the black spruce (*Picea mariana*) – moss (*Bryophyta*) domain, while the southern part is transitional between the black spruce – moss and the balsam fir (*Abies balsamea*) – white birch (*Betula paperifera*) domains (Robitaille and Saucier, 1998). The understory of the black spruce – moss domain is mainly composed of mosses, ericaceous shrubs, and forbs (mostly *Cornus canadensis*, *Clintonia borealis*, and *Maianthemum canadense*). The most common tree species are black spruce, balsam fir, jack pine (*Pinus banksiana*), white birch, and trembling aspen (*Populus tremuloides*). Within the balsam fir – white birch domain, the most abundant tree species are balsam fir, white birch, white spruce (*Picea glauca*), and black spruce as well as trembling aspen. Topography is characterized by low rolling relief ranging between 250 and 900 m (Robitaille and Saucier, 1998). Mean annual temperature varied between -2ºC and 0ºC, and mean annual precipitation ranged between 1,000 mm and 1,300 mm, 30% to 35% of which fell as snow, while mean daily temperature during the calving period (21st May – 20th June) varied between 10°C and 16°C (Robitaille and Saucier, 1998).

3. Methods

3.1. Capture and determination of calving site

Between 2004 and 2011, we captured a total of 38 female caribou using a net-gun fired from a helicopter (Potvin and Breton, 1988), and equipped them with GPS collars (Lotek 2200L or 3300L, Telonics TGW-3600). We programmed the GPS collars to attempt location fixes every 4 hours. Capture and handling procedures were approved by the Animal Welfare Committee of the Université du Québec à Rimouski (certificate no. CPA-30-08-67). Following Pinard et al. (2012), we examined the movement pattern of each female during the calving period (21st May – 20th June) to assess the location of its calving site. Typically, females increase movement rates (from one to ten times) a few days prior to calving (Bergerud et al., 1990), and then suddenly become sedentary for approximately 3 days post-calving (Ferguson and Elkie, 2004) because of the restricted mobility of the new-born calf (Pinard et al., 2012). The movement rate of females then slowly increases (Ferguson and Elkie, 2004) as their calves become more agile. When we observed this movement pattern for a female during a given calving season, we estimated the calving site location as the centroid of all GPS locations recorded during the period of restricted mobility (~ 3 days). Because our method did not allow us to find the placenta or other evidence of the parturition site, we use the term “calving location” to account for the fact that we could not accurately determine the true calving site.

3.2. Data analysis

As habitat selection is a hierarchical process and scale of selection may reveal the influence of different limiting factors (Rettie and Messier, 2000), we assessed calving location selection by female caribou at three different spatial scales: the annual home range scale, the calving home range scale, and the forest stand scale. At the annual home range and calving home range scales, we used 1:20,000 digital ecoforest maps, published by the Ministère des Ressources naturelle et de la Faune du Québec, to describe caribou habitat. We updated these maps annually to include habitat modifications resulting from forestry practices and natural disturbances. Minimum mapping unit size was 4 ha for forested polygons and 2 ha for non-forested areas (e.g., water bodies, bogs). Based on previous studies (Hins et al., 2009; Leblond et al., 2011), we combined polygons available on ecoforest maps into 8 habitat types (Table 1) known to be important for caribou. We also created a digital elevation model using topographic maps.

We contrasted habitat use and availability by comparing the calving location with 10 locations randomly distributed within each individual annual home range (for the annual home range scale) or calving (21st May – 20th June) home range (for the calving home range scale) based on simulations obtained using the Pitman efficiency of the Mantel-Haenszel test for stratified data (Mandrekar and Mandrekar, 2004). We defined home ranges using 100% MCP (Mohr, 1947), because kernel estimation provides biased estimates when animals exhibit site fidelity behaviour (Hemson et al., 2005) such as caribou in our study area (Faille et al., 2010). MCPs are known to overestimate home range size by including unused habitats (Grueter et al., 2009). However, our objective was not to assess home range size but habitat selection, and MCPs were more likely to provide the desired contrast between used and available habitat types to highlight habitat selection. To consider the influence of the surrounding environment on habitat selection and match the accuracy of calving location, we calculated the elevation, proportions of coniferous stands, open lichen woodlands, peatlands, young (≤ 5 years-old) and old (6 – 40 years-old) cutovers as well as road density, within 829-m radius circular buffers centered on each calving and random location. We used an 829-m buffer size as it represented the median daily distance traveled by females during the calving period. We conducted all spatial analyses using ArcGIS 10.0 (ESRI Inc., Redlands, California, USA).

