

# Historical Changes and Current Distribution of Caribou, *Rangifer tarandus*, in Quebec

REHAUME COURTOIS<sup>1,2,3</sup>, JEAN-PIERRE OUELLET<sup>2</sup>, ANDRÉ GINGRAS<sup>4</sup>, CLAUDE DUSSAULT<sup>5</sup>, LAURIER BRETON<sup>1</sup> and JEAN MALTAIS<sup>6</sup>

<sup>1</sup>Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, 675, René-Lévesque, Est, 11<sup>e</sup> étage, boîte 92, Québec, Québec G1R 5V7 Canada; e-mail: rehaume.courtois@fapaq.gouv.qc.ca

<sup>2</sup>Université du Québec à Rimouski, Département de biologie et des sciences de la santé, Centre d'études nordiques, 300, Allée des Ursulines, Rimouski, Québec G5L 3A1 Canada

<sup>3</sup>Université Laval, Département de foresterie et de géomatique, Cité Universitaire, Ste-Foy, Québec G1K 7P4 Canada

<sup>4</sup>Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune, 818, boulevard Laure, Sept-Îles, Québec G4R 1Y8 Canada

<sup>5</sup>Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune, 3950 boulevard Harvey, 4<sup>e</sup> étage, Jonquière, Québec G7X 8L6 Canada

<sup>6</sup>Conseil de l'industrie forestière du Québec, 1175, avenue Lavigerie, Bureau 200, Sainte-Foy, Québec G1V 4P1 Canada

Rehaume Courtois, Jean-Pierre Ouellet, André Gingras, Claude Dussault, Laurier Breton, and Jean Maltais. 2003. Historical changes and current distribution of Caribou, *Rangifer tarandus*, in Quebec. *Canadian Field-Naturalist* 117(3): 399–414.

We examined published historical information, reports on aerial surveys conducted since 1953, and harvest data collected since 1971 to describe changes in the distribution and abundance of Caribou (*Rangifer tarandus*) in Québec. The southern limit of the Caribou distribution diminished considerably in the late 19<sup>th</sup> century, and the decline in numbers probably continued until the 1960s and 1970s east of the 62<sup>nd</sup> meridian. South of the 49<sup>th</sup> parallel, only four small populations still persist. Despite the fact that all Caribou of the province were assigned to the same sub-species (*R. t. caribou*), three ecotypes with specific habitats and behaviour are found. The Barren-Ground ecotype, the only migratory form, is found north of the 52<sup>nd</sup> parallel. This ecotype currently occupies  $\approx 255\,000\text{ km}^2$  in fall and winter, mainly in the ecological subzones of the forest tundra and the taiga. The Barren-Ground Caribou was characterized by a very low abundance from the end of the 19<sup>th</sup> century until the mid-1950s, but increased markedly thereafter reaching over a million individuals at the beginning of the 1990s. Populations of the Mountain ecotype have been identified in the southeastern and, possibly, in the northeastern parts of the province. The latter Mountain population is virtually unknown. The southeastern population is sedentary and uses mainly the boreal forest. This population has decreased over the last century and currently numbers only  $\approx 140$  individuals. Finally, the Forest-Dwelling ecotype is found discontinuously, mainly between the 49<sup>th</sup> and 55<sup>th</sup> parallels. Its current distribution covers  $\approx 235\,000\text{ km}^2$ , mainly east of the 72<sup>nd</sup> meridian. This sedentary ecotype is found almost exclusively in the boreal forest, principally in areas with long forest fire cycles. Its abundance has also decreased over the years. Large Forest-Dwelling populations still persisted during the 1950s and 1960s, but they apparently disappeared. The current abundance is not known precisely, but based on density estimates and considering the current distribution, it probably does not exceed 3000 individuals. Current data are insufficient to identify precisely the causes of the population decline, although hunting seems to be an important proximal cause.

Key Words: Caribou, *Rangifer tarandus*, Moose, *Alces alces*, distribution, ecotype, history, hunting, Québec.

Nous avons utilisé les données historiques publiées, les rapports d'inventaires aériens réalisés depuis 1953 et les statistiques de récolte sportive colligées depuis 1971 pour décrire les changements dans la répartition et l'abondance du Caribou (*Rangifer tarandus*) au Québec. La limite méridionale de l'aire de répartition a beaucoup diminué à la fin du 19<sup>e</sup> siècle et la régression s'est probablement poursuivie durant les années 1960 et 1970 à l'est du 62<sup>e</sup> méridien. Au sud du 49<sup>e</sup> parallèle, on ne retrouve plus que quatre petites populations. Bien que tous les caribous du Québec soient considérés appartenir à la même sous-espèce (*R. t. caribou*), on distingue trois écotypes fréquentant des milieux différents et arborant des comportements spécifiques. Au nord du 52<sup>e</sup> parallèle, on retrouve l'écotype Toundrique, lequel est migrateur. Ces Caribous se répartissent sur  $\approx 255\,000\text{ km}^2$  durant l'automne et l'hiver, principalement dans les sous-zones écologiques de la toundra forestière et de la taïga. Cet écotype était peu abondant entre la fin du 19<sup>e</sup> siècle et le milieu des années 1950, mais il s'est accru considérablement pour atteindre plus d'un million d'individus au début des années 1990. Une population de l'écotype Montagnard est présente au sud-est de la province et une autre existe possiblement au nord-est. Cette dernière n'est pas bien connue. Celle du sud-est utilise principalement la forêt boréale. Cette population sédentaire a diminué considérablement depuis une centaine d'années et elle ne compte plus qu'environ 140 individus. Finalement, l'écotype Forestier est présent de façon discontinue, principalement entre les 49<sup>e</sup> et 55<sup>e</sup> parallèles. Ces Caribous sont également sédentaires. On les retrouve presque exclusivement en forêt boréale, principalement là où le cycle des feux de forêt est long. Leur répartition actuelle couvre  $\approx 234\,000\text{ km}^2$ , principalement à l'est du 72<sup>e</sup> méridien. D'importantes populations forestières existaient encore durant les années 1950 et 1960, mais elles semblent avoir disparu. L'abondance actuelle n'est pas connue mais elle pourrait difficilement dépasser 3000 individus si l'on se base sur les estimations de la densité et de l'aire de répartition. Les données disponibles sont insuffisantes pour identifier les causes exactes des diminutions d'effectifs bien que la chasse semble une cause proximale importante.

Mots clés : Caribou, *Rangifer tarandus*, Original, *Alces alces*, chasse, écotype, historique, Québec, répartition.

In North America, the oldest fossils of Caribou (*Rangifer tarandus*) are 50 000 years old (Banfield 1961; Brassard 1979). The species appears to have been abundant in the taiga, from the edge of the glaciers to New Mexico. Subsequent climatic changes seem to have considerably modified its distribution. At the arrival of the first Europeans, Caribou were found in areas currently occupied by all the Canadian provinces as well as the American states bordering on Canada. In the eastern part of the continent, Caribou were found in the present-day states of New York, Vermont, New Hampshire and Maine (Moisan 1956). However, today the Gaspésie Caribou population in eastern Quebec is the only remaining population south of the St. Lawrence River.

Despite the fact that all Caribou of the province were assigned to the same sub-species (*R. t. caribou*), three ecotypes (Barren-Ground, Mountain, Forest-Dwelling) can be identified based on habitat use, behaviour and genetics (Courtois et al. 2003). Many studies have examined the abundance, population dynamics and habitat of the Barren-Ground Caribou in northern Quebec and of the Gaspésie Mountain Caribou. The spectacular increase in numbers of the first ecotype and the precarious status of the second have made them favourite subjects for limitation and regulation mechanism studies (Messier et al. 1988; Crête and Desrosiers 1995; Couturier et al. 1996; Crête et al. 1996). Some studies have also been carried out on northern populations affected by hydroelectric developments (Brown et al. 1986; Paré 1987) and on the isolated populations in southern Quebec (Vandal 1985; Jolicoeur 1993\*; Paré and Brassard 1994\*; Crête and Desrosiers 1995; Ouellet et al. 1996). However, the Forest-Dwelling Caribou in the central part of the province remains largely unknown. Studies carried out on these populations are limited to surveys conducted in the 1960s and 1970s and, as no synthesis of available data has been done, their current distribution and status remain speculative.

