BEHAVIOURAL STRATEGIES TOWARDS HUMAN DISTURBANCES EXPLAIN INDIVIDUAL PERFORMANCE IN WOODLAND CARIBOU

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ABSTRACT – Behavioural strategies may have important fitness, ecological and evolutionary consequences. In woodland caribou, human disturbances are associated with higher predation risk. Between 2004 and 2011, we investigated if habitat selection strategies of female caribou towards disturbances influenced their calf's survival in managed boreal forest with varying intensities of human disturbances. Calf survival was 53% and 43% after 30 and 90 days following birth, respectively and 52% of calves that died were killed by black bear. The probability that a female lose its calf to predation was not influenced by habitat composition of her annual home range, but decreased with an increase in proportion of open lichen woodland within its calving home range. At the local scale, females that did not lose their calf displayed stronger avoidance of high road density areas than females that lost their calf to predation. Further, females that lost their calf to predation and that had a low proportion of ≤5-year-old cutovers within their calving home range were mostly observed in areas where these young cutovers were locally absent. Also, females that lost their calf to predation and that had a high proportion of ≤5-year-old cutovers within their calving home range were mostly observed in areas with a high local density of ≤5-year-old cutovers. Our study demonstrates that we have to account for human-induced disturbances at both local and regional scales in order to further enhance effective caribou management plans. We demonstrate that disturbances not only impact spatial distribution of individuals, but also their reproductive success.

Key words: Anthropogenic disturbances, calf survival, functional response, habitat selection, reproductive success.

INTRODUCTION

Anthropogenic disturbances are widely spread across all ecosystems (Sanderson et al. 2002). Some species benefit from anthropogenic activities, however others, like those associated with undisturbed habitats, are often negatively affected (Fisher and Wilkinson 2005). As outlined by Johnson and St-Laurent (2011), anthropogenic infrastructure or disturbances may affect animal physiology (Wikelski and Cooke 2006), behaviour (Blumstein et al. 2005), energetic balance (Williams et al. 2006), survival (Phillips and Alldredge 2000), as well as populations and communities (Addessi 1994).

The boreal forest, a biome representing 33% of the Earth's forest cover, is increasingly impacted by forestry activities (Burton et al. 2003). The threatened woodland caribou *Rangifer tarandus caribou* is recognized as being negatively impacted by both human-induced and natural disturbances (Vors et al. 2007; Festa-Bianchet et al. 2011), and increased predation risk in highly disturbed environments is considered the most important proximate limiting factor explaining the widespread population declines (Wittmer et al. 2007; Festa-Bianchet et al. 2011). Forestry activities benefit wolf *Canis lupus* (Seip 1991), the main predator of adult caribou, and black bear *Ursus americanus* which is another potential predator of caribou calves (Gustine et al. 2006; Pinard et al. 2012). Although adult female survival is the most important determinant of population dynamics, calf survival is highly variable among years and populations (Seip and Cichowski 1996; Gustine et al. 2006; Pinard et al. 2012) and it also has a great influence on population dynamics (Gaillard et al. 2000; Raithel et al. 2007).

During the calving period, female caribou behavioural adjustments are aimed at reducing predation risk for their calf (Gustine et al. 2006; Pinard et al. 2012), and their habitat selection is oriented toward 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). Females also select areas located at high elevations or in rugged terrain, while avoiding cutovers, regenerating areas and roads (Leclerc et al. 2012; Leblond et al. 2013). Caribou attempt to isolate themselves spatially from predators, and their habitat selection pattern appears to be effective in avoiding predation by wolves (James et al. 2004). However, calves also suffer from black bear predation in landscapes where the human footprint is extensive (Mahoney and Virgl 2003; Pinard et al. 2012). Some authors have suggested that wolf-avoidance strategies displayed by caribou could result in increased bear predation (Faille et al. 2010; St-Laurent and Dussault 2012), a potentially maladaptive behaviour due to recent increases in bear densities across the caribou range.

During the last decade, an increasing number of studies have investigated differences in behaviour (Réale et al. 2010) which can occur between and within populations of the same species (Wilson 1998). For example, individuals may express different habitat selection (Mabille et al. 2012) or movement patterns while foraging (Austin et al. 2004) or different intensities of boldness or shyness (Wilson et al. 1994; Réale and Festa-Bianchet 2003). Because different behavioural strategies may lead to different survival probabilities or reproductive rates, behavioural strategies may have fitness, ecological and evolutionary consequences (Sih et al. 2004; Smith and Blumstein 2008; Réale et al. 2010). Therefore it is important to consider the range of behavioural strategies displayed by individuals when assessing the impacts of human-induced disturbances on wildlife, particularly in caribou, as human disturbances are associated with higher predation risk for that species (Courtois et al. 2008; Whittington et al. 2011).