For the forest stand scale, we conducted vegetation surveys in the field that allowed us to investigate fine scale habitat characteristics that cannot be assessed on ecoforest maps but that might be crucial for the calving location selection. We contrasted habitat use and availability by comparing vegetation characteristics found at the calving location with three random locations distributed within the same habitat type (see Table 1) in the calving home range of each female. We measured visual obstruction provided by vegetation (i.e., lateral cover) below 1 m above ground level in the four cardinal directions, shrub density in three 4 m^2 plots spaced 15 m apart along a north – south axis, basal tree area using a factor 2 prism, and percent ground cover of forbs, grasses, and terrestrial lichens in three 1 m^2 plots spaced 15 m apart along a north – south axis. We conducted vegetation surveys during the calving period in 2010 and 2011 to measure environmental conditions experienced by females at that time of the year. Specifically for the forest stand scale, we overlaid calving locations on ecoforest maps and removed calving events from our analysis when a major disturbance occurred after a calving event but before field surveys were conducted (2010 and 2011).

3.3. Statistical analysis

We used Resource Selection Functions (RSF; Manly et al., 2002) to assess calving location selection at each spatial scale. We conducted conditional logistic regressions using the library *Survival* in R 2.13.0 (R Development Core Team, 2011) to compare the calving location (use) to random locations (availability), and used a combination of female – year to define the conditional stratum. Prior to statistical analyses, we assessed multicolinearity between independent variables using the variance inflation factor, and confirmed that multicolinearity was absent from our dataset (VIF<10; Graham, 2003). We performed model selection (Burnham and Anderson, 2001) and evaluated different candidate models (see below) using the Quasi-likelihood under Independence Criterion (QIC; Pan, 2001), since conditional logistic regression provides pseudo-likelihood estimates (Pan, 2001). We used model averaging for models with a Δ QIC < 2.

We considered five hierarchically-structured candidate models for the annual and calving home range scales as well for the forest stand scale (each containing different variables). The ELEVATION, NATURAL, ROAD, CUTOVER, and COMPLETE models (see Table 2 for model description) allowed us to assess the joint influence of cutovers and elevation on calving location selection. As we expected that caribou might experience trade-off between predation risk and food availability (Barten et al., 2001; Gustine et al., 2006), we added elevation × % young cutovers and elevation × % old cutovers interactions in more complex models.

We determined the fit of the best supported model at each spatial scale by using a k-fold cross-validation (Boyce et al., 2002). We calculated parameter estimates using 80% of the strata (i.e., female – year combination), and applied the resulting equation to calculate the logit values of the remaining 20%. We then ranked logit values in each stratum and summed the number of real calving locations (used) in each rank. We calculated a Spearman correlation between the rank and the number of real calving locations (used) in each rank (Leblond et al., 2011), and repeated this procedure 1000 times.

4. Results

We identified and analyzed 51, 55, and 48 different calving locations at the annual home range, calving home range and forest stand scales, respectively. The number of calving locations differ among scales since we discarded calving locations where a major disturbance occurred between the calving event and field surveys (forest stand scale), and we were not able to define annual home ranges when a female died during a calving year. At the larger spatial scales, i.e., the annual and calving home range scales, the most parsimonious model was the ROAD model (Table 3). However, we conducted model averaging at the annual home range scale because the CUTOVER model was equivalent to the ROAD model (Δ QIC < 2, Table 3). At both scales, females selected calving locations at high elevations with a low road density (Table 4). Moreover, females selected coniferous stands while avoiding young and old cutovers at the annual home range scale, and peatlands at both the annual and calving home range scales (Table 4). The validation procedure indicated that the most parsimonious models were robust to cross-validation (r_s ± SD; annual home range scale = 0.76 ± 0.11 and calving home range scale = 0.70 ± 0.14).

At the forest stand scale, 43 of the 48 calving locations were in coniferous stands, 3 in old cutovers, and 2 in peatlands. The best supported model from the candidate set was the COMPLETE model (Table 3). At this fine scale, females still selected calving locations away from roads and we found a tendency toward selection of higher elevations (Table 4). Caribou response to young cutovers changed with elevation (Table 4). At a relatively low elevation, the distance to young cutover did not have a strong influence on calving location selection, while females selected calving location farther from young cutovers more frequently than randomly expected at higher elevations (Figure 1). Females also avoided calving in areas where lateral cover was dense and basal area of mature trees, especially balsam fir, was high (Table 4). Finally, females selected calving locations where the abundance of forbs, terrestrial lichens, and grasses was lower than their availability at random sites (Table 4). The most parsimonious model at the forest stand scale was also robust to cross-validation (r_s ± SD = 0.74 ± 0.24).