This study had three main objectives: (1) to provide a comprehensive analysis of available data on Caribou in order to describe historical changes in Quebec; (2) to determine the current distribution of Caribou with the aim of identifying areas where this species should be considered a priority in forest management, and (3) to explore potential causes of temporal changes in Caribou abundance. As the magnitude of the harvest provides a relative index of abundance (Crête and Dussault 1987), we used harvest data to verify whether Caribou and Moose (*Alces alces*) harvests were inversely correlated. Because Wolf (*Canis lupus*) and Moose abundance are positively correlated (Messier 1994, 1995; Larivière et al. 2000), a decrease in Caribou harvest while Moose were increasing would suggest that Caribou abundance could be limited by Wolf predation (Bergerud 1974, 1988; Martin 1980; Ber-

gerud and Mercer 1989; Jolicoeur 1993\*; Seip 1992). Otherwise, Caribou could be limited to a greater extent by changes in harvest rate.

## Methods

The historical distribution range was determined using published information (newspaper articles, activity reports, legislation and interviews; Moisan 1956; Martin 1980; Guay 1983; Bellehumeur et al. 1985\*; Gingras et al. 1989; Jolicoeur 1993\*). The distribution and abundance of Caribou from the 1950s to the 1970s were derived from 42 aerial survey reports (> 70 surveys). Various techniques were used. Until the early 1980s, surveys mainly consisted of systematic coverage of large blocks (9000 to 92 700 km<sup>2</sup>) carried out between late February and mid-April, by airplane (Dornier 28-B, DC-3, Cessna 185), using north-south or east-west transects spaced 16.1 km apart at an altitude of 250-350 m (Brassard 1967\*; Le Hénaff 1976a,b\*). Animals were counted from each side of the aircraft at a distance of 500 m. The crews included a pilot, a navigator-observer and two other observers seated in the rear of the aircraft. The crews abandoned the flight lines to count all the Caribou when large groups (>75 individuals) or extensive track networks were observed (Le Hénaff 1976a\*). The study sites were then post-stratified according to the numbers observed (population ≥ 75 individuals; scattered Caribou). The average density calculated for the transects in each stratum were extrapolated to obtain the total population per stratum and for the entire study area, without calculating the confidence interval or correcting for the visibility bias. The counts were likely underestimates, but these surveys provide a reliable picture of the distribution of Caribou on a regional scale. Beginning in the 1970s, surveys were carried out using sample plots, usually of 60 km<sup>2</sup>, in order to calculate the variance of the estimates (Joly and Brassard 1980\*; Brassard 1982\*; Barnard 1983\*; Gingras and Malouin 1993\*; Bourbonnais et al. 1997\*).

Caribou observations have been obtained through various sources since 1954 by the Société de la faune et des parcs du Québec (FAPAQ) and stored in a geographic information system (Anonymous 1996). The database includes 3825 records (< 1980: 436 records; 1980-1989: 1344; 1990-1999: 2045) from aerial surveys of Caribou conducted within limited areas (1333), chance observations made by individuals or aircraft pilots or by FAPAQ personnel (967), during aerial surveys of Moose (98), and finally, observations made during telemetry work in various regions (1427). Sport and subsistence hunting (234 191), as well as other known causes of mortality (e.g., poaching, road accidents, some cases of predation: 1302) documented since 1971 (Sebbane and Courtois 2001\*) were also included. To give equal weight to the various sources of information, data were utilized in the form of a presence/absence index calculated for every 10 km<sup>2</sup> of the

\*Internal reports are listed in the Document Cited section

province. Zones of continuous distribution were identified by means of the fixed kernel method using the 90% distribution probability, a grid cell of 0.1 and a smoothing factor of 0.4 (Hooge and Eichenlaub 1997). The same technique with 70% distribution probability was used to determine the extent of the zones of intensive use. Kernels were superimposed onto ecological (Anonymous 2000\*) and forest fire cycle maps (Gauthier et al. 2001) to identify ecological zones, sub-zones and forest fire cycle of areas frequented by Caribou.

Finally, the sport harvest was used to describe changes that have occurred since 1971, in terms of abundance (Caribou harvested) and population structure (males and calves per 100 females, % of calves), in the zones of intensive use. The fall (1 August – 30 November) and winter (1 December – 30 April) harvests were considered separately when two hunting seasons existed. Characteristics of the harvest are likely to differ during the two seasons since the winter hunt mainly targets Barren-Ground Caribou. The Spearman coefficient was used to test the relationships between Caribou and Moose harvests as well as between Caribou harvest and productivity (% of calves, calves per 100 females) and harvest rate (males per 100 females) indices derived from hunting statistics. Correlation analyses were conducted for the 1971-1999 period, for each population separately.

## Results

### *Historical Trends*

In Québec, the first explorers noted the presence of Caribou on both shores of the St. Lawrence River, from the present-day location of Québec City (46° 48' N, 71° 15' W) to Gaspé (48° 49' N, 64° 30' W), and over the entire Laurentian plateau, in the centre of the Québec-Labrador peninsula (Martin 1980; Jolicoeur 1993\*) (Figure 1). Initially, the Caribou was not heavily exploited, but hunting increased during the 19<sup>th</sup> century with the growth of the human population and as the colonists moved farther into the backcountry. The Caribou had disappeared from the St. Lawrence valley by 1850 (Martin 1980; Guay 1983). However, between 1865 and 1875, it could still be found on the north shore of the St. Lawrence River (Laurentides National Park, 47° 44' N, 71° 26' W; Montréal, 45° 33' N, 73° 39' W; Outaouais, 45° 42' N, 76° 00' W; Saint-Maurice, 46° 37' N, 72° 43' W) and from the Matapedia valley (48° 22' N, 67° 29' W) to the eastern part of the Gaspé Peninsula (Moisan 1956; Guay 1983; Gingras et al. 1989). By the early 20<sup>th</sup> century, the Caribou was already rare in inhabited areas, even in the Québec City region and farther east, as far as the Matapedia valley (Guay 1983). Hunting remained significant in the eastern part of Laurentides National Park (the part occupied today by Parc des Grands-Jardins: 47° 48' N, 70° 49' W) up until 1914, but the Caribou also disappeared from that area during the 1920s (Jolicoeur 1993\*).

The situation evolved in a similar manner in the Saint-Maurice valley. For example, Caribou were observed and hunted regularly by the Triton Club up until the early 20<sup>th</sup> century, but were considered rare by 1915 (Gingras et al. 1989). It was only observed exceptionally after 1920, although one Caribou was observed in 1941, after many years with no sightings. The same situation was noted in southwestern Quebec. Caribou were still found there in the late 1800s, but seem to have been heavily exploited (Guay 1983). Further north, in Témiscamingue (46° 48' N, 79° 00' W) and Abitibi (48° 15' N, 79° 02' W), Caribou probably decreased in abundance at the beginning of colonization, during the 1920s-1930s. In eastern Ontario, Cumming and Beange (1993) place the southern limit of the Caribou at about the 48<sup>th</sup> parallel in 1900, at the 49<sup>th</sup> in 1950, and at the 50<sup>th</sup> in 1990. The trends were probably similar in western Quebec.

In northern Quebec, the narrative history of the Native peoples suggests the presence of three populations, one near Hudson Bay in the region of lakes Guillaume-Délisle (56° 15' N, 76° 30' W) and à l'Eau Claire, a second population to the east, which spent the summer on the high plateaus of Labrador and migrated to the George River (55° 16' N, 65° 53' W) in winter, and a third population which moved between summer and winter, from southern Ungava Bay (58° 37' N, 67° 48' W) to the Caniapiscou River (54° 48' N, 69° 50' W), in east-central Quebec (Brassard 1979). These populations are thought to have decreased between the mid-19<sup>th</sup> century and the mid-1950s, but then to have increased, similarly to other northern populations (Bergerud 1988; Couturier et al. 1996; Morneau and Payette 1998). In contrast, the southern Forest-Dwelling populations apparently did not recover.