The study of functional responses in habitat selection may help to highlight the different behavioural strategies within a population. A functional response in habitat selection is defined as a change in the selection of a habitat attribute as a function of its availability or the availability of other habitat attributes (Mysterud and Ims 1998; Hebblewhite and Merrill 2008). Functional responses in habitat selection have been reported to occur in large ungulates such as moose *Alces*

alces (Mabille et al. 2012; Beyer et al. 2013), red deer *Cervus elaphus* (Godvik et al. 2009) and caribou (Hansen et al. 2009; Moreau et al. 2012). The study of functional responses towards human disturbances is important for managers as the impacts of disturbances can vary according to their local and regional density. Furthermore, functional responses in habitat selection that are triggered by human disturbances might have important fitness implications and ultimately alter animal's adaptive value. Despite such important potential consequences on population dynamics, few studies have tried to link functional responses in behaviour to fitness (except Dussault et al. 2012). In this study, we used GPS collars to track female caribou in managed landscapes with varying intensities of human disturbances in the boreal forest of Québec, Canada. We first evaluated calf survival and then investigated if habitat selection strategies of females towards major human disturbances influenced their reproductive success. Further, we examined if functional responses in habitat selection of adult female caribou towards human-induced disturbances could explain the fate of their calf.

MATERIALS AND METHODS

Study area

The study area (Supplemental Figure S1) included two caribou ranges, i.e., Charlevoix (5086 km^2; 47°40' N, 71°15' W) and Saguenay–Lac-St-Jean (26 686 km^2; 48°28'-50°59' N, 69°59'-72°15' W), both typical of the boreal forest but contrasted in terms of human footprint. In both regions, the landscape was dominated by coniferous stands composed of black spruce *Picea mariana* and balsam fir *Abies balsamea* with few mixed or deciduous stands composed of white birch *Betula papyrifera*, trembling aspen *Populus tremuloides*, and maples *Acer spp*. Topography was characterized by low rolling relief ranging between 250 and 900 m in Saguenay–Lac-St-Jean, and between 500 and 1000 m in Charlevoix (Robitaille and Saucier 1998). Mean precipitation was 1500 mm y^{-1} in Charlevoix and 1200 mm y^{-1} in Saguenay–Lac-St-Jean, and snow accumulations could reach >3 m (Robitaille and Saucier 1998). The Charlevoix study region encompassed 3 National Parks (Grands-Jardins, Jacques-Cartier, and Hautes-Gorges-de-la-Rivière-Malbaie) where forest harvesting was prohibited; the study region also includes a large part of the Laurentides Wildlife Reserve where forestry activities were allowed, such as in Saguenay–Lac-St-Jean. Human-disturbed stands (cutovers of varying ages only) occupied ca. 44% of the caribou range in Charlevoix and 32% in Saguenay–Lac-St-Jean. When applying a 500-m buffer to anthropogenic disturbances (cutovers < 50 year-old and roads) according to the Environment Canada (2011) model, the proportion of each caribou range under the influence of human-induced disturbances reached ca. 99% in Charlevoix and 77% in Saguenay–Lac-St-Jean. Other large mammals inhabiting the study area were moose, black bear, and grey wolf. White-tailed deer *Odocoileus virginianus* were also occasionally seen in Charlevoix.

Capture and monitoring

Between 2004 and 2011, we captured female caribou using a net-gun fired from a helicopter (Potvin and Breton 1988), and equipped them with GPS collars (model 2200L or 3300L from Lotek, Newmarket, Ontario, Canada or model TGW4600 from Telonics, Mesa, AZ, USA). We programmed GPS collars to attempt location fixes every 1, 2, 3 or 4 hours depending upon the collar model and study site.

From 2004 to 2007 (Charlevoix) and 2009 to 2011 (Saguenay–Lac-St-Jean), we captured as many calves as possible from females equipped with GPS collars. To do so, we conducted telemetry flights spaced < 3 days apart during the calving period (21-May to 20-June) to locate collared females and visually confirm if a newborn calf was absent or present. When a calf was first detected, we evaluated if we could capture it immediately (calf standing firmly or moving with its mother) or delayed capture to the next day (wet fur, lying down, low mobility). We captured each calf by hand wearing latex gloves, determined its sex, and fitted it with a VHF expandable collar equipped with a mortality sensor (model LMRT-3 from Lotek, Newmarket, Ontario, Canada or model M2510B from Advanced Telemetry Systems, Isanti, MN, USA). We have no evidence that the capture of a calf affected its survival probability as our survival estimates were consistent with the cow : calf ratio observed in the population during aerial surveys (Courtois et al. 2007; Pinard et al. 2012). All capture and handling procedures were approved by the Animal Welfare Committee of the Université du Québec à Rimouski (certificates #36-08-67 and #27-07-53) and of the Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs du Québec (certificate #07-00-02).

We monitored calf survival by flying over the study area to detect any VHF mortality signals at least twice a week from birthing to the end of June (flights being on average 1.8 ± 1.5 [SD] days apart), and every 2 weeks thereafter until late August (flights being on average 10.8 ± 6.7 [SD] days apart), and finally once per month in September and October. When a mortality signal was detected, we located the collar within 72 hours of detection and investigated the carcass and its surroundings to determine cause of mortality. We considered the presence of tooth marks, blood or disarticulated, dispersed or crushed bones as evidence of predation, and we determined the predator species with evidence such as faeces, tracks, hairs, and scratching signs (Pinard et al. 2012). We used the date of telemetry flights, evidence left at the mortality site, and unusually long movements of a calf's mother, based on their GPS locations, to estimate the mortality date more precisely.

