

The reintroduction of boreal caribou as a conservation strategy: A long-term assessment at the southern range limit

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Abstract: Boreal caribou were extirpated from the Charlevoix region (Québec) in the 1920s because of hunting and poaching. In 1965, the Québec government initiated a caribou reintroduction program in Charlevoix. During the winters of 1966 and 1967, a total of 48 boreal caribou were captured, translocated by plane, and released within enclosures; only their offspring (82 individuals) were released in the wild. Between 1967 and 1980, a wolf control program was applied to support caribou population growth. The caribou population, however, remained relatively stable at 45–55 individuals during this period. During the 1980s, the population grew slowly at a rate of approximately 5% each year to reach a peak of 126 individuals in 1992. At that time, Bergerud & Mercer (1989) reported that the Charlevoix experiment was the only successful attempt at caribou reintroduction in the presence of predators (in North America). Afterwards, the population declined and since then it has been relatively stable at about 80 individuals. Here we reviewed the literature regarding the ecology and population dynamics of the Charlevoix caribou herd since its reintroduction, in an attempt to critically assess the value of reintroduction as a conservation tool for this species. Indeed, the Charlevoix caribou herd is now considered at very high risk of extinction mostly because of its small size, its isolation from other caribou populations, and low recruitment. The Charlevoix region has been heavily impacted by forestry activities since the early 1980s. Recent studies have indicated that these habitat modifications may have benefited populations of wolves and black bears—two predators of caribou—and that caribou range fidelity may have exposed caribou to higher predation risk via maladaptive habitat selection. As females are ageing, and females and calves suffer high predation pressure from wolves and bears respectively, we suggest that the future of this reintroduced herd is in question and that they are facing a high probability of extinction in the near future if further action is not taken.

Key words: boreal caribou reintroduction; Charlevoix herd; conservation tool; decline and extirpation; landscape disturbance; predator-prey relationships.

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Introduction

Throughout North America, woodland caribou (*Rangifer tarandus*) have undergone severe population declines and range recession in the last century (Vors & Boyce, 2009). Numerous local populations have

been extirpated, essentially because of overhunting and poaching, but also due to anthropogenic habitat modifications such as forest harvesting and road networks—both of which locally favour large predator populations (Schaefer, 2003; Racey & Arsenault,

2007; Vors *et al.*, 2007). Now recognized as a threatened species by COSEWIC, woodland caribou receive much political attention and are considered of high conservation value (Mallory & Hillis, 1998; Environment Canada, 2008a).

In the past decades, several jurisdictions have advocated caribou reintroduction as a conservation strategy to support declining populations or to re-establish extirpated herds. Bergerud & Mercer (1989) published a critical review of caribou reintroduction experiments in which they identified a series of factors influencing the success of these reintroductions. Namely, they attributed failures to high predation pressure (e.g., in St. Ignace, Ontario and northern Minnesota) and to low lichen supplies (e.g., in Cape Breton, Nova Scotia and Mt. Katahdin, Maine). They also highlighted that the presence of white-tailed deer (*Odocoileus virginianus*), which may transmit a meningeal worm (*Parelaphostrongylus tenuis*) infection to caribou, may be an important factor limiting the success of caribou reintroductions.

Other factors reported as potentially compromising successful ungulate reintroductions include an incomplete understanding or characterisation of historical distributions, husbandry practices, patterns of space use, feeding habits, habitat relationships, population structure (age and sex), number of animals that should be released, mitigation of the extirpation causes, site/range fidelity and dispersal capacities, individual experience or naivety of animals vs. local risks of mortality, guilds of predators and competitors, parasitism, genetic diversity and the evolution of genetic polymorphism of the reintroduced animals (Griffith *et al.*, 1989; Wolf *et al.*, 1996; Fischer & Lindenmayer, 2000; Komers *et al.*, 2000; Larter *et al.*, 2000; Armstrong & Seddon, 2007; Frair *et al.*, 2007; Kidjo *et al.*, 2007; Bell & Dieterich, 2010).

As elsewhere across the historical range of caribou in North America, caribou in Québec underwent severe declines beginning in the early 1800s. The most important declines occurred at the southern edge of the boreal forest, close to human settlements. Range recession towards the north resulted in three isolated herds south of the continuous species range, namely the relict herds of Gaspé National Park, Val-d'Or, and Charlevoix. The Val-d'Or herd is a remnant of the larger herds which historically inhabited the boreal forest near the Québec–Ontario border. The status of this herd is now critical, with only 25 individuals remaining (MRNF, unpubl. data). The herd associated with the summits of Gaspé National Park contains about 150 individuals and represents the last vestige of the populations once occupying the southern shore of the St. Lawrence River, from New

England to Nova Scotia (Ouellet *et al.*, 1996). The last of these three isolated herds is unique in that the herd was reintroduced in the Charlevoix region, north of Québec City, during the late 1960s. Interestingly, Bergerud & Mercer (1989) reported that the Charlevoix experiment was the only successful attempt at caribou reintroduction in the presence of predators (in North America). Although the Charlevoix herd managed to persist until now, recent findings suggest that it might face new threats in the near future.