### *Recent Trend According to Aerial Surveys*

The first aerial surveys carried out in Quebec were regional in scope. In 1953 and 1954, Moisan (1957) surveyed the Gaspésie Caribou population, which then comprised between 700 and 1500 Caribou. Two surveys were carried out in northern Quebec in 1954 and 1956, and the population of the Ungava Peninsula was then estimated at 6120 Caribou (Banfield and Tener 1958). In 1963, Desmeules and Brassard (1963\*) estimated that 60 000 Caribou were living in central and eastern Quebec.

The first wild ungulate aerial survey program was carried out between 1963 and 1968 (Brassard 1968\*). It confirmed a reduction in the distribution range of Caribou in Quebec. South of the 49<sup>th</sup> parallel, only two isolated populations were found, in Gaspésie and Val-d'Or. Farther north, numerous isolated groups (called scattered Caribou by the author) and four areas of high concentration were found: one on the North Shore at the Labrador border, two in central Quebec in the Bienville and Caniapiscou Lake regions, and finally, one in the northeastern part of the province at the Labrador border. The total population of the

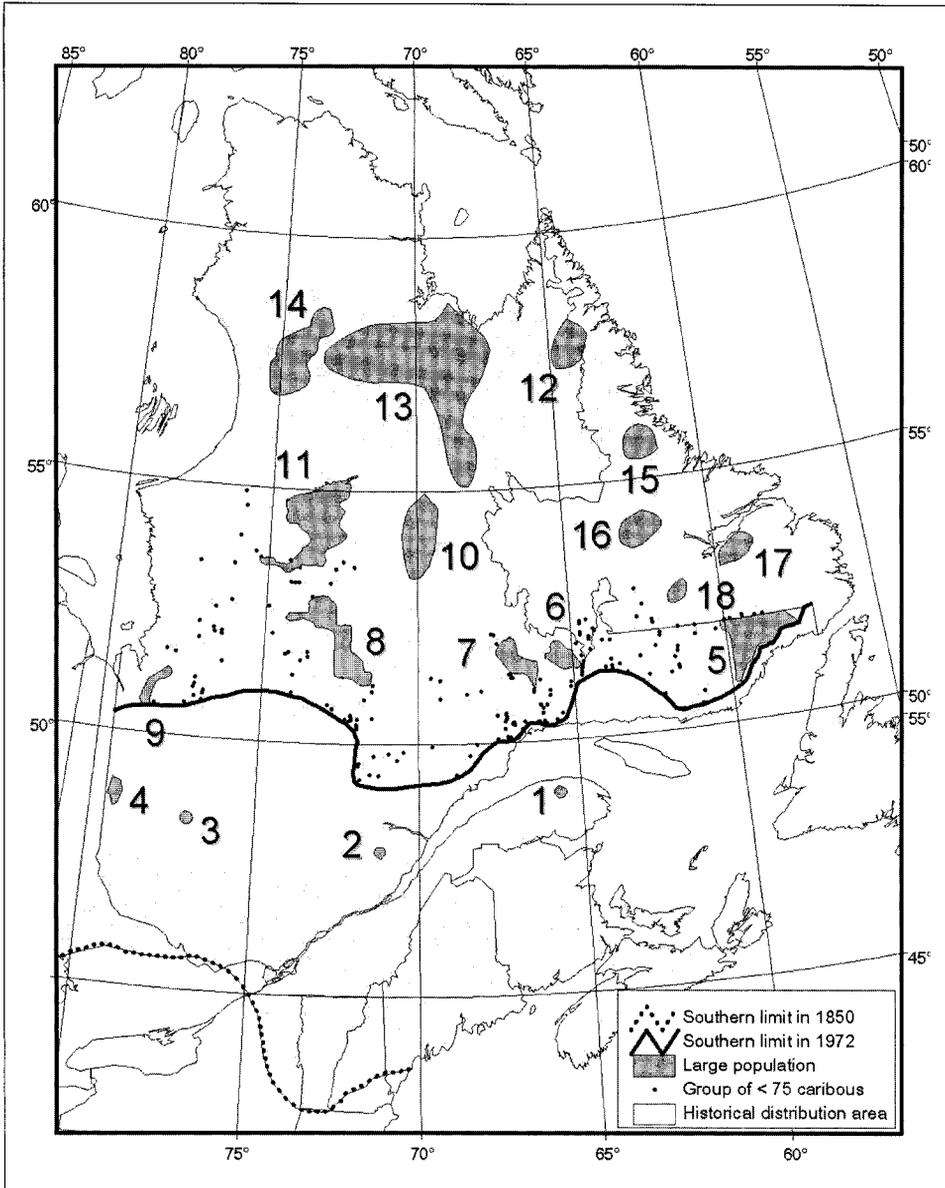


FIGURE 1. Distribution of Caribou in Quebec and adjacent jurisdictions before 1850 and in 1972-1973. Numbers refer to main populations located in 1972 and 1973: (1) Gaspésie; (2) Charlevoix; (3) Val-d'Or; (4) La Sarre; (5) Saint-Augustin; (6) Magpie River (Lac Joseph); (7) Petit Lac Manicouagan; (8) Mistassini Lake; (9) Rupert; (10) Caniapiscau Lake; (11) Bienville Lake; (12) Torngat Mountains; (13) George River (spring); (14) Leaf River; (15) George River (winter); (16) Red Wine Mountains; (17) Mealy Mountains; (18) Dominion Lake (Bergerud 1967; Brassard 1968\*, 1972\*, 1979, 1982\*; Pichette and Beauchemin 1973\*; Barnard 1983\*; Paquet 1997\*).

province was then estimated at between 68 000 and 90 000 Caribou, spread over an area of 1 007 432 km<sup>2</sup> (7-9 Caribou/100 km<sup>2</sup>).

The first exhaustive inventories were carried out in 1972 and 1973, when Quebec and Labrador were entirely covered from the 49<sup>th</sup> parallel up to Hudson Strait

(Brassard 1972\*; Pichette and Beauchemin 1973\*). The northern populations appeared to be concentrated between the south of Ungava Bay and the east of Hudson Bay (Figure 1). About 20 Forest-Dwelling populations were identified, of which six comprised a few hundred to a few thousand Caribou. At that time the