Spatial analyses

We used 1 : 20 000 digital ecoforest maps, published by the Quebec government, to describe caribou habitat. We updated these maps annually to include new 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). We combined polygons available on ecoforest maps into 10 habitat types based on caribou ecology: (1) ‘Coniferous’ and (2) ‘Mixed and deciduous’ stands included stands with dominant coniferous or mixed and deciduous tree strata ≥50-year-old, respectively; (3) ‘Open lichen woodlands’ referred to coniferous forest with terrestrial lichens and low tree density; (4) ‘Peatlands’ were poorly drained open areas (mainly bogs and fens); cutovers were divided using time since disturbance, resulting in (5) ‘≤5-year-old cutovers’, (6) ‘6-20-year-old cutovers’, (7) ‘20-40-year-old cutovers’ and (8) ‘Open no regeneration’ which referred to areas originating from a natural disturbance but with no established tree and shrub strata; (9) ‘Water bodies’ and (10) ‘Others’, which primarily included non-forested areas. We also created a digital elevation model (cell size: 30 × 30 m) using 1 : 20 000 topographic maps.

We investigated the link between habitat selection of adult females and the fate of their calf at three spatial scales: 1) the annual home range scale, 2) the calving home range scale, and 3) the local scale. To do so, we subsampled the GPS telemetry database to get location intervals of 3 or 4 h. At both the annual and calving home range scales, we compared the home range composition between females that lost and those that did not lose their calf. We defined home ranges using 100% minimum convex polygon (MCP).

At the local scale, we contrasted habitat use and availability by comparing locations of each female caribou to an equal number of locations randomly distributed within their annual home range (3rd order of selection, *sensu* Johnson 1980). We defined home ranges using 100% MCP. We determined elevation, and calculated the proportion of each undisturbed and disturbed habitat type, as well as road density within an 816-m radius circular buffer centred on each GPS and random location. This allowed us to consider the influence of the surrounding environment on habitat selection at the local scale (Leblond et al. 2011). We used an 816-m buffer size because it represented the median daily distance travelled by females during the calving period. We conducted all spatial analyses using ArcGIS 10.0 (ESRI Inc., Redlands, California, USA).

Statistical analyses

We assessed calf survival rate using a Cox Proportional Hazards regression model (Cox 1972; McLoughlin et al. 2005) and tested the effect of year, sex, and date of birth on calf survival using the "Survival" library in R 2.15.1 (R Development Core Team 2012). For this survival analysis, we only used calves from the Saguenay–Lac-St-Jean region as calf survival curves for the Charlevoix region were published by Pinard et al. (2012). We nevertheless graphed the survival functions of both regions.

For the habitat selection analyses, we used GPS locations of females from Saguenay–Lac-St-Jean and Charlevoix for which we also had calf survival data. Females that lost their calf from a cause other than predation were removed from our analysis, as our focus was on mortality by predation and not total mortality (McLoughlin et al. 2005; Dussault et al. 2012). We further removed 3 other females from our habitat selection analyses because we did not retrieve their GPS collar ($n = 2$) or we did not have ecoforest maps for their location ($n = 1$).

At the annual and calving home range scales, we used mixed effects logistic regressions to determine the influence of the annual and calving home range composition on female reproductive success. We used calf fate (0 = alive, 1 = dead from predation) as the dependent variable and mean elevation, proportion of each undisturbed and disturbed habitat type, and road density within the female annual and calving home ranges as independent variables. We also considered the region (i.e., Saguenay–Lac-St-Jean or Charlevoix) as a random effect. We performed model selection and evaluated different alternative hypotheses (3 candidate models; see Table 1) using Akaike's Information Criterion (AIC). Further, we tested if the best-supported model was statistically different from the null model using the likelihood ratio test.

At the local scale, we aimed to highlight the habitat selection strategies of females, not the differences between the mortality site and previous locations (which would have required using Cox models; Cox 1972). Therefore, in order to compare habitat selection between females that lost their calf to predation and females for which the calf survived throughout the study period, we used Resource Selection Functions (RSFs; Manly et al. 2002). Following Dussault et al. (2012), we randomly matched a female for which the calf was killed by a predator to a female whose calf survived. This approach did not yield a true pairing in a statistical sense since there was no link between females within a pair, but it allowed us to perform balanced regression models, i.e. with an equal number of females that lost and that did not lose their calf. For each pairing, we restricted the dataset of each female with a calf that survived to the same number of days as the one that died, the counting starting at calving. Doing so allowed us to compare habitat selection of females while controlling for calf age, and prevented us from detecting differences due only to increased calf mobility or environmental changes which both changed along with calf age (Dussault et al. 2012). We pooled the resulting datasets and used this new file to conduct RSFs. We used mixed logistic regressions to compare habitat characteristics at recorded female locations (use) to those at random locations (available) and considered the calf nested in female, nested in region, as a random effect. We repeated this process 999 times, each time with a different pairing of calves that died and that survived. In each iteration, we used the new database to calculate RSFs and evaluate different candidate models (Table 1) using AIC. In candidate models 4 to 12, we added the interaction between calf fate and habitat type covariates in order to evaluate if habitat selection strategies of females could be linked to the fate of their calf. Further, in models 7 to 12, we added triple interactions to explore if functional responses in habitat selection could explain calf fate. Thus, for each candidate model, we obtained 1000 coefficient estimates that we used to calculate the mean coefficient and associated 95% CIs (determined as the 2.5 and 97.5 percentiles). Prior to all habitat selection analyses, we assessed multicollinearity between independent variables using the variance inflation factor (VIF; threshold of 5; Graham 2003) and consequently removed the '% of coniferous stands' variable from the candidate models. We conducted all statistical analyses using R 2.15.1.