5. Discussion

Our objective was to investigate calving location selection by caribou at three different spatial scales. Our results were consistent with the hypothesis that predation was the primary limiting factor guiding calving location selection at large spatial scales. Further, our results indicate that food availability did not influence calving location selection at a finer spatial scale, providing limited support to the hypothesis that caribou could limit predation risk at large scale and select for food availability at fine scale (Rettie and Messier, 2000).

At the annual home range scale, calving females selected coniferous stands and avoided young and old cutovers. Previous studies have suggested that female caribou avoid calving in areas supporting a high vegetation biomass, such as cutovers, as they perceive those habitats as more risky (Gustine et al., 2006). Conifer stands, on the other hand, are recognized as suitable caribou habitat (Mahoney and Virgl, 2003; Hins et al., 2009) that may favor spatial segregation between caribou and their predators and alternative prey (James et al., 2004; Bowman et al., 2010). Roads and elevation, two variables associated with predation risk, were also the two most important variables driving selection of calving location at large spatial scales (Bergerud et al., 1984; Pinard et al., 2012). Although we did not directly assess wolf predation risk, roads and other linear corridors are known to facilitate wolf's movements across the landscape (James and Stuart-Smith, 2000; Whittington et al., 2005), and caribou were shown to have a higher probability of crossing a wolf's path along roads (Whittington et al., 2011), resulting in increased predation risk (James and Stuart-Smith, 2000). Higher elevation could help caribou to detect oncoming predator and escape more efficiently (Chekchak et al., 1998; Carr et al., 2007) in addition to segregate from wolves (Bergerud et al., 1984; Seip, 1991). Although variation in elevation in Québec is not as important as in other parts of the caribou range (e.g. British Columbia or Alberta), studies conducted in the same study area or close to our study area demonstrated that wolves (Tremblay-Gendron, 2012; Lesmerises et al., 2012) and moose (Dussault et al., 2007; Leblond et al., 2010) strongly react to elevation or differences in elevation, preferring to use lower elevation and gentle slope to move through the landscape. These findings, in addition to calving females not showing strong selection toward food-rich habitat types, support the hypothesis that predation is the main limiting factor influencing calving site selection at large spatial scales (Gustine et al., 2006; Pinard et al., 2012).

The influence of elevation and roads on calving site selection was also present at the smallest spatial scale investigated (Carr et al., 2007; Pinard et al., 2012), suggesting that caribou could not sufficiently attenuate predation risk through habitat selection at larger scales. In addition, females selected calving locations supporting a low basal area of black spruce (Pinard et al., 2012) and balsam fir at the finest spatial scale. In agreement with Pinard et al. (2012) but contrary to Carr et al. (2007), they also selected calving locations with a low percentage of lateral cover. We hypothesize that the enhanced visibility in these stands could help caribou detecting predators more rapidly (Poole et al., 2007).

Caribou selected calving locations away from cutovers regardless of the elevation and, contrary to our prediction, displayed stronger avoidance towards cutovers at high elevations. We hypothesize that the capacity of caribou to avoid cutovers may be fully expressed at high elevation, where cutovers are less ubiquitous, and that caribou are forced to use areas with more abundant cutovers at lower elevation. A *post-hoc* analysis demonstrated that the proportion of cutovers in the landscape is lower at higher elevations (35.4% at < 650 m and 28.7% at > 650 m), but that suitable coniferous stands are more common (42.5% at < 650 m and 52.7% at > 650 m). Females were also found to select calving locations where the abundance of food resources (i.e., terrestrial lichens, grasses, and forbs) was lower compared to random areas located in similar habitat types. This finding suggests that food resources were clearly not an important variable in the selection of a calving location, and predation risk remained the most important limiting factor at fine spatial scale.

Females avoided peatlands at the calving home range scale, which is surprising because this habitat type was previously reported to be selected (Rettie and Messier, 2000; Mahoney and Virgl, 2003), presumably because peatlands favor spatial segregation from predators (James et al., 2004; McLoughlin et al., 2005). In our case, we argue that peatlands were avoided because females selected areas located at higher relative elevations to calve while peatlands are found on flat terrain at lower elevations relative to the surrounding environment. Moreover, peatlands in our study area were a relatively rare habitat type (2.1%) and were much smaller in size (average 6 ha) than the bog – fen complexes found elsewhere in the caribou range (e.g., Newfoundland, Alberta). Given the low abundance and size of peatlands in our study area, we believe that this may have limited the capacity of caribou to use this habitat type to segregate from predators and alternative prey.