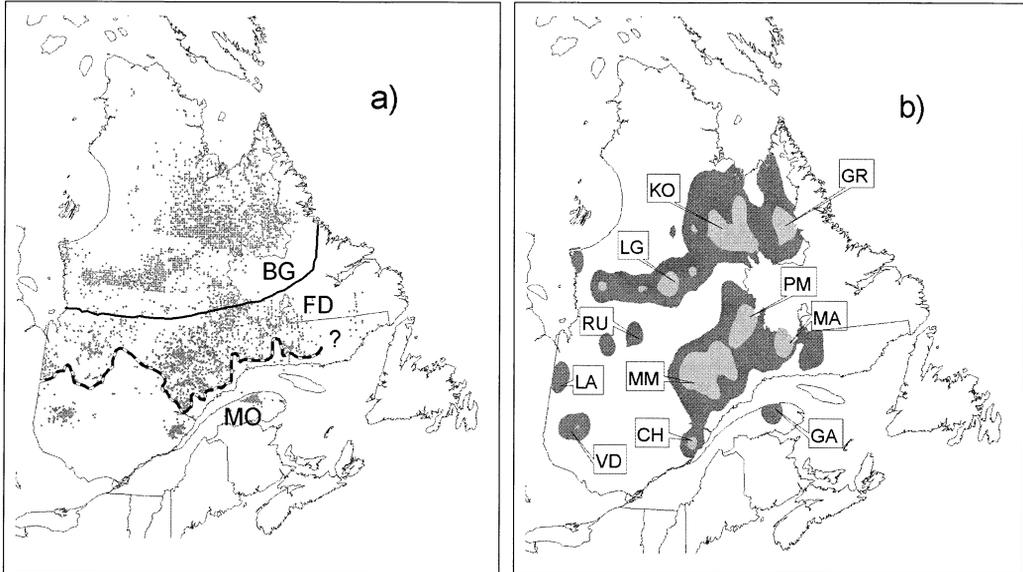


FIGURE 2. Main areas frequented by Caribou in Quebec. (a) presence per 10 km<sup>2</sup>; and southern limit of Barren-Ground (BG: solid line), Forest-Dwelling (FD: broken line) and Mountain (MO) ecotypes distribution; southern limit of Forest-Dwelling ecotype unknown in eastern Quebec (?); (b) zones of continuous distribution (90% kernels) and zones of intensive use (70% kernels) of Barren-Ground (KO: Koksoak; LG: LG-4; GR: George River), Mountain (GA: Gaspésie) and Forest-Dwelling (CH: Charlevoix; VD: Val-d'Or; LA: La Sarre; RU: Rupert; MM: Manouane-Manicouagan; PM: Petit Lac Manicouagan; MA: Magpie) ecotypes.

Quebec population had been estimated at  $\approx 120\,000$  Caribou north ( $16.5/100\text{ km}^2$ ) and  $12\,000$  south ( $3.7/100\text{ km}^2$ ) of the 52<sup>nd</sup> parallel (Brassard 1979).

Subsequent surveys, usually carried out in the high concentration areas identified in 1972 and 1973, showed an expansion in the northern populations and a reduction in the southern ones. The northern Barren-Ground Caribou numbers rose from 3500 in the mid-1950s to about 1 000 000 individuals in 1993 (Couturier et al. 1996). The southern populations, more dispersed and sometimes rather indistinct, were monitored less intensively. The Gaspésie (140-200 Caribou) and Charlevoix (100-125 Caribou) populations were the best studied, the first one due to its precarious status, and the second because it was recently reintroduced. More details on known populations are provided in Audet (1979), Courtois et al. (2001\*), and de Bellefeuille (2001\*).

#### Current Distribution According to Presence Indices

Information derived from sport hunting, large mammal surveys and chance observations show that the Caribou distribution has not changed drastically since 1972 (Figure 2a). Barren-Ground Caribou ecotype is found north of the 52<sup>nd</sup> parallel. With the exception of the Charlevoix ( $47^{\circ} 48' \text{ N}$ ,  $70^{\circ} 49' \text{ W}$ ), Val-d'Or and La Sarre ( $48^{\circ} 46' \text{ N}$ ,  $79^{\circ} 07' \text{ W}$ ) isolated populations, the Forest-Dwelling ecotype is found exclusively between the 49<sup>th</sup> and 55<sup>th</sup> parallels whereas the Gaspésie Mountain ecotype is the only population south of the

St. Lawrence River. The main difference from the 1972 survey is the near absence of Caribou in the eastern part of the province, south of Labrador.

The 90% kernels revealed two important zones of continuous distribution (Figure 2b). The first ( $255\,138\text{ km}^2$ ), oriented on a north-east axis in northern Quebec, corresponds to the area frequented by the Barren-Ground Caribou during fall and winter. The second important 90% kernel ( $234\,538\text{ km}^2$ ), also oriented on a north-east axis and located between the Saguenay fjord and Labrador, corresponds to the area mainly used by the Forest-Dwelling Caribou. Other 90% kernels identify isolated populations: the Gaspésie Mountain population, and the Forest-Dwelling populations of Charlevoix, Val-d'Or and La Sarre, as well as two groups east of James Bay. The latter two, identified in 1991 (Anonymous 1992\*), correspond either to the Rupert Forest-Dwelling population identified by Brassard (1972\*) or to subsets of the George River or Leaf River Barren-Ground populations.

The 70% kernels (zones of intensive use) cover  $115\,282\text{ km}^2$  and delimit three main areas in the north and three others in central Quebec. The three northern 70% kernels probably correspond to sub-groups of the George River population, exploited at different annual and seasonal periods. The western kernel is located in the region of the LG-4 hydroelectric dam, the second corresponds to the location of the George River population as identified by Pichette and Beau-

TABLE 1. Percentage of the zones of intensive use and the zones of continuous distribution of Caribou by ecological zone (in bold) and sub-zone (italics). The extent of intensive use and continuous distribution zones was determined using presence indices obtained from harvest, aerial surveys, scientific research and chance observations of Caribou. See Figure 2 for location of the zones of intensive use. The ecological classification follows Anonymous (2000\*).

	Zones of intensive use (70% kernels)					Zones of continuous distribution (90% kernels)					
	NT - MF <sup>a</sup>	B - BF <sup>b</sup>	B - T <sup>c</sup>	B - FT <sup>d</sup>	A - LA <sup>e</sup>	NT - MF	B - BF	B - T	B - FT	A - LA	km <sup>2</sup>
Barren-Ground population (George River)											
LG-4	-	-	100.0	-	-						
Koksoak	-	-	66.9	33.1	-						
George River	-	-	12.9	77.3	9.8			46.4	48.3	5.3	255 138
Mountain population											
Gaspésie	-	-	-	-	-						
Forest-Dwelling populations											
Charlevoix	4.3	95.7	-	-	-	17.2	82.8	-	-	-	6818
Val-d'Or	-	100.0	-	-	-	20.8	79.2	-	-	-	10 954
La Sarre	-	-	-	-	-	37.3	62.7	-	-	-	13 849
Eastern James Bay	-	-	-	-	-	-	100.0	-	-	-	8463
Manouane-Manicouagan	-	100.0	-	-	-	-	99.1	0.9	-	-	12 238
Petit Lac Manicouagan	-	67.4	32.6	-	-	0.5	85.5	14.0	-	-	171 040
Magpie	-	100.0	-	-	-	-	93.0	7.0	-	-	17 994

<sup>a</sup> **Northern temperate** - *mixedwood forest*: forest of northern hardwoods and conifers (bioclimatic domain of balsam fir - yellow birch forest).

<sup>b</sup> **Boreal** - *boreal forest*: continuous forest, dominated by relatively dense formations of boreal coniferous or shade intolerant hardwood species (bioclimatic domain of balsam fir-white birch forest and spruce-moss forest).

<sup>c</sup> **Boreal** - *taiga*: open coniferous forest with lichen mat (bioclimatic domain of spruce-lichen forest).

<sup>d</sup> **Boreal** - *forest-tundra*: mosaic of forest of varying density and tundra dominated by shrubs and lichens (bioclimatic domain of forest tundra).

<sup>e</sup> **Arctic** - *low arctic*: absence of trees, presence of continuous permafrost, tundra vegetation dominated by shrubs, herbaceous species, grass-like plants, mosses and lichens (bioclimatic domain of shrub arctic tundra).

\*The zones of continuous distribution of these groups overlapped; no specific data were available.

chemin (1973\*), near the Koksoak River, while the eastern kernel coincides with the site identified by Bergerud (1967), at the source of the George River. The first southern 70% kernel, north of the Saguenay, corresponds to the Manouane-Manicouagan populations, identified as scattered Caribou by Brassard (1972\*). The second southern kernel, northeast of the first, likely corresponds to the Petit Lac Manicouagan population, hunted in fall in the 1970s and 1980s, but also in winter concurrently with Barren-Ground Caribou since the early 1990s. The kernel south of Labrador represents the Magpie River population (also called the Lac Joseph population).

Nearly all the areas of the zones of continuous use and the zones of intensive use were located in the boreal ecological zone (Table 1). The extent of the ecological sub-zones differed among kernels, but the boreal forest and the taiga dominated, except for the Barren-Ground ecotype which used the forest tundra and the taiga equally. The populations in Gaspésie, Charlevoix and Val-d'Or were the only ones located at the edge of the mixedwood forest.