Here we review the history of the Charlevoix caribou herd, focusing on the population dynamics since the reintroduction. We review the causes of their original decline and extirpation, describe habitat modifications and population surveys, and synthesize the results from past and recent research projects. We demonstrate that, even 40 years following reintroduction, population persistence is not ensured. Ultimately, we discuss the feasibility and potential limitations of using caribou reintroduction as a conservation strategy.

Description of the Charlevoix region

The area traditionally used by the Charlevoix caribou herd covers approximately 5500 km² and is located ~50 km north of Québec City (Québec, Canada). The range overlaps the Laurentides Wildlife Reserve and three protected areas—Jacques-Cartier National Park (670 km²), Grands-Jardins National Park (310 km²), and Hautes-Gorges-de-la-Rivière-Malbaie National Park (225 km²) (Fig. 1). Located within the Jacques-Cartier ecoregion, the area is characterised by broken topography, a coniferous-dominated forest cover, and an important current and historical habitat disturbance regime (Li *et al.*, 1997). The forest is dominated by balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* Mill.), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.). An important wintering area of the Charlevoix caribou herd is found in Grands-Jardins National Park, in a section characterised by alpine tundra vegetation and a highly-rugged topography with some of the highest peaks in southern Québec (up to 1100 m) (Li *et al.*, 1997). The Charlevoix region is subject to harsh weather conditions. Mean annual temperatures range between -2.5 and 0.0 °C, with a daily minimum of -15 °C in January and a maximum of 15 °C in July (Environment Canada, 2008b). The region typically receives 1000 to 1600 mm of precipitation annually, with 400 to 700 mm falling as snow. Mean snow depth reaches ~150 cm each year.

The forested landscape of the study area has been frequently modified by natural disturbances. Since

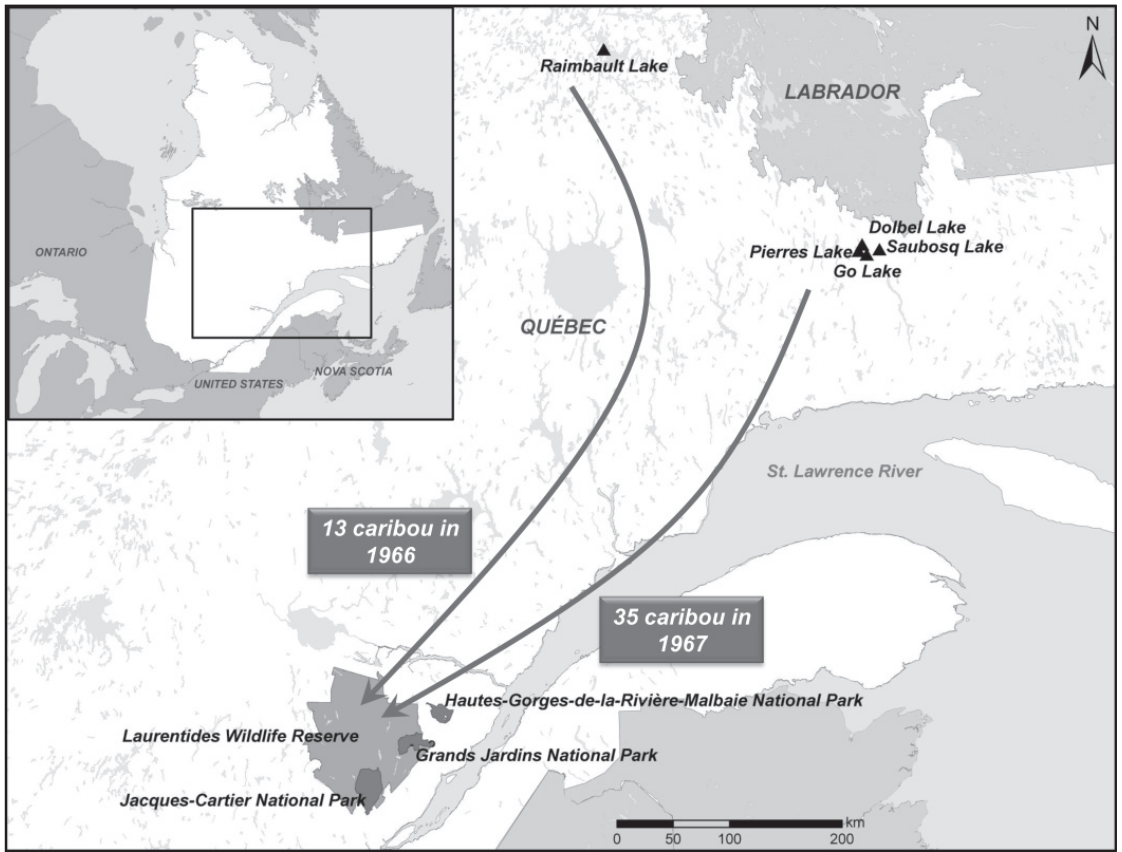


Fig. 1. Location of the sites where caribou were captured for reintroduction in the Charlevoix area in 1966 and 1967. The current location of the Laurentides Wildlife Reserve, the Jacques-Cartier National Park, the Grands-Jardins National Park and the Hautes-Gorges-de-la-Rivière-Malbaie National Park is also indicated (adapted from Sebbane *et al.*, 2008).