We benefited from previous studies conducted in the same study area to develop a more comprehensive understanding of caribou selection of a calving location. Faille et al. (2010) found that female caribou display range fidelity, especially during the calving period. Nevertheless, fidelity to a calving location could be detrimental to calf survival in cases where females continue to select a formerly suitable calving habitat that has changed following major disturbances. If habitat selection is constrained by range fidelity or is not sufficient to mitigate the influence of a dominant limiting factor, we could expect responses to take place at other biological scales (*sensu* Johnson and St-Laurent, 2011), such as the physiological scale or the energetic balance. A companion study recently demonstrated that caribou suffer physiological stress in response to anthropogenic disturbances associated with forestry activities (Renaud, 2012). In addition to demonstrating the negative influence of roads at all spatial scales, these studies suggest that females could not completely escape road and cutover influence at any scale, and are likely being forced to calve in suboptimal environments.

5. Management implications

Caribou selected particular habitat features to calve (Table 4). Our findings add further support to earlier research which reported that woodland caribou are trying to avoid predation at the coarsest spatial scale (Bergerud et al., 1990; Rettie and Messier, 2000), especially during the calving period (Hins et al., 2009; Pinard et al., 2012). We demonstrated that anthropogenic disturbances originating from forestry activities, namely roads and cutovers, are avoided at large spatial scales by females when seeking a calving location. These anthropogenic features are decreasing the quality of caribou calving habitat, as the distribution of roads and cutovers is known to shape predation risk across the landscape by increasing black bear and wolf density both locally and regionally (Landers et al., 1979; Potvin et al., 2005; Seip, 1991). Avoidance of roads and cutovers was still detectable at the finest spatial scale investigated, suggesting that females were not able to mitigate the negative influence of such disturbances at larger scales. In order to reduce the negative impacts of roads and cutovers during this critical phase of the caribou life cycle, we recommend conserving large tracts of mature forest exempt from anthropogenic disturbances, where caribou may find suitable and safe calving locations (Courtois et al., 2007, 2008; Lesmerises, 2011). In regions where such large, undisturbed areas are no longer available, we suggest concentrating logging activities in low-lying sectors to facilitate spatial segregation between caribou and predators (Bergerud et al., 1984; Pinard et al., 2012). We believe that such strategies would limit overlap between suitable calving locations and anthropogenic features originating from forestry activity, helping to maintain sustainable woodland caribou populations within highly managed landscapes.

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Table 1. Description of the different habitat types used to assess calving location selection by woodland caribou in Saguenay – Lac-Saint-Jean (Québec, Canada) between 2004 and 2011.

Habitat type	Description	Availability within the study area (%)
Forested habitat types		
Coniferous	Coniferous stands with dominant tree strata ≥ 50-yr-old	45.3
Mixed and deciduous	Mixed and deciduous stands with dominant tree strata ≥ 50-yr-old	4.1
Open lichen woodland	Coniferous forest with low tree density and usually terrestrial lichens	0.7
Peatlands	Poorly drained open areas (bogs and fens)	2.1
Disturbed habitat types		
Young cutover	Cutovers aged ≤ 5-yr-old	7.8
Old cutover	Cutovers aged 6 to 40-yr-old	28.5
Non-forested habitat types		
Water bodies	Lakes and rivers	9.3
Others	Others non-forested areas	2.1

Table 2. Descriptions of the candidate models at the annual home-range scale, calving home-range scale, and forest stand scale used to assess the effect of elevation and anthropogenic disturbances on calving location selection by caribou in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011.

Model	**Variables**
	Annual and calving home-range scales
ELEVATION	Elevation
NATURAL	ELEVATION + % coniferous + % open lichen woodland + % peatlands
ROAD	NATURAL + road density
CUTOVER	ROAD + % young cutovers + % old cutovers
COMPLETE	CUTOVER + Elevation × % young cutovers + Elevation × % old cutovers
	Forest stand scale
ELEVATION	Elevation
NATURAL	ELEVATION + basal area of black spruce, balsam fir, white birch + lateral cover + density of black spruce shrubs + % ground cover of forbs, grasses, lichens
ROAD	NATURAL + distance to the nearest road
CUTOVER	ROAD + distance to the nearest young cutover + distance to the nearest old cutover
COMPLETE	CUTOVER + Elevation × distance to the nearest young cutover + Elevation × distance to the nearest old cutover

Table 3. Results of the model selection process (see Table 2 for descriptions) to assess calving location selection by female caribou at the annual home-range scale, calving home-range scale, and forest stand scale in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011. Candidate models are listed with their Log-likelihood (LL), number of parameters (K), the difference in Quasi-likelihood under Independence Criterion compared to the best model (Δ QIC), and the model weight (w_i).