Forest fire cycle maps (Gauthier et al. 2001) indicated that most Caribou observations were made in areas with long fire cycles (Table 2). The zones of continuous distribution were dominated by long or very long fire cycles (200-500 years: 77.8% of the area; 100-200 years: 5.8%; <100 years: 16.4%), and 95.7% of the zones of intensive use were located in sites having fire cycles of 200-500 years. Forest fire cycles were not available for the Barren-Ground Caribou kernels but Payette et al. (1989) reported very long fire cycles (> 7800 years) in the forest tundra and the taiga.

*Change in Harvest Characteristics Since 1971*

Over the last 30 years, Caribou hunting has been permitted in the hunting zones where the six main 70% kernels were located (Table 3). Total harvest and harvest per unit area were particularly high in the three kernels of the Barren-Ground populations but also in the Magpie and Petit Lac Manicouagan populations. In contrast to Caribou, Moose harvest per unit area decreased from south to north.

Trends in harvest differed between kernels (Figure 3). A significant drop was noted in the George River 70% kernel. This decrease was compensated by an increase of the same magnitude in the Koksoak kernel in the mid-1980s, and later in the LG-4 kernel. In the Manouane-Manicouagan, Petit Lac Manicouagan and Magpie populations, the fall harvest decreased slightly or drastically during the 1970s or the 1980s.

Winter hunting was permitted in the Petit Lac Manicouagan kernel and in the northern populations. In northern Quebec, the fall and winter harvests for each kernel showed a similar trend, probably because the same populations were exploited during the two hunting seasons. For Petit Lac Manicouagan, the harvest was about 50 times higher in winter than in fall. The winter season was instituted in order to harvest the

TABLE 2. Percentage of the area of the zones of intensive use and the zones of continuous distribution of Caribou according to length of fire cycle. The extent of the zones was determined using presence indices obtained from harvest, aerial surveys, scientific research and chance observations of Caribou.

	Zones of intensive use (70% kernels)			Zones of continuous distribution (90% kernels)			
	n.d. <sup>1</sup>	< 100 years	100-200 years	n.d.	< 100 years	100-200 years	200-500 years
Mountain population							
Gaspésie	-	-	-	17.2	-	-	82.8
Forest-Dwelling populations							
Charlevoix	4.3	-	95.7	14.0	-	-	86.0
Val-d'Or	-	-	100.0	36.9	-	63.1	-
La Sarre	-	-	-	-	-	100.0	-
Eastern James Bay	-	-	-	60.4	39.6	-	-
Manouane-Manicouagan	-	4.4	95.6	48.3	9.2	0.1	42.3
Petit Lac Manicouagan	100.0	-	-	-	-	-	-
Magpie	100.0	-	-	-	-	-	-

<sup>1</sup>No data available.

\*The zones of continuous distribution of these groups overlapped; no specific data were available

TABLE 3. Mean annual Caribou harvest ( $\pm$  standard error [ $n$  = number of years]), and Caribou and Moose annual harvest per surface area between 1971 and 1999 in the zones of intensive use (70% kernels) where hunting was permitted<sup>a</sup>.

	Caribou harvest		Harvest / 100 km <sup>2</sup>
	Fall	Winter	
Barren-Ground population			
George River			
LG-4	842 $\pm$ 402.8 (8)	2037.4 $\pm$ 579.9 (11)	0.03 $\pm$ <0.01 (9)
Koksoak	1240.7 $\pm$ 228.1 (27)	1042.4 $\pm$ 190.5 (24)	<0.01 $\pm$ - (1)
George River	574.9 $\pm$ 81.4 (28)	264.1 $\pm$ 25.0 (25)	0.01 $\pm$ <0.01 (2)
Forest-Dwelling populations			
Manouane-Manicouagan	22.2 $\pm$ 2.4 (28)	-	-
Petit Lac Manicouagan	10.7 $\pm$ 1.3 (27)	384.4 $\pm$ 108.4 (15)	0.45 $\pm$ 0.03 (29)
Magpie	84.3 $\pm$ 72.0 (16)	53.4 $\pm$ 24.5 (10)	0.16 $\pm$ 0.01 (29)
			0.21 $\pm$ 0.02 (29)

<sup>a</sup> No data are available for the Mountain populations; hunting of the Gaspésie population has not been allowed since 1929 (Moisan 1956), and the Tornat Mountain population was not identified by a 70% kernel, because the harvest was either too low or undocumented.

Barren-Ground Caribou during its southern migration. The high winter harvest suggests that the flux from the George River population was important at the start of the 1990s. In the absence of important changes in hunting effort, the decline in winter harvest after 1992 suggests that the Barren-Ground Caribou did not migrate far enough south to reach the Petit Lac Manicouagan area.

The structure of the harvest also differed between kernels. In northern Quebec, an increase in productivity was noted up until the mid-1980s, at least in the George River kernel, but then underwent a significant decrease (Figure 4). The number of males per 100 females diminished in the George River kernel, whereas it increased in the Koksoak and the LG-4 kernels suggesting that hunters were more selective probably due to a population increase in these areas (Figure 5). The percentage of calves and the number of males per 100 females varied from year to year in the southern populations without conclusive explanation.

The fall harvest of Caribou between 1971 and 1999 was negatively correlated to the Moose harvest in the LG-4 kernel, positively correlated in the Manouane-Manicouagan population, whereas these two variables appeared to be independent in other kernels (Table 4). The temporal change in Caribou harvest was positively correlated to the number of males and calves per 100 females as well as to the percentage of calves in two of the six kernels examined.

## Discussion

Caribou populations seem to have undergone significant growth on a worldwide scale during the 1980s (Bergerud 1988). However, this increase has been mainly due to the Barren-Ground populations, estimated at about 3 000 000 Caribou in the mid-1980s, that is, practically double the numbers estimated a decade earlier. During the same period, the Forest-Dwelling populations barely comprised 325 000 individuals and appeared to have undergone notable but inaccurately quantified decreases (Bergerud 1988; Cumming 1992; Mallory and Hillis 1998). However, some authors express reservations as to the magnitude of the changes due to the inaccuracy of historical information (Bradshaw and Hebert 1996).

### Historical Distribution

There is no doubt as to an historical reduction in the Caribou distribution in Quebec. Except for the Gaspésie population, the species is no longer present south of the St. Lawrence River, where it was frequently sighted until about 1875 (Martin 1980; Guay 1983). However, its precise historical distribution and abundance in the St. Lawrence valley are not known. This area is at present dominated by hardwood and mixedwood forest, unsuitable for Caribou. Mature hardwoods also dominated the forest landscape in the early 19<sup>th</sup> century (Richard 1993), which indicates that Caribou were probably not abundant southwest of