RESULTS

Between 2009 and 2011, we captured 30 calves in Saguenay–Lac-St-Jean. In this region, mean calf survival rate was 53% and 43% after 30 and 90 days following birth, respectively (Table 2, Fig. 1). Nine of the 17 (53%) calves that died were killed by black bear, the most important mortality agent, and no calf died of wolf predation. Four calves (13%) died from an unknown natural cause (Table 2). Most calf mortalities occurred during the first month of life and survival rate stabilized after 90 days (Fig. 1). Survival rate did not vary with calf sex ($\chi^2 = 0.3$; df = 1; $P = 0.559$), year ($\chi^2 = 1.5$; df = 2; $P = 0.471$), and birth date ($\chi^2 = 22.2$; df = 16; $P = 0.136$). In Charlevoix, mean calf survival rate was 47% after 90 days and black bear was also the primary mortality agent (see Pinard et al. 2012 for more information).

We conducted the habitat selection analyses using GPS locations of 22 mothers from the Saguenay–Lac-St-Jean region, from which 11 calves survived and 11 died from predation, and 35 mothers from Charlevoix, from which 16 calves survived and 19 died from predation. At the two largest spatial scales, calf fate did not depend on the reaction of their mother toward human disturbances. At the annual home range scale, the best-supported model describing calf fate only included undisturbed habitat types (Table 3). However, this model did not differ from the null model ($\chi^2 = 2.09$; df = 4; $P = 0.718$). At the calving home range scale, the best-supported model also included undisturbed habitat types only (Table 3) but in this case, it was statistically better than the null model ($\chi^2 = 10.36$; df = 4; $P = 0.035$). The probability that a female lose its calf to predation decreased as the proportion of open lichen woodlands in its calving home range increased (Table 4).

At the local scale, the best-supported model revealed that calf fate was linked to habitat selection strategies of adult females toward human disturbances (Table 3). Three major results emerged from this analysis. First, all females avoided areas of high road density, but females that did not lose their calf displayed stronger avoidance of high road density areas than females that lost their calf to predation (Table 4). Second, females that did not lose their calf to predation displayed stronger selection of mixed and deciduous stands (Table 4). Finally, calf fate depended on the combined local (within the 816-m buffer) density of ≤5-year-old cutovers and on the proportion of ≤5-year-old cutovers within the calving home range (Table 4, Fig. 2). This functional response towards ≤5-year-old cutovers highlights two different habitat selection strategies that resulted in the same calf fate. Females that lost their calf to predation and that had a low proportion of ≤5-year-old cutovers within their calving home range were mostly observed in areas where ≤5-year-old cutovers were locally absent (Fig. 2). Also, females that lost their calf to predation and that had a high proportion of ≤5-year-old cutovers within their calving home range were mostly observed in areas with a high local density of ≤5-year-old cutovers (Fig. 2).

DISCUSSION

Our study demonstrates that differences in behavioural strategy towards human-induced disturbances led to different calf fate outcomes in a large ungulate, the threatened woodland caribou. Different habitat selection strategies displayed by females toward ≤5-year-old cutovers and roads resulted in different outcomes in reproductive success. At the local scale, all human disturbances induced female caribou behavioural changes, but not all had consequences on the fate of their calf. Female's habitat selection patterns at the largest spatial scale (annual home range) did not influence the probability that her calf died from predation, suggesting that females avoided predation risk at smaller spatial and temporal scales. Nevertheless, including open lichen woodlands, an undisturbed habitat type known to be important to caribou for spatially segregating them from predators and alternative prey (Hins et al. 2009), in a calving home range appears to increase a calf's survival probability.

We further demonstrated that the functional response in habitat selection by females towards ≤5-year-old cutovers explained some variation in calf fate. During the lactation period, the energetic requirements of females double (Chan-McLoed et al. 1994) so that fine scale habitat selection might be oriented towards habitat types with higher food availability (Lantin et al. 2003; Carr et al. 2007). The use of ≤5-year-old cutovers, a highly productive habitat type, likely resulted in more frequent foraging opportunities for female caribou (Bergerud 1972; Bock and Van Rees 2002). We suggest two plausible hypotheses to explain the adaptive use of ≤5-year-old cutovers by female caribou after calving. Higher food availability may result in 1) higher milk production and in 2) more time available for maternal care, both of which should promote calf growth (White 1983; Rognmo et al. 1983), and shorten the period during which calves are highly vulnerable to predators. However, when the proportion of ≤5-year-old cutovers within the landscape reaches higher levels, the positive effect of increased food availability is superseded by the negative effect of increased predation risk. Disturbed habitat types, such as ≤5-year-old cutovers, are often associated with higher predation risk (Wittmer et al. 2007; Festa-Bianchet et al. 2011) and the proportion of disturbed habitat types within caribou habitat has been negatively correlated with calf recruitment (Environment Canada 2011). The increased proportion of disturbed habitat types triggers numerical (Seip 1991) and functional (Houle et al. 2010) responses of caribou predators. Indeed, wolves are known to increase their selection of recent cutovers when these areas are more abundant in the landscape (Houle et al. 2010). A similar functional response towards ≤5-year-old cutovers could also exist for other predators of caribou calves, such as black bear.