Model	LL	K	Δ QIC	w_i
Annual home-range scale (n=51)				
ELEVATION	-99.49	1	37.00	0.00
NATURAL	-85.63	4	13.73	0.00
ROAD	-77.88	5	0.00	0.58
CUTOVER	-77.38	7	1.70	0.25
COMPLETE	-77.07	9	2.38	0.17
Calving home-range scale (n=55)				
ELEVATION	-114.85	1	21.45	0.00
NATURAL	-111.28	4	19.74	0.00
ROAD	-101.11	5	0.00	0.82
CUTOVER	-100.68	7	3.51	0.14
COMPLETE	-99.88	9	6.30	0.04
Forest stand scale (n=48)				
ELEVATION	-59.14	1	17.75	0.00
NATURAL	-50.84	9	13.00	0.00
ROAD	-45.87	10	2.39	0.20
CUTOVER	-44.92	12	2.80	0.16
COMPLETE	-42.73	14	0.00	0.64

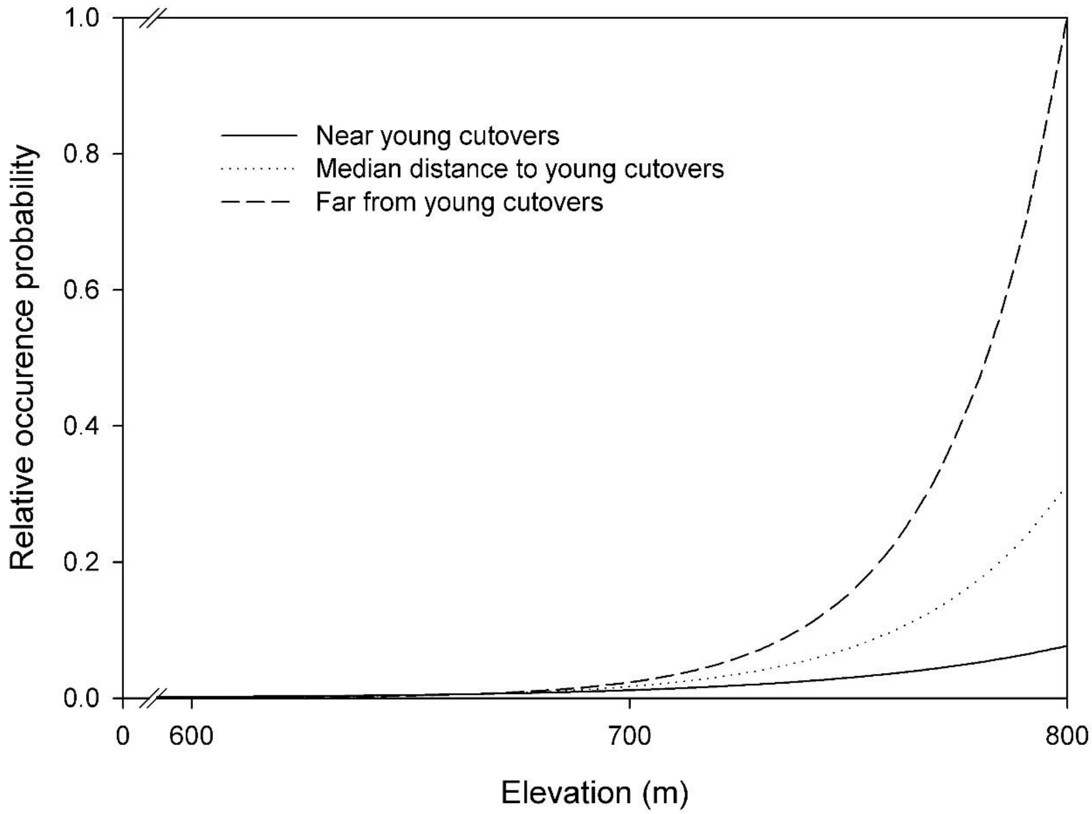
Table 4. Mean (± SE) used and availability in the dataset and the coefficients of the variables included in the best supported models, or in the averaged model at the annual home-range scale, to assess calving location selection by female caribou at the annual home-range scale, calving home-range scale, and forest stand scale in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011. Each variable is presented with its coefficient (β), robust standard error (SE), and 95% confidence interval of odds ratio.