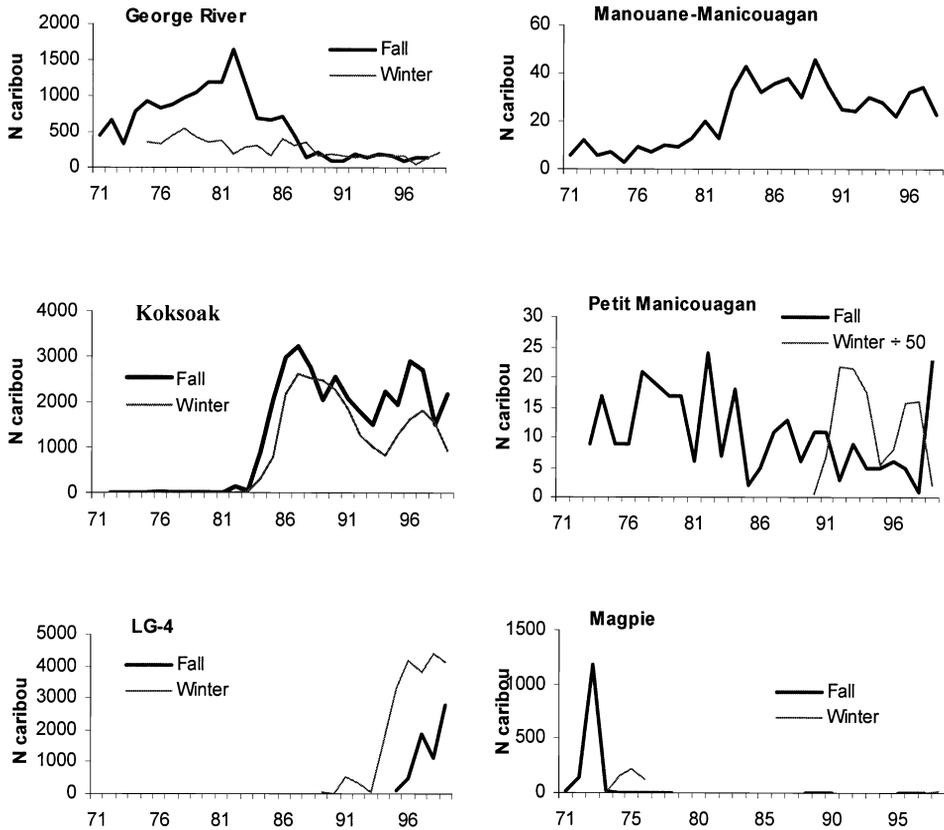


FIGURE 3. Harvest of Caribou in the zones of intensive use (70% kernels) where hunting was allowed between 1971 and 1999.

Quebec City, even at that time. Its distribution was probably limited to sites dominated by coniferous trees.

The main direct causes of the Caribou decline appear to have been overharvesting and predation, and in some cases, the transmission of the Meningeal Worm (*Parelaphostrongylus tenuis*) by White-tailed Deer (*Odocoileus virginianus*) (Bergerud 1974, 1988; Martin 1980; Bergerud and Mercer 1989; Jolicoeur 1993\*). In addition, the development of agriculture and forestry probably led to growth in Moose and deer populations due to conversion of conifer stands to deciduous and mixed stands, which may have favoured an increase in Wolf abundance and, consequently, predation on Caribou (Bergerud 1974; St-Vincent 1981\*; Bellehumeur et al. 1985\*; Gingras et al. 1989; Jolicoeur 1993\*). These habitat modifications may also have favoured the growth of Black Bear (*Ursus americanus*) populations and predation on Caribou calves. There is mounting evidence that habitat changes and increased predation contribute to the decline of Woodland Caribou (Bergerud and Elliot 1986; Seip 1992; Seip and Cichowski 1996).

The effect of any particular cause is difficult to quantify, since habitat changes that led to expansions in Moose, deer and Wolf populations occurred at a time when hunting was very intense. Nevertheless, Caribou disappeared from the southern part of its distribution range simultaneously all across North America. To explain this situation, Bergerud (1974) examined (1) changes in the availability of lichens due to forest fires and logging, (2) the impact of hunting and predation, (3) the combined effects of the availability of lichens and predation, and finally, (4) the simultaneous impact of social pressures (following population growth) and predation. According to Bergerud (1974), only the second hypothesis seemed probable. Caribou can use open habitats and often take traditional routes when travelling; they live in groups, and are not fearful, making them very vulnerable to hunting. Although there may not necessarily be a cause and effect relationship, stories about excessive hunting abound and the disappearance of the Caribou coincides with the arrival of the repeating rifle (St. Cyr 1873; Moisan 1956; Martin 1980; Guay 1983;

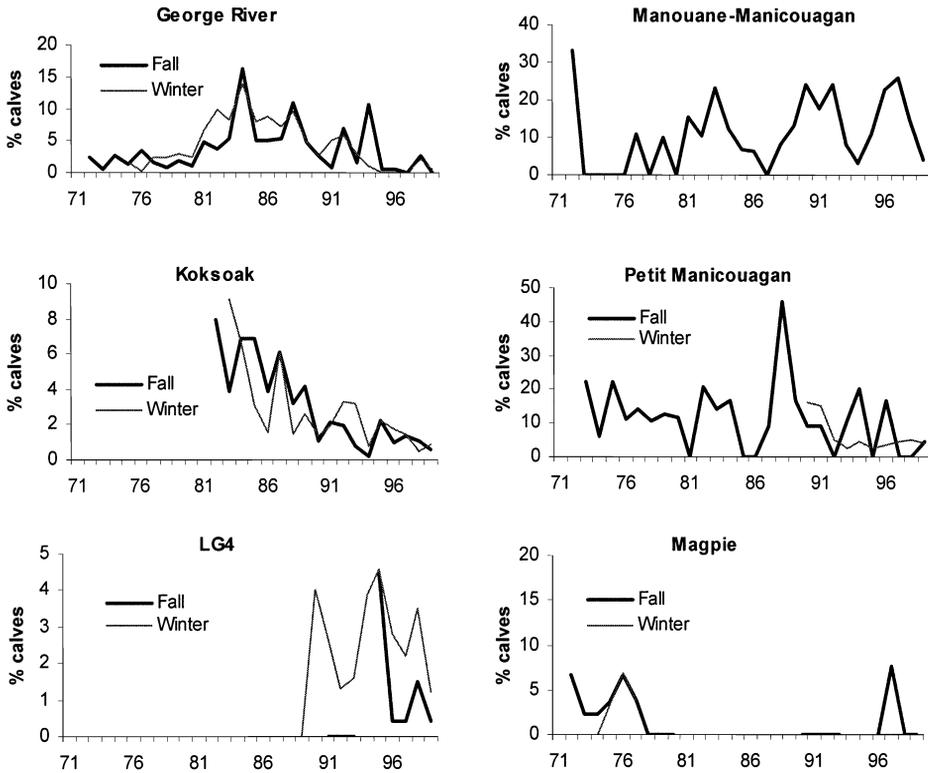


FIGURE 4. Percentage of calves in Caribou harvest in the zones of intensive use (70% kernels) where hunting was allowed between 1971 and 1999.

Jolicoeur 1993\*). The impact of limiting factors is exacerbated by the low productivity of Caribou, with females giving birth to only one calf per year.

#### Current Distribution

In western Quebec, Caribou has been virtually absent south of the 50<sup>th</sup> parallel and west of the 78<sup>th</sup> meridian for at least 50 years. A 1968 survey covering northern Abitibi (74°00'–79°30' W, 48°00'–50°00' N) noted only six Caribou track networks over 92 715 km<sup>2</sup> and no mention was made of any previous observations (Anonymous 1968\*). Moreover, Caribou presence was not reported in surveys carried out southwest of this area (Vallée and Poitras 1973\*). A few isolated populations have been known since the 1950s, because Seton (1953) marvelled at the absence of antlers in many females in northwestern Quebec. Brassard (1968\*) identified the Val-d'Or population without mentioning its abundance, obviously because he observed only a few individuals. Several surveys conducted during the 1970s revealed the presence of a few individuals in Val-d'Or and near the Ottawa River (47° 52' N, 78° 26' W, between Rapide-Sept and Rapide-Deux, perhaps individuals from the Val-d'Or

population), and chance observations were reported near Val-Paradis (La Sarre population) and Matagami (49° 46' N, 77° 40'; probably individuals from the Rupert population) (St-Vincent 1981\*). These populations appear to have been the only ones totally or partially located south of the 50<sup>th</sup> parallel, west of the Charlevoix region.

Data available for the east-central part of the province have suggested low but relatively stable densities since the early 1980s. The distribution of Caribou on the North Shore was re-evaluated in 1982 using 120 60-km<sup>2</sup> sample plots (Brassard 1982\*). The total population was not estimated, but the presence of Caribou track networks was noted in 41% of the plots. In 1988, Caribou were present in 33 of the 84 (40%) plots surveyed west of Natashquan on the North Shore and in the Saguenay region (Gingras et al. 1989\*). In 1991, 12 plots out of 30 (40%) contained Caribou track networks in the western part of the North Shore.

