

DIRECTION DE LA RECHERCHE SUR LA FAUNE
in collaboration with the
Institut for Environmental Monitoring and Research
and the
Department of Environment and Conservation
Government of Newfoundland and Labrador

**GENE FLOW PATTERNS BETWEEN
MIGRATORY, MONTANE, AND SEDENTARY
CARIBOU HERDS OF NORTHERN QUÉBEC
AND LABRADOR: LESSONS FROM SATELLITE
TRACKING, MICROSATELLITE GENOTYPING,
AND POPULATION SIMULATIONS**

Marylène Boulet ^{1,2}
Serge Couturier ^{1,2,3}
Steeve D. Côté ^{1,2}
Robert Otto ⁴
and
Louis Bernatchez ¹

¹ Département de biologie, Université Laval

² Centre d'études nordiques, Université Laval

³ Secteur Faune Québec, Direction de la recherche sur la faune

⁴ Department of Environment and Conservation, NF & Labrador

MINISTÈRE DES RESSOURCES NATURELLES ET DE LA FAUNE

June 2005

To be cited as:

BOULET, M., S. COUTURIER, S. D. CÔTÉ, R. OTTO and L. BERNATCHEZ. 2005.
Gene flow patterns between migratory, montane, and sedentary caribou herds of
northern Québec and Labrador: lessons from satellite tracking, microsatellite
genotyping, and population simulations. Ministère des Ressources naturelles et de la
Faune, Direction de la recherche sur la faune. Québec. 46 p.

Legal deposit – Bibliothèque nationale du Québec, 2005

ISBN : 2-550-45229-1

ABSTRACT

Modelling metapopulation dynamics between animal populations requires an accurate delineation of groups and an assessment of gene flow between populations. This information is essential for establishing effective conservation planning. Here, we combine satellite-tracking data of migratory caribou during the rutting and calving seasons, microsatellite markers, and population simulations to evaluate potential and realised gene flow and to understand metapopulation dynamics between seven caribou (*Rangifer tarandus*) herds of northern Québec and Labrador representing three ecotypes (two migratory, four sedentary, and one montane). Satellite-telemetry data indicated that overlap of rutting ranges occurred frequently between the two migratory herds (Rivière-George and Rivière-aux-Feuilles) and averaged 10% of their combined rutting range annually. In addition, 9.4% of the satellite-tracked females from the migratory herds switched calving sites at least once in their lifetime, re-enforcing the possibilities for high gene flow. Some migratory individuals also migrated south into the range of the sedentary herds, suggesting possibilities of gene flow between these groups. These results were reflected in the weak but significant global genetic differentiation among herds (global $F_{ST}= 0.015$). The sedentary Mealy Mountain herd was the most differentiated. The differentiation between sedentary herds was significant and influenced by the geographic distance separating herds. High gene flow with the remote migratory herds, however, removed the pattern of isolation-by-distance among sedentary herds. Indeed, historical estimates of gene flow suggested a large impact of the migratory herds on the sedentary herds via direct immigration or genetic exchanges during the rut. Population simulations suggested that an effective immigration rate of 0.0005 was sufficient to obtain the observed F_{ST} value of 0.015. More importantly, the differentiation has remained stable through time, suggesting that caribou herds of northern Québec-Labrador have interacted as a metapopulation.

RÉSUMÉ

Modéliser une dynamique de métapopulation entre différentes populations animales nécessite une délimitation spatiale précise et une évaluation des flux géniques entre les populations. Cette information est indispensable afin d'établir un plan de conservation efficace. Dans cette étude, nous utilisons des données de repérages par satellite du caribou migrateur pendant la saison du rut et de la mise bas, des marqueurs microsatellite et des simulations de populations afin d'évaluer le flux génique potentiel et réel pour comprendre les dynamiques de métapopulation entre sept troupes de caribous (*Rangifer tarandus*) du Nord-du-Québec et du Labrador qui représentent trois écotypes (deux migrants, quatre sédentaires et un montagnard). Les données de télémétrie satellitaire ont indiqué des chevauchements fréquents des aires de rut des deux troupes migrantes (Rivière-George et Rivière-aux-Feuilles) atteignant en moyenne 10% de leurs aires combinées. De plus, 9,4% des femelles suivies par satellite provenant de troupes migrantes ont changé de site de mise bas au moins une fois dans leur vie, ce qui augmente les possibilités d'un flux génique élevé. Quelques-uns des individus migrants se sont aussi déplacés vers le sud dans les terres des troupes sédentaires constituant des possibilités de flux génique entre ces deux écotypes. Ces résultats se reflètent dans la faible, mais tout de même significative, différenciation génétique globale des troupes (F_{ST} global= 0,015). Le troupeau sédentaire des Mealy Mountains était le plus distinct. La discrimination entre les troupes sédentaires était significative et influencée par la distance géographique les séparant. Toutefois, ce patron d'isolation par distance est disparu à cause du flux génique élevé avec les troupes migrantes éloignées. En effet, les estimés historiques de flux génique laissaient croire à un impact important des troupes migrantes sur les troupes sédentaires par l'immigration directe ou par les échanges génétiques durant le rut. Les simulations de population suggéraient qu'un taux d'immigration réel de 0,0005 était suffisant afin d'obtenir la valeur de F_{ST} observée de 0,015. De façon plus importante encore, la différenciation est demeurée stable à travers le temps, ce qui suggère que les troupes de caribous du Nord-du-Québec et du Labrador ont interagi suivant un modèle de métapopulation.