the reintroduction of caribou, four major forest fires (1977, 1991, 1996, and 1999) have affected approximately 100 km² of habitat frequented by caribou (Jasinski, 2004). In Grands-Jardins National Park alone, at least 13 different forest fires have burned across about 40% of the park's area (~120 km²) since the beginning of the 20th century. In addition, two severe spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks occurred in 1976–1977 and in 1981–1985, with considerable impact on the balsam fir stands in the region (Jasinski, 2004). Logging activity began at the end of the 19th century, but it became more important in the early 1940s, and since the 1970s the forestry industry has had a strong presence in the region. For instance, when Grands-Jardins National Park was created in 1981, around 40% of the territory was composed of early seral stage forests as a result of logging activities that occurred between 1942 and 1967 (Jasinski, 2004). Today, the area frequented by the Charlevoix caribou herd is

considered to be one of the most heavily impacted areas inhabited by forest-dwelling caribou in Québec (Faille *et al.*, 2010), with the most important habitat modifications occurring during the last four decades (see details below).

Causes of decline and extirpation

Similar to other woodland caribou populations (Vors & Boyce, 2009), the Charlevoix caribou herd underwent a rapid and continuous decline at the end of the 19th century. The population size decreased from an estimated 10 000 individuals (Potvin, 1945) in the 19th century to a complete extirpation in the early 1920s. The most important sources of mortality were hunting and poaching. During the first few centuries of European colonization in the province of Québec, caribou harvest was rather low—likely due to the use of high plateaus by caribou during the winter and their ability to move through deep snow with

ease (Martin, 1980). At the end of the 19th century, caribou harvest rates increased rapidly in association with the use of repeating rifles and increased access to hunting territory (as road and railway networks were developing). The rapid expansion of human settlements, logging, and clearing of forested areas for agriculture also resulted in degraded habitat conditions for caribou and changes in predator-prey relationships (Gaudreault & Fortin, 1988; Jolicoeur *et al.*, 1993).

An increase in predation mortality is the second most important factor explaining the decline of the Charlevoix caribou herd. Habitat modifications, such as logging and natural disturbances, increased the abundance of early successional stands in the area—this change in forest structure and composition provided moose (*Alces alces*) with more high-quality habitat (Courtois *et al.*, 1998; 2007). As reported by pioneer naturalists, and in the harvesting records of the Charlevoix region, moose densities began to increase in the late 1890s (Jolicoeur *et al.*, 1993). Increased prey (i.e., moose) availability for wolves (*Canis lupus*) translated into increased wolf density and, indirectly, increased predation risk for caribou (Bergerud & Elliot, 1986; Seip, 1992; Rettie & Messier, 1998; Wittmer *et al.*, 2007). Anthropogenic habitat modifications also favoured the northward expansion of white-tailed deer range and an increase in beaver (*Castor canadensis*) densities. The increase in density of these prey species likely resulted in higher wolf numbers and a consequent increase in predation pressure on caribou (Latham *et al.*, 2011).

Reintroduction of caribou

Following the extirpation of the Charlevoix caribou herd in the 1920s, the Québec government decided to reintroduce the species in the region in the late 1960s. Two capture sessions were organized approximately 700 km northeast of Québec city, along the Québec–Labrador border. Thirteen individuals were

captured in March 1966 near Raimbault Lake, while 35 individuals were captured in March 1967 near Pierres, Dolbel, Go, and Saubosq Lakes (Fig. 1). Individuals were captured by being herded by aircraft towards nets on a frozen lake. All captured caribou were adults and were temporarily maintained within a small enclosure prior to transportation to the reintroduction site.

The caribou were transported to Charlevoix via plane, followed by a short trip by truck to the relocation site. Prior to travel, caribou were chemically immobilised with succinyl chloride, physically restrained with a harness in a sternal position, and blindfolded. They were first released in a 0.5-ha enclosure (Lake Turgeon, Grands-Jardins National Park) and then in a 2.1-ha enclosure (Grand Lac Jacques-Cartier, Laurentides Wildlife Reserve). Despite all the precautions taken, 7 of the 48 caribou died from myopathy soon after their release. For 3 years caribou were kept in captivity and fed daily with 8 kg of lichens (wet weight) and 2 kg of a specially prepared animal feed. The caribou reproduced successfully in captivity, increasing their numbers within the enclosure to 102 (both adults and calves) in the summer of 1969. Only captive-born offspring were released because translocated individuals were expected to exhibit site fidelity toward their native range and could potentially return there. A total of 83 caribou were released in the wild on three different occasions between 1969 and 1972 (Table 1).

Wolf control program

The Québec government conducted a wolf control program from 1967 to 1979 in the area to be frequented by the reintroduced caribou (Jolicoeur *et al.*, 2005). It is not obvious from the population survey data whether the wolf control program had a significant positive impact on caribou demography. Surprisingly, caribou abundance only started to increase shortly after the end of the control program (Ban-

Table 1. Characteristics of the 83 caribou released in Charlevoix between 1969 and 1972, following breeding in captivity.