Calf survival was primarily influenced by black bear predation in Saguenay–Lac-St-Jean (Pinard et al. 2012). Wolves killed 5% of calves in Charlevoix and none in Saguenay–Lac-St-Jean, suggesting that the wolf-avoidance strategy used by female caribou during the calving period is currently effective in these areas. This wolf-avoidance strategy mainly consists of selecting higher elevations (Leclerc et al. 2012; Pinard et al. 2012) as wolves usually use lower elevations to move through the landscape (Whittington et al. 2011; Lesmerises et al. 2012). However, by avoiding wolves, the predator with which caribou co-evolved, caribou could be at increased predation risk by black bear, as the latter also selected higher elevations during spring (Mosnier et al. 2008). We also hypothesize that females might have difficulties in assessing calf predation risk by bears because they rarely attack adult caribou (Ballard 1994). Although black bears killed the most calves in our system, Bastille-Rousseau et al. (2011) suggested that bears prey only opportunistically on caribou calves during their frequent movements between food-rich habitat patches such as regenerating stands.

We also demonstrated that linear infrastructure negatively influenced caribou behaviour and calf survival. All females avoided areas with high road density, but females that avoided these linear features more strongly were less likely to lose their calf to predation. Caribou avoidance of roads has been demonstrated to be a means of avoiding wolves (James and Stuart-Smith 2000; Leclerc et al. 2012) because roads are associated with higher predation risk by wolf

(James and Stuart-Smith 2000; Whittington et al. 2011). Roads may also increase black bear predation risk as roadsides are highly productive environments that are selected by bear during spring (Bastille-Rousseau et al. 2011).

Females that lost and those that did not lose their calf to predation displayed different habitat selection strategies towards young cutovers. Some females selected ≤5-year-old cutovers even if it resulted in higher predation risk for their calf. We suggest that such behavioural response could result in an ecological trap when an individual continues to frequent a formerly suitable habitat patch that was modified by human activities (Schlaepfer et al. 2002). This maladaptive behaviour, although expressed only by some females, could jeopardize caribou recruitment particularly in highly managed boreal forest regions where black bear densities are high, and could at least partially explain the mechanism linking habitat alteration with the global decline of woodland caribou.

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Table 1. Candidate models tested to assess the relationship between the habitat selection of female caribou and the fate of their calf (i.e., died from predation or survived) in the boreal forest of Québec, Canada between 2004 and 2011. In candidate models 4 to 12, we added the interaction between calf status and habitat covariates to investigate if habitat selection strategies could explain calf fate. In models 7 to 12, we added three-way interactions to explore if functional responses in habitat selection could explain calf fate.

Candidate model no.	Variables
1*	Elevation + % Peatlands + % Open lichen woodlands + % Mixed and deciduous
2	% ≤5-year-old cutovers + % Old 6-20-year-old + % 20-40-year-old cutovers + % Open no regeneration + Road density
3	Model 1 + Model 2
4	Model 1 + Elevation × Calf status + % Peatlands × Calf status + % Open lichen woodland × Calf status + % Mixed and deciduous × Calf status
5	Model 2 + % ≤5-year-old cutovers × Calf status + % 6-20-year-old cutovers × Calf status + % 20-40-year-old cutovers × Calf status + % Open no regeneration × Calf status + Road density × Calf status
6	Model 4 + Model 5
7	Model 5 + % ≤5-year-old cutovers × % ≤5-year-old cutovers in the calving home range × Calf status

8	Model 5 + % 6-20-year-old cutovers × % 6-20-year-old cutovers in the calving home range × Calf status
9	Model 5 + % ≤5-year-old cutovers × % ≤5-year-old cutovers in the calving home range × Calf status + % 6-20-year-old cutovers × % 6-20-year-old cutovers in the calving home range × Calf status
10	Model 6 + % ≤5-year-old cutovers × % ≤5-year-old cutovers in the calving home range × Calf status
11	Model 6 + % 6-20-year-old cutovers × % 6-20-year-old cutovers in the calving home range × Calf status
12	Model 6 + % ≤5-year-old cutovers × % ≤5-year-old cutovers in the calving home range × Calf status + % 6-20-year-old cutovers × % 6-20-year-old cutovers in the calving home range × Calf status

*****The % of coniferous stands was removed to prevent multicollinearity

Table 2. Survival rate and mortality agent of caribou calves (*n* = 30) monitored during their first 140 days of life from 2009 to 2011 in Saguenay–Lac-St-Jean, Québec, Canada.

	Year			
Variable	2009	2010	2011	Total
No. of calves	9	11	10	30
Survival rate	44.4%	36.4%	50.0%	43.3%
Mortality agent (*n*)				
Black bear	3	2	4	9 (52.9%)
Wolf	0	0	0	0 (0.00%)
Unknown predator	2	0	1	3 (17.6%)
Drowning	0	1	0	1 (5.88%)
Unknown*	0	4	0	4 (23.5%)

*Mortalities of unknown cause occurred when the carcass was seemingly untouched and there was no evidence of predation.

Table 3. Rankings of the candidate models tested at three spatial scales to assess the relationship between habitat selection by female caribou and the fate of their calf (i.e., died from predation or survived; *n* = 57) in the boreal forest of Québec (Canada) between 2004 and 2011. Candidate models are listed with log-likelihood (LL), numbers of parameters (K), difference in Akaike Information Criterion value versus the best-supported model (**Δ**AIC), and their relative weight (AICw).