TABLE OF CONTENT

ABSTRACT	iii
RÉSUMÉ	v
TABLE OF CONTENT	vii
LIST OF TABLES	ix
LIST OF FIGURES	xi
1. INTRODUCTION	1
2. MATERIAL AND METHODS	5
2.1 Characteristics of caribou herds.....	5
2.2 Satellite-tracking data	7
2.3 Potential gene flow during the rutting season.....	8
2.4 Potential gene flow during the calving season.....	9
2.5 Sampling and DNA analyses	10
2.6 Genetic diversity and Hardy-Weinberg equilibrium.....	10
2.7 Genetic population structure	11
2.8 Barriers to gene flow.....	11
2.9 Historical levels of realized gene flow.....	12
2.10 Simulations of levels of gene flow between herds.....	12
3. RESULTS	15
3.1 Opportunities for gene flow during the rut	15
3.2 Opportunities for gene flow during the calving seasons.....	15
3.3 Polymorphism and Hardy-Weinberg equilibrium	18
3.4 Genetic differentiation between herds	21
3.5 Barriers to gene flow.....	23
3.6 Historical estimates of gene flow.....	23
3.7 Simulations of historical scenarios	25
4. DISCUSSION	29
4.1 Lessons learned from the integration of data.....	29
4.2 Gene flow dynamics between herds: a hierarchical metapopulation?.....	33
4.3 Limitations: the difficulty of assessing gene flow	35

4.4 Conservation implications	36
ACKNOWLEDGEMENTS	37
5. REFERENCES	38

LIST OF TABLES

Table 1. Opportunities for gene flow based on satellite-tracking data of caribou from northern Québec-Labrador during the rutting season: range overlap between migratory herds, between migratory and sedentary herds, and between the migratory Rivière-George herd and the montane Torngat herd.	16
Table 2. Occurrences of calving site switching by female caribou between migratory Rivière-aux-Feuilles (L) and Rivière-George (G) herds during successive calving seasons (June 1986 to June 2003).....	18
Table 3. Number of alleles observed at each locus (A), allelic richness standardized for the smallest sample size with complete scoring ($n= 11$, AR_{11}), observed heterozygosity (H_o), expected heterozygosity (H_e), and mean number of alleles / loci (A_{mean}) found in the caribou herds of northern Québec and Labrador.....	19
Table 4. Genetic differentiation in allele frequencies between caribou herds of northern Québec and Labrador at seven microsatellite loci. Numbers above the diagonal refer to the number of loci that showed significant differences in allele frequencies, whereas numbers below the diagonal refer to multilocus P -values obtained following Fisher's method (Raymond & Rousset, 1995).	22
Table 5. Pairwise estimates of genetic differentiation (F_{ST}) between caribou herds of northern Québec and Labrador (above diagonal) and corresponding P -values (below diagonal).	22
Table 6. Overall F_{ST} values between all caribou herds for simulations of historical scenarios of fragmentation of an initial herd into five herds of varying size (see parameters below) and varying effective immigration rates.....	27