Year	Number of caribou	Sex		Age class		
		Male	Female	Adult	Yearling	Calf
1969	42	19	23	18	19	5
1971	23	14	9	12	11	0
1972	18	6	12	0	7	11
Total	83	39	44	30	37	16

ville, 1998) (Figure 2). Even if the link between caribou increase and wolf control was not obvious, the Québec government has continued to encourage wolf harvest by local trappers (Banville, 1998). Special training was even offered to trappers in an attempt to increase trapping efficiency (Sebbane *et al.*, 2008).

New data, however, suggest that wolf abundance may have increased substantially in recent decades (Sebbane *et al.*, 2003). For example, the density of the wolf's primary prey species, moose, is estimated to have increased from 0.6 to 2.2 individuals/10 km² between 1978 and 1994 (Crête & Dussault, 1987; St-Onge *et al.*, 1995; Sebbane *et al.*, 2008), reaching 4.1 moose/10 km² in 2009 (MRNF, *unpubl. data*)—a density considered by Bergerud (2007) to be far too high to maintain caribou.

Despite a high wolf harvesting rate between 1995 and 1998 (estimated at 41%, Jolicoeur, 1998), there are still seven packs inhabiting the Charlevoix region, several of which have a territory overlapping the caribou distribution area; and recent data suggest that wolf harvest is still high in the region (about 40%; Dussault & St-Laurent, *unpubl. data*). Although the predation rate of wolves on the caribou population has not been evaluated precisely, Tremblay *et al.* (2001) have estimated that the summer diet of wolves in the Charlevoix region in 1996–1997 was composed of 29 to 92% moose, 1 to 24% caribou, and 7 to 73% beaver.

Population monitoring

Caribou abundance and population structure have been monitored regularly by aerial survey since the reintroduction. The abundance of the reintroduced caribou population remained stable at around 50 individuals during the 1970s and increased rapidly from 38 animals in 1978 to 126 animals in 1992 (Fig. 2). Between 1978 and 1992, recruitment—defined here as the proportion of calves in the population during late winter—was high (18–30%), as were annual survival rates of both adults (87–95%) and calves (79%). Following the peak abundance of 126 individuals recorded in 1992, the population declined steadily to a minimum of 61 in 2001 (Fig. 2). During

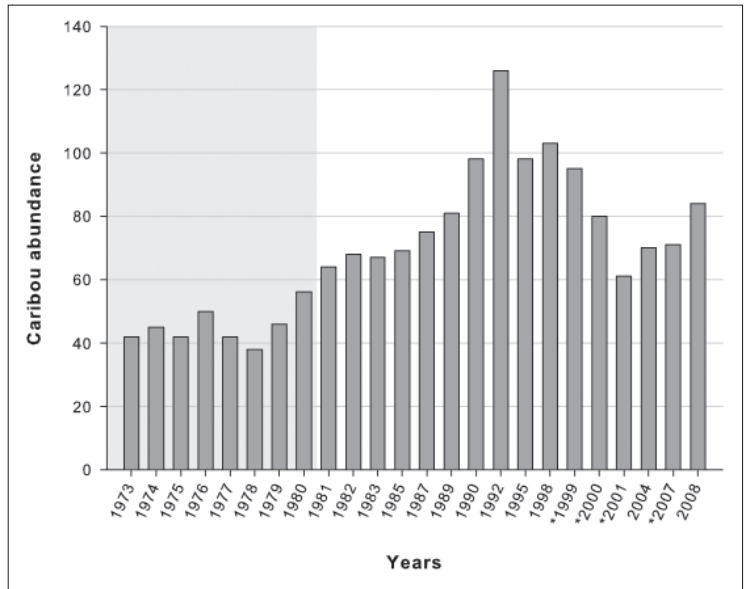


Fig. 2. Variation in abundance of the reintroduced caribou herd estimated from aerial surveys conducted in Charlevoix between 1973 and 2008. An asterisk (*) identifies years when caribou abundance was estimated rather than counted by aerial surveys.

the decline, recruitment was low (~15 %) and annual survival rate of adults was low (69%); and lower in winter (77%) than in summer (90%; Sebbane *et al.*, 2003). Based on a telemetry survey, Sebbane *et al.* (2003) noted that 46% of the females fitted with a VHF collar died from natural causes (e.g., predation, cliff falls, malnutrition, and calving complications).

Woodland caribou are known to have low productivity and high mortality rates, which often result in stable or slightly declining population trends (Bergerud, 1980; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998; Mahoney & Virgl, 2003). The high mortality rates observed in Charlevoix since 1992 illustrate the precarious state of this reintroduced population. Between 1992 and 2008, the annual growth rate (λ) was estimated at 0.95 (see methods in Akçakaya *et al.*, 1997), indicating an approximate 5% decline in caribou abundance annually. Since 2004, the Charlevoix caribou population appears to be relatively stable at approximately 75–80 individuals (Sebbane *et al.*, 2008; Fig. 2).