Candidate	Annual home range scale*				Calving home range scale*				Fine scale			
model no.	LL	K	**Δ**AIC	AICw	LL	K	**Δ**AIC	AICw	LL	K	**Δ**AIC	AICw
1	-38.38	5	0	0.54	-34.25	5	0	0.73	-6865	5	2094	0.00
2	-37.57	6	0.38	0.44	-35.04	6	3.58	0.12	-6772	6	1910	0.00
3	-36.85	10	6.39	0.02	-30.84	10	3.18	0.15	-6146	10	666	0.00
4									-6829	10	2032	0.00
5									-6636	12	1650	0.00
6									-6004	20	402	0.00
7									-6509	16	1404	0.00
8									-6547	16	1480	0.00
9									-6429	20	1252	0.00
10									-5873	24	148	0.00

11		-5916	24	234	0.00
12		-5795	28	0	1.00

*At the annual and calving home range scales we only tested candidate models 1, 2 and 3.

Table 4. Coefficient (β) and their 95%CI of the covariables present in the best-supported model at the calving home range (left panel) and local (right panel) scales assessing the link between a female calf 's fate (*n* = 57; i.e., died from predation coded 1, survived coded 0) and the composition of its calving home range (left panel) or its habitat selection strategy (right panel) in the boreal forest of Québec (Canada) between 2004 and 2011.

	Calving home range scale		Local scale	
Variable	β	95%CI [Lower : Upper]	β	95%CI [Lower : Upper]
Intercept	0.768	[-3.201 : 4.677]	-4.221	[-5.063 : -3.745]
Elevation (km)	-0.516	[-5.048 : 4.016]	8.457	[7.956 : 9.272]
Peatlands (%)	17.278	[-9.857 : 44.416]	-8.002	[-8.172 : -7.814]
Open lichen woodland (%)	-34.459	[-64.054 : -4.865]	0.729	[0.673 : 0.809]
Mixed and deciduous (%)	-1.360	[-11.368 : 8.648]	-2.666	[-2.833 : -2.521]
Road density (km/km^2)			-5.286	[-5.414 : -5.169]
≤5-year-old cutovers (%)			-7.643	[-7.786 : -7.457]
6-20-year-old cutovers (%)			-5.053	[-5.405 : -4.680]
20-40-year-old cutovers (%)			-4.650	[-4.709 : -4.544]

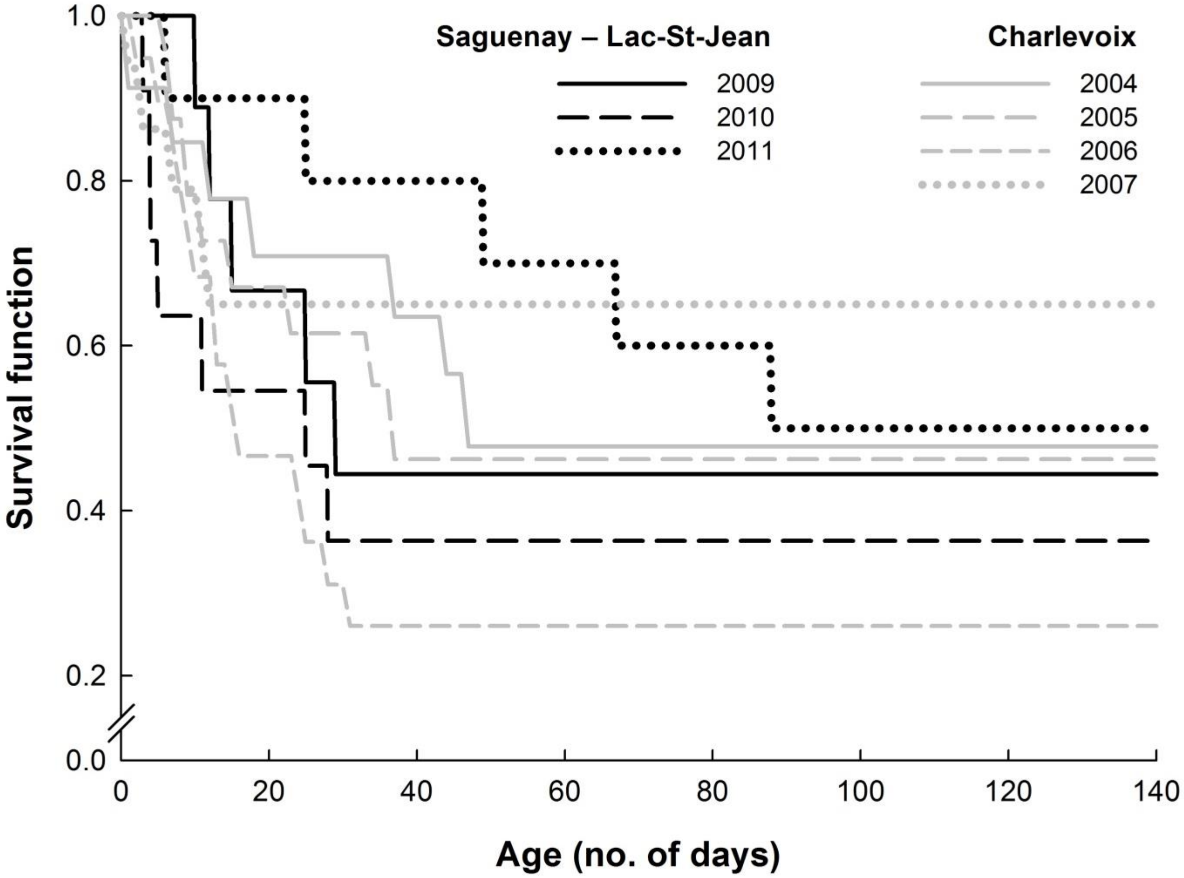
Open no regeneration (%)	-5.498	[-5.567 : -5.450]
Calf alive	-0.340	[-3.589 : 2.106]
≤5-year-old cutovers in calving home range (%)	-4.934	[-6.439 : -3.020]
6-20-year-old cutovers in calving home range (%)	-3.953	[-5.482 : -2.756]
Elevation (km) × calf alive	0.755	[-2.910 : 5.532]
Peatlands (%) × calf alive	-0.104	[-4.821 : 4.591]
Open lichen woodland (%) × calf alive	-3.735	[-8.732 : 0.375]
Mixed and deciduous (%) × calf alive	4.405	[0.991 : 7.659]
Road density (km/km^2) × calf alive	-9.383	[-18.472 : -1.962]
≤5-year-old cutovers (%) × calf alive	4.501	[1.918 : 7.193]
6-20-year-old cutovers (%) × calf alive	-6.312	[-21.614 : 4.208]
20-40-year-old cutovers (%) × calf alive	0.657	[-1.648 : 3.185]
Open no regeneration (%) × calf alive	-1.568	[-18.892 : 6.212]
≤5-year-old cutovers (%) × ≤5-year-old cutovers in calving home range (%)	37.696	[36.699 : 38.481]
≤5-year-old cutovers in calving home range (%) × calf alive	1.854	[-1.202 : 3.984]