LIST OF FIGURES

- Figure 1. Map of northern Québec and Labrador showing the annual ranges of the migratory Rivière-George herd (horizontal shading, Minimum convex polygon [MCP] area for 1991-2003), migratory Rivière-aux-Feuilles herd (vertical shading, MCP area for 1993-2003), four sedentary caribou herds (Lac Joseph, Mealy Mountains, Red Wine Mountains: following Schmelzer, *et al.*, 2004; Jamésie: approximate annual range), and montane Torngat herd (Schaefer & Luttich, 1998). The calving ground is shown for both migratory herds. The sedentary ecotype range is located south of the 54° N (northern extreme limit) and 53° N (average northern limit). Sample locations for DNA analysis are also shown within each annual range. Only animals of known herd origin were used (i.e. they must have been captured when the migratory herds were clearly separated based on satellite-telemetry). 6
- Figure 2. Rutting ranges of migratory caribou Rivière-George herd (light shading located in the south-east portion of the map), migratory Rivière-aux-Feuilles herd (stripped-motif shading located in the north-west) and montane Torngat herd at the peak of the rut (ca. 23 October) from 1994-2001. The sedentary ecotype range is located south of the 54° N..... 17
- Figure 3. Frequency distribution of alleles present among the seven microsatellite loci analysed for caribou herds of northern Québec and Labrador: A) RT1, B) RT5, C) RT6, D) RT7, E) RT9, F) RT24, and G) RT27. Herds are labelled as follow on the y-axis: #1= Lac Joseph, #2= Mealy Mountains, #3= Red Wine Mountains, #4= Jamésie, #5= Torngat, #6= Rivière-aux-Feuilles, and #7= Rivière-George. Each allele found in a particular herd is represented by a circle proportional to the frequency of this allele within the herd..... 20
- Figure 4. Barriers to gene flow in caribou herds of northern Québec and Labrador identified by the SAMOVA analysis when $k= 2$. The barrier suggests that gene flow is lowest between the Mealy Mountains herd and all other herds. Abbreviations are: GEOR= Rivière-George, LEAF= Rivière-aux-Feuilles, LACJ= Lac Joseph, MEAL= Mealy Mountains, REDW= Red Wine Mountains, JAME= Jamésie, and TORN= Torngat..... 24
- Figure 5. Historical gene flow estimates between (A) the migratory caribou GEOR and LEAF herds versus the sedentary herds, and (B) among all sedentary herds. Numbers refer to the number of immigrants per generation and their respective 95% confidence intervals. Bold arrows represent directions between herd pairs in which the immigration rate was significantly asymmetric. Abbreviations are: GEOR= Rivière-George, LEAF= Rivière-aux-Feuilles, LACJ= Lac Joseph, MEAL= Mealy Mountains, REDW= Red Wine Mountains, JAME= Jamésie, and TORN= Torngat. 25

1. INTRODUCTION

Modelling metapopulation dynamics requires determining how the populations are structured, assessing the number of distinct populations in the study area, and measuring the level of gene flow between populations (Awise, 2004). This information is crucial for establishing effective conservation planning. Estimating historical and contemporary gene flow, however, is particularly challenging and it is only recently due to technological advances that ecologists and conservationists have been able to more accurately measure gene flow between existing populations.

Three main approaches can be used to measure gene flow: natural phenotypic markers (i.e., distinct body marks), tagging programs (i.e., bands, ear tags, VHF collars, satellite-collars) and genetic markers (DNA) (Awise, 2004). While natural markers such as scars and patterns on skin may be useful for identifying large marine mammals such as whales at a relatively low cost (Witteveen *et al.*, 2004), tags are mostly used to obtain detailed information on the movements and life-histories of individuals, especially in terrestrial ecosystems (Boulanger *et al.*, 2004). Genetic markers are heritable, phenotypic markers may have a heritable component that can be influenced by the environment, and physical tags have no heritable component. Thus, only genetic markers can provide information that is directly linked to population genetics.

A comprehensive integration of these three approaches can result into an increased understanding of the processes (e.g. contemporary gene flow, sex-biased dispersal, recent and historical divergence) that can explain the observed structure among animal populations (Bensch *et al.*, 1999; Paetkau *et al.*, 1999; Blouin-Demers & Weatherhead, 2002; Proctor *et al.*, 2004; Witteveen *et al.*, 2004). Markers such as VHF collars and satellite-tracking collars can be affixed to large mammals to characterize movements during successive months to years (Rettie & Messier, 2001). In addition, a wide array of nuclear DNA markers (i.e., microsatellite loci) is available for quantification of realized gene flow among groups and populations of large mammals (Wilson *et al.*, 1997; Røed, 1998; Røed & Midtjell, 1998). Yet, in species with large home ranges or high movement

rates such as bears, wolves and ungulates, much of the ecological applications of VHF and satellite tracking have been devoted to the characterization of habitat use and movement rates. Studies integrating the two aspects of population exchanges, i.e., the potential for gene flow via movement patterns during the mating season and on-going immigration, and the realized gene flow, are still very rare (but see polar bear *Ursus maritimus* studies by Bethke & Taylor 1996, Paetkau *et al.*, 1999; Taylor *et al.*, 2001).