Although the Charlevoix caribou herd has managed to persist in a human-altered landscape since its reintroduction, it has exhibited a relatively low population growth rate. Further, it was troubling to note that following 1992 the status of the herd deteriorated. Possible explanations for this apparent stabilization of the population at a low density suggest the interaction of several aspects of caribou ecology,

such as genetics, fecundity, forage quality and availability, habitat modifications, and relationships with predators. In the following sections, we synthesize the results of several research projects conducted on the reintroduced Charlevoix herd to assess the different hypotheses raised to explain the precarious status of the population.

Population intrinsic hypotheses

Although food is usually not a major limiting factor for forest-dwelling caribou in the boreal forest (Bergerud & Mercer, 1989), it may become more important or interact with other limiting factors in highly managed landscapes (Briand *et al.*, 2009; Hins *et al.*, 2009). Caribou consume about 5.0 kg and 3.5 kg of lichen every day in winter and summer, respectively, for a total of 1135 kg/yr (Cumming, 1992). Consequently, open lichen woodlands and coniferous forests rich in lichens have been identified as important habitat types in Charlevoix (Charbonneau, 2011) as elsewhere in eastern Canada (Mahoney & Virgl, 2003; Briand *et al.*, 2009; Hins *et al.*, 2009). To determine whether caribou could be limited by food availability in Charlevoix, Sebbane *et al.* (2003) estimated the winter carrying capacity in the herd's distribution area, based on terrestrial (TL) and arboreal lichen (AL) biomass produced in open lichen woodlands (4160 kg/ha for TL and 7–14 kg/ha for AL) and in other coniferous stands (588–609 kg/ha for TL and <1.4 kg/ha for AL). Considering annual lichen production and lichen damage caused by caribou trampling, they estimated that terrestrial lichens could support 117 individuals and arboreal lichens could support 17 individuals, which is similar to the maximum abundance of the reintroduced herd in 1992 ($n = 126$). Although we have no precise information on caribou body condition since the reintroduction, we could hypothesize that food – at least lichen – may have partially limited the growth of the Charlevoix caribou herd; but lichen abundance alone cannot explain why caribou abundance has remained so low since 2001. Food abundance could, however, interact with other limiting factors such as habitat loss and fragmentation (i.e., food accessibility) or predation.

Another plausible hypothesis to explain the decline of the Charlevoix herd is low genetic diversity (i.e., heterozygosity). Genetic analyses confirmed that the reintroduced caribou were of the forest-dwelling ecotype, and that the Charlevoix herd exhibited lower genetic diversity than larger populations inhabiting the continuous range (Courtois *et al.*, 2003). However, the number of alleles per locus and expected

heterozygosity for the reintroduced herd were twice as high as those of the insular Svalbard reindeer (Côté *et al.*, 2002). Courtois *et al.* (2003) thus concluded that the genetic diversity of the Charlevoix herd was sufficient to prevent problems with productivity and/or mortality, at least on a short-term basis. They concluded that the Charlevoix herd was more likely vulnerable to extinction caused by stochastic variation in population dynamics than to inbreeding, a situation observed in many isolated animal populations (Caughley, 1994; Levin, 1995).

The last hypothesis that could explain the observed decline in the Charlevoix population is related to fecundity problems. Pinard *et al.* (2012) estimated the calving rate at approximately 80% between 2004 and 2007. They reported that this was a similar rate to those observed elsewhere in the continuous caribou range of Québec (e.g., Courtois *et al.*, 2007) and consequently discarded this hypothesis.

Habitat degradation

The forest structure and composition within the range of the Charlevoix herd has been greatly modified since their reintroduction. By comparing caribou behaviour during two distinct time periods using VHF telemetry surveys (1978–1981 and 1998–2001), Sebbane *et al.* (2008) demonstrated that these habitat modifications resulted in the expansion of the herd's range and influenced habitat selection patterns. Between the late 1970s and late 1990s, the herd's range almost doubled, increasing from 1185 km² to 3127 km². Caribou expanded their population range and their individual home ranges to include open coniferous forests (Sebbane *et al.*, 2008), a behaviour recognized recently as an anti-predator strategy (Charbonneau, 2011; Pinard *et al.*, 2012). In comparison, closed-canopy coniferous stands, which were selected for by caribou in the late 1970s, were avoided in the late 1990s.

An ongoing GPS telemetry monitoring program (2004–present) showed that the Charlevoix herd is now occupying a range of approximately 6500 km², which is heavily disturbed by logging (Fig. 3). Even though 16% of the herd's range is found within protected areas (i.e., national parks), most of the range (71%) overlaps a wildlife reserve where logging is permitted. Consequently, their range is essentially dominated by disturbed stands (48%) with 18% of clearcuts being < 20 years old. Nearly half of the herd's range (46%) is composed of mature forests (>50 years old) suitable for caribou, but these suitable patches are dispersed in a highly fragmented landscape intersected by numerous forest roads (0.97 km/

km²; Fig. 3a). Regenerating stands (mainly old clearcuts, 20-50 years old) occupy 25% of the distribution range, while natural disturbances (insect outbreaks, fires, and windthrows) account for only 4% of the range (Fig. 3b). Recreational infrastructure (both private and commercial cabins) are also well-distributed across the landscape (0.14/km²), suggesting that the road network is active.