In contrast, Caribou appeared to be rare farther east. In 1993, Bourbonnais et al. (1997\*) observed Caribou in only seven (20%) of the 60 plots surveyed in the Natashquan region. Still farther east, only one (6%) of

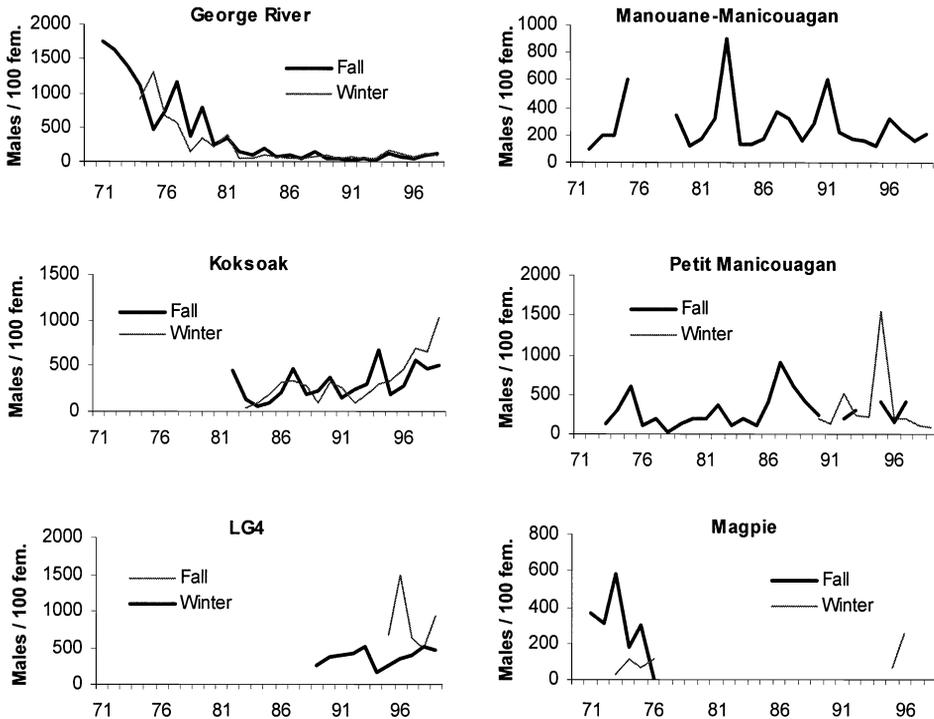


FIGURE 5. Number of males per 100 females in Caribou harvest in the zones of intensive use (70% kernels) where hunting was allowed between 1971 and 1999.

the 18 sample plots covered in 1983 contained Caribou (Barnard 1983\*). According to available data, the Saint-Augustin population seems very reduced or extirpated, although the Native people hunt an indeterminate number of Caribou. However, the dearth of information available for this relatively inaccessible and uninhabited region should be kept in mind. No sport hunting has been allowed in that area since 1979, and it has not been surveyed for almost 20 years.

The range probably shrank between the 1960s and 1980s in the eastern part of the North Shore. However, the major change that has come about south of the 52<sup>nd</sup> parallel since the late 1950s is undoubtedly the disappearance of large Forest-Dwelling populations that frequented the North Shore and southern Labrador. The magnitude of the changes cannot be accurately quantified due to the imprecision of the first surveys, the absence of recent inventories, and changes in the areas flown and the methods used. However, the decline itself is not in doubt. Desmeules and Brassard (1963\*) estimated that there were 9774 Caribou on the North Shore, within an 80-km wide strip, between Sept-Îles (50° 13' N, 66° 23' W) and Saint-Augustin (51° 13' N, 58° 40' W). Brassard and Bouchard (1968\*) evaluated the population at 5629 individuals

within an even larger area than in 1963. In 1972, the population was estimated at 7500 Caribou for the entire North Shore south of the 51<sup>st</sup> parallel (Brassard 1972\*). In 1978, it was estimated at  $13\,158 \pm 6\,590$  individuals south of the 53<sup>rd</sup> parallel (Audet 1979\*). Based on surveys of large blocks carried out in the 1990s, density could be of the order of 0.97 to 1.6 Caribou per 100 km<sup>2</sup> (Gingras and Malouin 1993\*; Bourbonnais et al. 1997\*; Maltais 1997\*). Assuming that no large population has been missed and that the zones of continuous distribution provide a reasonable estimate of the area currently occupied, there would be between 1900 and 3200 Forest-Dwelling Caribou north of the Saguenay fjord.

The most frequently cited causes of decline are excessive hunting, predation and insufficient recruitment (Bergerud 1967; Audet 1979\*; Cinq-Mars 1977\*; Folinsbee 1979). Hunting is probably the main cause. Bergerud (1967) estimated the harvest rates to be from 26-27% between 1958 and 1963 in the Mealy Mountain population, south of Labrador. Taking into account losses from natural causes, the total mortality rate was 31% per year, whereas the recruitment was barely 11%. The Saint-Augustin population, adjacent to and perhaps an extension of the Mealy Mountain population,

TABLE 4. Correlation between fall harvests of Caribou on the one hand, and Moose harvest, males / 100 females, calves / 100 females and % calves in Caribou harvest on the other hand in the zones of intensive use (70% kernels) between 1971 and 1999.

Zone of intensive use	Spearman $r$ ( $P$ ) <sup>a</sup>			
	Moose harvest	Males / 100 females	Calves / 100 females	% calves
Barren-Ground population				
George River				
LG-4	-0.64 (0.01)	0.20 (0.70)	-0.03 (0.95)	0.60 (0.11)
Kokoak	-0.15 (0.45)	0.39 (0.10)	-0.18 (0.45)	0.26 (0.89)
George River	0.00 (0.99)	0.58 (<0.01)	0.56 (<0.01)	0.26 (0.18)
Forest-Dwelling populations				
Manouane-Manicouagan	0.85 (<0.01)	-0.03 (0.87)	0.15 (0.47)	0.31 (0.11)
Petit Lac Manicouagan	0.14 (0.44)	-0.14 (0.52)	0.47 (0.02)	0.43 (0.02)
Magpie	0.11 (0.57)	0.68 (0.05)	0.43 (0.23)	0.79 (<0.01)

<sup>a</sup>  $14 \leq n \leq 29$ .

probably experienced a similar fate (Brassard 1972\*). The Magpie River population, exploited simultaneously in Quebec and in Labrador, comprised about 5000 Caribou in the mid-1960s but only 1300 to 3000 by the mid-1970s. According to Folinsbee (1976\*, 1979), this population appeared to have been overexploited. At that time, subsistence hunting took at least 176 to 254 Caribou per winter, to which natural mortality ( $\approx 150$ ), sport hunting ( $\approx 120$ ) and illegal or undeclared hunting should be added. Annual harvest reported in our files varied between 128 and 1162 Caribou in the 70% kernel of the Magpie River between 1973 and 1977, meaning that the harvest rates exceeded 30% at that time.

It is not entirely impossible that the large populations have migrated into other sectors. Several surveys in the 1960s and 1970s showed population movements of many tens of kilometres. However, if such was the case, these groups would have been located during subsequent surveys of Moose and Caribou, but this has not occurred over the last two decades. Caribou are philopatric, and as observed at present in northern Quebec, site changes occur when densities increase, not when they decline (Bergerud 1974). One might also think that the large populations observed on the North Shore in the 1960s could have been extensions of migratory populations from northern Quebec. However, published survey maps show that the northern populations were located farther north, that they only started to increase in abundance in the 1950s, and that their distribution range did not expand considerably before the 1980s (Banfield and Tener 1958; Bergerud 1967; Pichette and Beauchemin 1973\*; Messier et al. 1988). Even today, the distribution of Barren-Ground Caribou does not extend south of the 52<sup>nd</sup> parallel (Schaefer et al. 1999).