					95% confidence interval	
Variable	**Use (mean ± SE)**	**Availability (mean ± SE)**	**β**	**SE**	**Lower limit**	**Upper limit**
		Annual home-range scale (n=51)				
Elevation (m)	652 ± 10	591 ± 4	0.016	0.003	1.010	1.023
% coniferous	0.599 ± 0.037	0.386 ± 0.011	2.193	1.336	0.613	131.165
% open lichen woodland	0.018 ± 0.007	0.031 ± 0.003	-2.510	2.656	>0.001	16.809
% peatlands	0.014 ± 0.002	0.030 ± 0.003	-14.048	7.719	>0.001	4.258
Road density (km/km^2)	0.399 ± 0.111	1.162 ± 0.052	-0.925	0.289	0.222	0.709
% young cutovers	0.067 ± 0.023	0.086 ± 0.008	-0.360	0.457	0.279	1.747

% old cutovers	0.156 ± 0.026	0.319 ± 0.013	-0.497	0.708	0.147	2.518
Calving home-range scale (n=55)						
Elevation (m)	652 ± 9	616 ± 3	0.022	0.005	1.013	1.031
% coniferous	0.596 ± 0.036	0.529 ± 0.011	-0.163	0.995	0.121	5.969
% open lichen woodland	0.016 ± 0.007	0.015 ± 0.002	-0.533	2.678	0.003	111.714
% peatlands	0.014 ± 0.002	0.024 ± 0.002	-17.350	6.871	<0.001	0.021
Road density (km/km^2)	0.417 ± 0.108	0.862 ± 0.048	-1.385	0.378	0.119	0.525
Forest stand scale (n=48)						
Elevation (m)	655 ± 9	634 ± 5	0.015	0.009	0.998	1.032
Lateral cover below 1m (%)	79 ± 3	80 ± 1	-0.025	0.013	0.952	1.000
Basal area of black spruce trees (m^2/ha)	15.5 ± 2.1	16.8 ± 1.2	-0.037	0.017	0.933	0.995
Basal area of balsam fir trees (m^2/ha)	3.5 ± 0.9	6.4 ± 0.72	-0.099	0.037	0.842	0.974
Basal area of white birch trees (m^2/ha)	0.5 ± 0.4	0.3 ± 0.1	-0.056	0.067	0.829	1.078
Black spruce shrub density (stems/4m^2)	7.6 ± 0.9	7.3 ± 0.6	0.041	0.031	0.980	1.107
Forbs ground cover (%)	16.7 ± 2.6	16.3 ± 1.6	-0.014	0.015	0.959	1.015

Grass ground cover (%)	3.4 ± 0.9	3.2 ± 0.8	-0.055	0.028	0.896	0.998
Terrestrial lichens ground cover (%)	2.8 ± 1.1	4.7 ± 1.1	-0.065	0.028	0.887	0.990
Distance to the nearest road (km)	1.7 ± 0.3	1.4 ± 0.1	1.621	0.663	1.371	18.678
Distance to the nearest young cutover (km)	2.1 ± 0.3	1.8 ± 0.2	-5.277	2.376	<0.001	0.537
Distance to the nearest old cutover (km)	1.1 ± 0.2	1.1 ± 0.1	-3.479	4.142	<0.001	103.395
Elevation × Distance to the nearest young cutover	-	-	0.008	0.003	1.001	1.015
Elevation × Distance to the nearest old cutover	-	-	0.004	0.006	0.993	1.016

Figure 1. Relationship between the relative occurrence probability of a caribou calving location and the elevation × distance to nearest young cutover interaction, as predicted by the COMPLETE model at the forest stand scale from data collected in Saguenay – Lac-St-Jean (Québec, Canada) between 2004 and 2011. We fitted 3 curves originating from the COMPLETE model to investigate the influence of the distance to the nearest young cutover using the 1^{st}, 2^{nd}, and 3^{rd} quartile of the distance to nearest young cutover values, i.e., 0.399 km, 1.621 km, and 2.629 km, respectively.


Near young cutovers
Median distance to young cutovers
Far from young cutovers
Relative occurence probability
1.0
0.8
0.6
0.4
0.2
0.0
0
600
700
800
Elevation (m)