Finally, the Charlevoix caribou range is fragmented (cut almost in half) by Highway 175 (density of 0.03 km/km²; Fig. 3a), an important paved road linking two major cities, Québec City and Ville Saguenay (total population >500 000). Though caribou are sometimes involved in collisions with vehicles, the barrier effect of the highway on caribou movements may have a much greater impact on population dynamics. Caribou are found on both sides of the highway and, as they usually avoid it (Leblond *et al.*, 2011), the already small population could become subdivided into even smaller units. The fragmenting effect of the highway has become an even greater concern for wildlife managers since 2006 when a very large road-work project aimed at

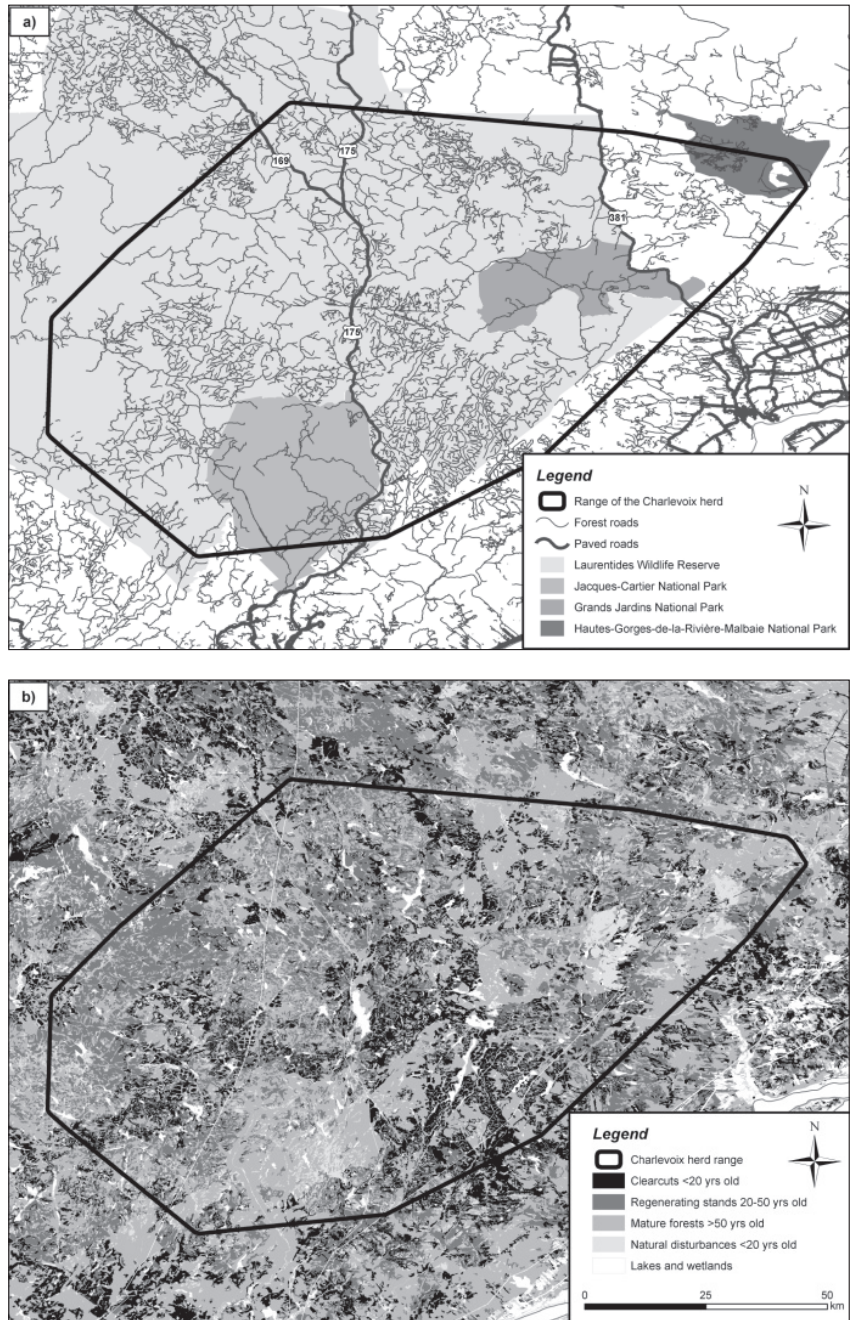


Fig. 3. Characterisation of the range occupied by the reintroduced caribou herd in Charlevoix between 2004 and 2010 (MCP 100%). Habitat characteristics were determined using ecoforest maps updated in 2009 by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF). (a) Map showing road density (both paved and forest roads) and boundaries of the Laurentides Wildlife Reserve, Jacques-Cartier National Park, Grands-Jardins National Park and Hautes-Gorges-de-la-Rivière-Malbaie National Park. (b) Map showing the abundance and configuration of clearcuts, regenerating stands, mature forest and naturally disturbed forest stands.

rebuilding the highway from a two-lane highway into a four-lane dual carriageway was initiated.