6-20-year-old cutovers (%) × 6-20-year-old cutovers in calving home range (%)	22.386	[19.505 : 25.259]
6-20-year-old cutovers in calving home range (%) × calf alive	-1.731	[-6.958 : 2.637]
≤5-year-old cutovers (%) × ≤5-year-old cutovers in calving home range (%) × calf alive	-19.936	[-31.583 : -3.178]
6-20-year-old cutovers (%) × 6-20-year-old cutovers in calving home range (%) × calf alive	20.820	[-16.650 : 73.138]

FIGURE LEGENDS

Figure 1. Survival functions of caribou (*Rangifer tarandus caribou*) calves monitored in Saguenay–Lac-St-Jean (2009-2011; *n* = 30) and in Charlevoix (2004-2007; *n* = 64; Pinard et al. 2012) for the first 140 days of life. Detailed information on calf survival for the Charlevoix region can be found in Pinard et al. (2012).

Figure 2. Relative probability of occurrence of female caribou (*Rangifer tarandus caribou*) that did or did not lose their calves to predation (*n*=57), as a function of the proportion of ≤5 year-old cutovers within the female calving home range, for three ≤5year-old cutover densities (i.e., 0.0%, 4.6%, 29.1% of 816-m radius circular buffer, corresponding to absent, low and high density of cutovers, respectively).



1.0
0.8
0.6
0.4
0.2
0.0
Survival function
0
20
40
60
80
100
120
140
Age (no. of days)
Saguenay – Lac-St-Jean
2009
2010
2011
Charlevoix
2004
2005
2006
2007

Figure 1.