#### *Causes of Temporal Changes in Barren-Ground Caribou*

The negative correlation noted between Caribou and Moose harvests in kernel LG-4 is probably accidental (Table 4). In northern Quebec, the density of Moose ( $< 0.3$  per 10 km<sup>2</sup>; Maltais et al. 1993\*) is probably too low to influence Wolf abundance, since 2.0 Moose/10 km<sup>2</sup> are required to support stable Wolf populations (Messier 1994). This situation is not likely to change in the future, since the habitat carrying capacity is low for Moose at this latitude, where shrubs near waterways are the only sites of interest for this species (Joyal 1987).

Within each group of northern Quebec, the fall and winter harvests had nearly identical characteristics, suggesting that the same populations are exploited during both hunting seasons. However, there were marked differences in harvest characteristics between the northern groups. The decline in the harvest in the George River kernel indicates that Caribou numbers have been diminishing at this location since the mid-1980s. If the migratory behaviour of males had not

changed, the decrease in the proportion of males in the harvest could suggest a reduction in the selectivity of hunters as a result of an increasingly difficult hunt. The decline could be attributed to a lower population productivity, as suggested by the structure of the sport harvest (Figure 4).

Changes in the abundance of the George River population are in line with the observations of Morneau and Payette (1998). Based on the scars left on tree roots by the passage of Caribou, these authors consider that the species was rare during the 1940s and 1950s in the George River region. The abundance increased in the early 1970s, reached a maximum between 1984 and 1989, and then declined significantly in the early 1990s. Changes in abundance suggested by Morneau and Payette (1998) corroborate population increases noted during aerial surveys conducted during the 1970s and the 1980s (Couturier et al. 1996). Telemetry data and computer simulations realized by Crête et al. (1996) suggest a slight decline in populations after 1986 which seems to concur with the observations of Morneau and Payette (1998) but to contradict the 1993 aerial survey and demographic data which suggest a reduction in the rate of increase rather than a decline (Couturier et al. 1996; Messier et al. 1988). Considering the limits of simulations models, we cannot exclude that the scars left on tree roots could have diminished due to a change in migration routes. The increased harvest in the Koksoak River and LG-4 reservoir region following the decline in the George River area support this hypothesis. Moreover, the increased representation of males in the harvest of Koksoak and LG-4 suggests a greater selectivity on the part of hunters following an increase in Caribou abundance. In the early 1980s, Brown et al. (1986) observed large groups of Caribou at the Caniapiscau reservoir, south-west of the George River and presumably belonging to the George River population. In the early 1990s, a few large groups of Caribou, probably migrators from George River or Leaf River, were also observed in west-central Québec, around the 51<sup>st</sup> parallel (Anonymous 1992\*).

#### *Causes of Temporal Changes in Forest-Dwelling Caribou*

The groups of Caribou identified do not constitute a homogeneous population. Hunting statistics show regional differences in terms of population density, structure and temporal changes. For example, the Magpie population produced large harvests for a few years, and then practically disappeared in the mid-1970s, well before hunting was closed in 1979. In the mid-1970s, the Manouane-Manicouagan population, located a few hundred kilometres farther west, provided a small harvest, which increased up until the 1980s even though the harvest was subject to quotas. The harvest in Petit Lac Manicouagan, located to the northeast of Manouane-Manicouagan, showed intermediate trends. The fall harvest declined in a nearly constant fashion,

which may have been caused by a reduction in the number of hunting permits during that season. However, a considerable increase in the winter harvest was noted between 1990 and 1995, but was followed by a sharp decrease. These changes can probably be attributed to the irregular migrations of the Barren-Ground Caribou, which are the focus of the winter hunt, and which account for most of the harvest in this sector. Nevertheless, the downward trend in the fall harvest could indicate a decline in the abundance of Forest-Dwelling Caribou, perhaps partly caused by incidental kills of that ecotype during the winter hunt of Barren-Ground Caribou.

We were expecting an increase in the Moose harvest at sites where the Caribou harvest had declined, which would have suggested an increase in predation following population growth in Moose and Wolf. This may have occurred south of the 49<sup>th</sup> parallel at the end of the 19<sup>th</sup> century (St. Cyr 1873; Gingras et al. 1989; Jolicoeur 1993\*). However, this hypothesis does not seem to be supported by harvest data collected during the last three decades. For example, Moose and Caribou harvests were positively correlated in the Manouane-Manicouagan population, implying that the annual variations were more tightly linked to changes in hunting pressure, since the harvest of both species is carried out simultaneously in that area. In the Petit Lac Manicouagan and Magpie populations, harvests of Caribou and Moose evolved independently and Caribou declines followed very large harvests. In the studied populations, forest disturbance was probably not large enough to significantly increase the importance of early successional forests and provoke an increase of Moose and Wolf abundance that would have favoured Caribou predation. Instead, our results suggest that declines in the Forest-Dwelling Caribou populations may have been mainly caused by excessive hunting, as previously proposed (Bergerud 1967; Folinsbee 1979; Cinq-Mars 1977\*).

A considerable increase in the Caribou harvest can be noted from south to north, due to the presence of the large Barren-Ground populations in the North. In winter, they could migrate as far south as the Petit Lac Manicouagan kernel. At this location, the characteristics of the fall and winter harvests differ considerably in terms of abundance and structure, suggesting the presence of different populations in both seasons. The winter harvest seems to be supported mainly by migratory populations since the decline in the harvest and the percentage of calves is similar to that noted for the George River population. The Forest-Dwelling Caribou populations farther south do not seem to be influenced directly by the migratory animals.

#### **Conclusion**

In Quebec, the range of Caribou has decreased considerably over the last 150 years. The disappearance of Caribou has usually been associated with excessive hunting as well as with the arrival of Moose and

Wolves following logging (Martin 1980; Bellehumeur et al. 1985\*; Jolicoeur 1993\*). Northern populations recovered, beginning in the mid-1950s, but the Mountain population in Gaspésie and the Forest-Dwelling populations have continued to decline. The decline of the Gaspésie population appears to be due to hunting in the early 20<sup>th</sup> century (Moisan 1957) and predation since the early 1970s (Crête and Desrosiers 1995). The decrease in Forest-Dwelling Caribou, which was particularly rapid until the mid-1970s, seems to be the result of excessive hunting in eastern Quebec. Sport hunting of Forest-Dwelling Caribou was subject to a quota in 1979 and has been banned since winter 2001, but subsistence hunting continues. At the present time, it is difficult to predict the population trend in a context where access to the northern forests is increasing and early successional forests are developing due to logging. Moreover, despite the fact that we did not detect any relationships between Moose and Caribou abundance, it would be premature to conclude that habitat changes have no influence on Caribou. The precision of historical data is relatively low, so a type II error cannot be ruled out. Falsely concluding that no decline is occurring would be a more serious error in biological conservation than falsely concluding that a decline is occurring (Caughley and Gunn 1996).

The real situation of the Forest-Dwelling Caribou and their future trend remain speculative due to the lack of recent surveys. Unfortunately, an aerial survey programme would require a large investment due to the low densities and the contiguous distribution of Forest-Dwelling Caribou. To limit the costs, priority should be given to surveying the zones of intensive use.

### Acknowledgments

The authors are indebted to Pierre Drapeau, James Schaefer, François Potvin and two anonymous referees who commented on an earlier version of this paper. This study would not have been possible without the contribution of the authors of the publications and documents consulted. We appreciated their clear-sightedness, and particularly admire the audacity and bravery they required to carry out the first aerial surveys, at a time when northern travel was often still done by means of dogsled. We also thank those who graciously reported their Caribou observations and those who set up systems for collecting this information. We wish to underscore the contribution of Daniel Banville, Mario Duchesne and Marcel Paré, among others.

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Received 5 October 2001

Accepted 4 March 2004