Changes in the predator – prey system

The apparent competition hypothesis (Bergerud & Elliot, 1986; Seip, 1992)—that links changes in forest age and structure following timber harvest and fire to increases in moose and wolf abundance—is now well accepted in the literature as one of the mechanisms involved in the North American caribou decline (James *et al.*, 2004; Wittmer *et al.*, 2005; Vors & Boyce, 2009). This hypothesis stipulates that caribou populations suffer from increased predation risk when wolf populations are maintained at high levels by alternative prey (Wittmer *et al.*, 2007), a precarious situation for endangered populations (DeCesare *et al.*, 2010).

In Charlevoix, the situation is slightly different as caribou demography is more constrained by black bear (*Ursus americanus*) predation on calves than by wolf predation on adults. Indeed, results of the telemetry surveys conducted since the caribou reintroduction indicate a variable annual survival rate for adults (69–95%; Cantin, 1991; C. Dussault, unpubl. data) but aerial surveys indicate relatively low recruitment for several years. In agreement, calf survival rate was estimated to be 61% between 1973 and 1990, and only 47% between 2004 and 2007. A recent study has indicated that bears were responsible for the majority (96%) of calf predation events and 65% of overall calf mortality, while wolves were responsible for only 3% of calf mortalities (Pinard *et al.*, 2012). Throughout the caribou range, black bears are often recognized as a major threat for neonates and calves (Adams *et al.*, 1995; Mahoney & Virgl, 2003). Although it is not known whether black bears have long been an important predator of calves in Charlevoix, it is possible that high bear predation pressure is linked to the considerable increase in early successional stands in the area, as these provide a high biomass of berries (Brodeur *et al.*, 2008; Mosnier *et al.*, 2008a), an important black bear food. Black bear density was estimated at 2.2 individuals/10 km² in the study area in 1989 (Jolicoeur, 2004) but more recent data are not available. However, few bears (< 10) were annually harvested until the late 1980s, whereas total annual harvest increased up to 24 individuals thereafter (Sebbane *et al.*, 2008), suggesting that the bear population may have increased since then. Wolf density is moderate in the Charlevoix caribou herd range (0.44 wolf/100 km²; Jolicoeur, 1998) and caribou anti-predator strategies appear to be effective in avoiding them (Pinard *et al.*, 2012).

As demonstrated by Frair *et al.* (2007) for elk (*Cervus elaphus*), we believe that in Charlevoix, caribou were not able to adapt quickly to new threats (i.e., growing bear density) in their environment and that this naivety might have resulted in the recruitment problems currently observed.

A recent study conducted in Charlevoix demonstrated that most black bears are not actively seeking caribou calves during spring, when calves are most vulnerable (Bastille-Rousseau *et al.*, 2011). Instead, they appear to move between vegetation-rich areas, and their frequent movements result in high rates of opportunistic encounters with caribou neonates. The overall impact of black bears on caribou recruitment may be substantial given the suspected high bear density in the heavily logged landscape of Charlevoix. Such opportunistic predation on calves by bears could be exacerbated by the high range fidelity observed for caribou in Charlevoix (Faille *et al.*, 2010), which could have two possible consequences. First, higher calf and female caribou survival could result from increased familiarity with food distribution, escape cover, and predation risk. However, high range fidelity in a modified landscape could also result in an ecological trap because predation risk increases in early successional forests that are attractive to black bears (Brodeur *et al.*, 2008). We strongly believe that this latter situation occurred in Charlevoix, where range fidelity led to high calf mortality. We therefore suggest that the decline of the Charlevoix herd could be explained, in part, by maladaptive habitat selection behaviour (i.e., range fidelity in an unsuitable habitat matrix; Faille *et al.*, 2010).

Uncertain future

Although caribou are still present in the Charlevoix region approximately 40 years after their reintroduction, it would be hasty to conclude that this reintroduction was a complete success, based on recent findings and as suggested by Bergerud & Mercer (1989). Continuous adaptive measures must be implemented to ensure population persistence. Indeed, this case-study exemplifies the fragile equilibrium between habitat, predators, and caribou. Caribou is a highly-adaptable species that may persist for a long time in adverse environments (Vors *et al.*, 2007); however, long time periods (> 40 years) are required for harvested stands to become unattractive to wolves and bears, and to become a suitable lichen-rich caribou habitat again. Telemetry flights recently revealed that many adult caribou in Charlevoix have died during the last few years, most of them from wolf predation. The Charlevoix herd has been experienc-

ing low recruitment over a long period of time, and many reproductive females are reaching the end of their effective reproductive life. For instance, several females have been followed via telemetry for >12 years, and we believe that these older females may become senescent and more vulnerable to predation, a situation that could lead to rapid population extirpation. Wittmer *et al.* (2010) underlined the negative impact of an increasing proportion of early successional forest stands on both adult female survival rate and caribou density, suggesting that caribou populations might face extinction within < 200 years.