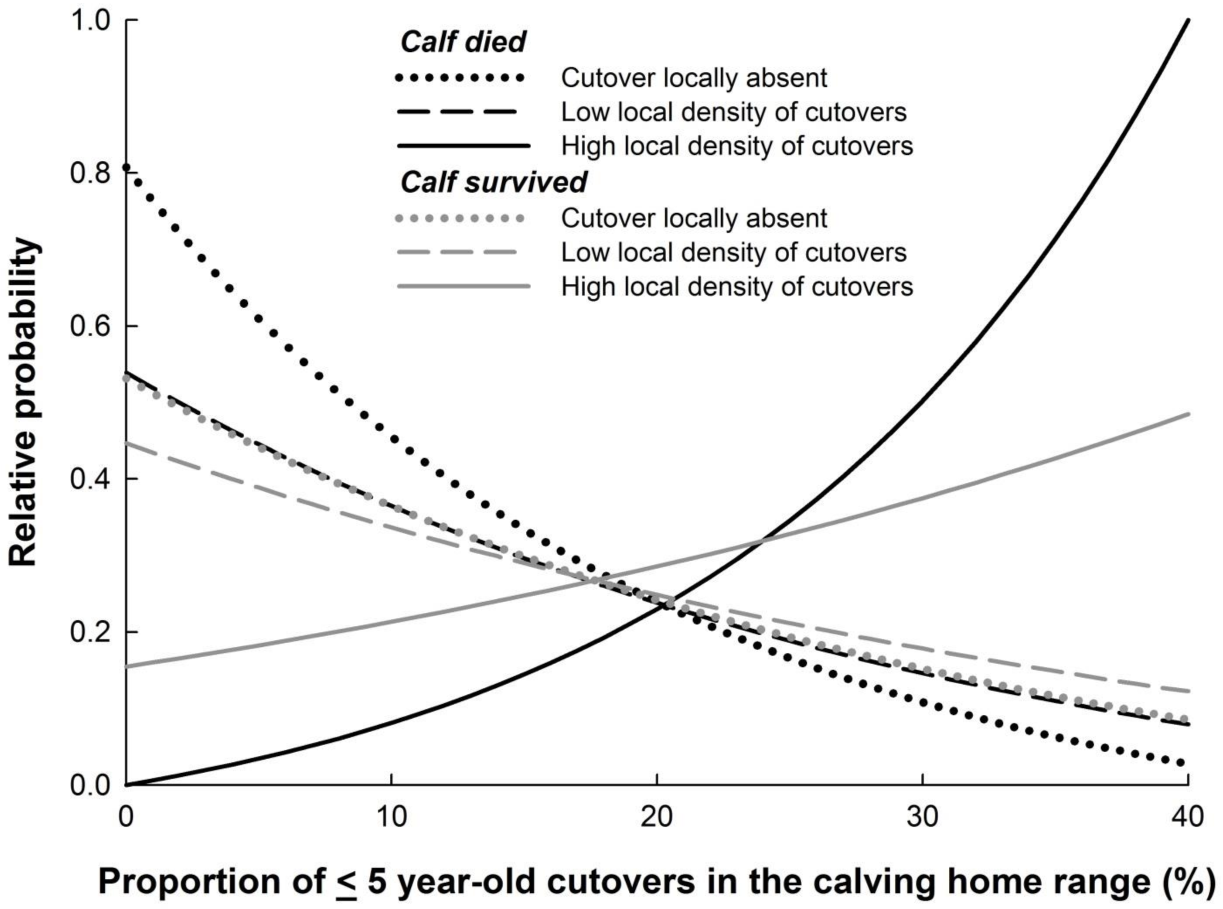

Calf died
Cutover locally absent
Low local density of cutovers
High local density of cutovers
Calf survived
Cutover locally absent
Low local density of cutovers
High local density of cutovers
Relative probability
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
Proportion of ≤ 5 year-old cutovers in the calving home range (%)

Figure 2.

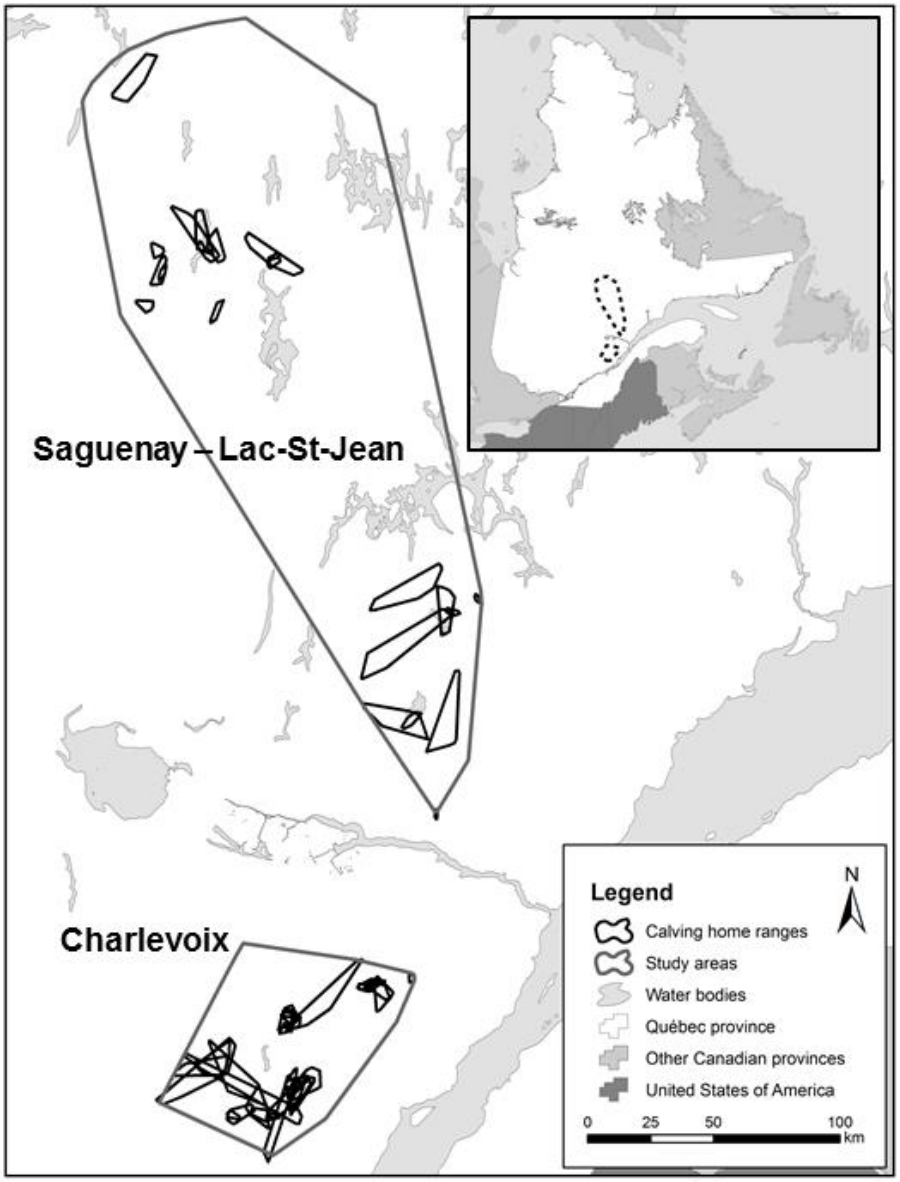


Figure S1. Map of the Saguenay–Lac-St-Jean and Charlevoix study areas and caribou calving home ranges (Québec, Canada).

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