Our review of the Charlevoix reintroduction supports the conclusions of many researchers regarding the proximate (i.e., numerical response of alternative prey and predators) and ultimate (i.e., profound habitat modifications) causes of the observed decline (Bergerud & Mercer, 1989; Racey & Arsenault, 2007; DeCesare *et al.*, 2010). Accordingly, we strongly suggest that immediate action be taken to preserve the reintroduced caribou population in Charlevoix. Both logging and recreational activities that are well established throughout the herd's range are resulting in a functional loss of suitable habitat for caribou while simultaneously favouring predator and alternative prey populations. Preserving caribou in a landscape such as in the Laurentides Wildlife Reserve, where human activities are entrenched, will require socio-economical and ecological compromises. A crucial step was recently taken by the Québec government with the publication of a caribou habitat management plan (Lafleur *et al.*, 2006). This plan is now in action and forest companies are requested to follow some important guidelines. It specifically aims to protect critical caribou habitat, maintain a minimum amount of suitable caribou habitat within the herd's range, and limit human disturbance and the development of road networks within critical caribou areas. Considering that recent research identified black bear as the most important threat to caribou recruitment in Charlevoix, we believe that the management plan could be complemented by requesting outfitters to increase bear harvest and forest managers to control deciduous species, especially grasses and berry-shrubs, within regenerating stands. Because wolf harvest is still important in this area and as wolves currently have only a slight influence on caribou recruitment according to Pinard *et al.* (2012), we do not believe that more pressure on the wolf population is necessary at this time. Similar to Environment Canada (2008a), we think that there is a habitat disturbance threshold above which the conservation of a small isolated herd like that of Charlevoix might become very difficult. We believe that the conserva-

tion of the Charlevoix caribou cannot be ensured solely by protection in protected areas, as exemplified by the recent extirpation of caribou in Banff National Park (Alberta, Canada; Hebblewhite *et al.*, 2010; see also Brashares, 2010).

As previously mentioned, the development of the road network continues in the Charlevoix caribou range—one of the largest roadwork projects in Canada in recent years. The overall impact of this road construction has yet to be explored in detail. In addition, a substantial proportion of the new right-of-way will be fenced to prevent moose–vehicle collisions, further limiting connectivity among caribou groups. An ongoing research project aims to assess the impacts of this new highway and fence on the Charlevoix caribou herd. We can only hope that current mitigation measures such as wildlife passages will allow caribou to move safely from one side to the other, thereby allowing access to some highly suitable winter habitats and, more importantly, increase connectivity between groups on both sides of the highway. Considering the above-mentioned threats, it is obvious that the reintroduced caribou herd of Charlevoix is facing an uncertain future and, if action is not taken soon, it is at high risk of being extirpated in the coming decades.

Lessons from the Charlevoix experiment

Improving the likelihood of a successful caribou reintroduction requires consideration of several very important factors. First, we believe that caribou reintroduction (as any other conservation effort) must be based on a rigorous, *a priori* estimation of the costs and probability of success (Schneider *et al.*, 2010), and must be supported by population viability analyses to assess the relative need for and benefits from animal translocation (DeCesare *et al.*, 2011). We judge that most reintroductions would be compromised if conducted in areas where predator and alternative prey populations are abundant and diversified, especially if translocated animals have not experienced similar predation risk and predator diversity (Frair *et al.*, 2007). Second, it is imperative to support reintroduction with a habitat management plan that will protect suitable caribou habitat, prevent habitat modifications favouring predator and alternative prey populations, and favour restoration of caribou habitat. Indeed, reintroduction success increases substantially when the causes of the original decline are removed (IUCN, 1987; Fischer & Lindenmayer, 2000; DeCesare *et al.*, 2011). Finally, if a reintroduction is attempted in a highly disturbed landscape, we consider that reducing predator (Bergerud, 2007)—and

even alternative prey (Latham *et al.*, 2011)—populations might be necessary. Predator control, although logistically difficult to implement and ethically sensitive in the public opinion (Latham *et al.*, 2011), has already proven efficient in increasing caribou recruitment in northern British Columbia (Seip, 1992) and in eastern Québec (Mosnier *et al.*, 2008b), at least on a short-term basis; it is also less expensive (relatively speaking) than protecting and restoring areas (Schneider *et al.*, 2010). Even though wolves are usually recognized as the main predators of caribou throughout the species' range, we urge managers not to overlook the role of bears as calf predators. We recognize that predator removal can be an effective short-term strategy to release pressure on an endangered prey species, but stress that it should be accompanied by suitable habitat management to dampen the influence of habitat alteration (an ultimate factor of caribou decline) on a long-term basis (DeCesare *et al.*, 2010). Moreover, wolf and bear control—if applicable—needs to be supported by detailed information on predator populations and pursued until the landscape becomes suitable to caribou and unsuitable to predators, which is hardly achievable on large territories. Despite difficulties inherent in applying such exceptional measures, we believe that conservation efforts should not be limited only to protection and restoration of habitats in highly disturbed landscapes (Bergerud, 2007). Because low recruitment is often a problem, reintroduced caribou populations will age and declines will likely ensue.

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