In North America, the status of caribou (*Rangifer tarandus*) herds is of high management concern because of the ecological, economical and traditional value of the species, especially for the First Nations (Miller, 2003). In addition, several caribou herds have recently experienced sharp declines and were listed under the *Species at Risk Act* (SARA) in Canada or under the *Endangered Species Act* (ESA) in the U.S.A. These include the Peary caribou herds in the Northwest Territories and Nunavut (endangered under SARA), the woodland Atlantic-Gaspésie herd in southern Québec (endangered under SARA), the sedentary woodland herds present in the boreal forests of Canada (threatened under SARA), and the woodland caribou herds of Washington and Idaho in the USA (endangered under the ESA) (COSEWIC, 2002, USFWS 2004, <http://endangered.fws.gov/mammals1.html#Lnk7u>).

Various types of markers have been used to characterize the genetic structure of caribou or reindeer (Eurasian vernacular name for caribou) herds in various parts of the northern Hemisphere, including allozymes (Røed & Whitten, 1986; Røed *et al.*, 1991), nuclear genes (Cronin *et al.*, 1995), mitochondrial DNA (Dueck, 1998; Gravlund *et al.*, 1998; Flagstad & Røed, 2003) and microsatellite loci (Côté *et al.*, 2002; Jepsen *et al.*, 2002; Courtois *et al.*, 2003; Cronin *et al.*, 2003; McLoughin *et al.*, 2004; Zittlau, 2004). Similarly, VHF and satellite-tracking collars are regularly used by researchers to study movements of caribou, but the majority of studies have focused on seasonal movement rates and patterns (Bergman *et al.*, 2000), annual and seasonal-range sizes (Rettie & Messier, 2001), site fidelity (Schaefer *et al.*, 2000), and movements and habitat selection at different spatial scales (Johnson *et al.*, 2002). Despite the ability of satellite-tracking to detect small-scale to large-scale movements over an extended period of time, very little

attention has been given to the consequences of varying levels of philopatry on the genetic structure of large mammal populations, especially caribou herds, the occurrence of dispersal movements between populations, and possible forays undertaken by migratory individuals during the period of reproduction into other migratory or sedentary populations. Knowing whether populations, for example caribou herds, of a given area are genetically distinct and whether they are more or less demographically connected through metapopulation dynamics is of crucial importance for designing appropriate management plans (Hanski & Simberloff, 1997; Hanski & Gaggiotti, 2004). Thus, the caribou represents an excellent candidate species for integrating genetic and satellite-telemetry techniques to understand exchanges and gene flow between animal populations at a large spatial scale.

Here we assessed the potential and realised gene flow and we modelled gene flow and metapopulation dynamics between seven caribou herds of northern Québec and Labrador representing three ecotypes (Bergerud, 1996; Mallory & Hillis, 1998). We combined the use of satellite-tracking technology and genetic analyses of microsatellite variation to address these goals. In terms of conservation implications, the four sedentary herds studied are classified within the woodland caribou boreal populations, which are designated as threatened in Canada due to a widespread decline of numbers throughout most of their range (COSEWIC, 2002). This designation excludes the migratory Rivière-George and Rivière-aux-Feuilles herds, which together include $\geq 1,000,000$ individuals (Couturier *et al.*, 2004) and the Torngat herd. To assess the spatial dynamics of potential and realized gene flow between herds, we focused on four objectives: 1) quantify potential gene flow by analysing movements of satellite-tracked animals of both sexes during the October rut and June parturition season; 2) assess the genetic structure and identify possible barriers to gene flow using spatial analyses; 3) quantify realised historical gene flow between herds; and 4) quantify the levels of gene flow required to explain the observed patterns of differentiation among herds by simulating various historical scenarios.

We predicted that : 1) there should be partial range overlaps and moderate possibilities of gene flow between migratory herds, weak range overlaps and few possibilities of gene flow between migratory and sedentary or montane herds based on the restricted movements of sedentary and montane ecotypes (Couturier *et al.*, 1990, Schaefer & Luttich, 1998; Schaefer *et al.*, 1999); 2) herds should be genetically structured according to their movement rates: differentiation would be highest between sedentary herds, intermediate between migratory and sedentary and montane herds and lowest between migratory herds; 3) gene flow should be asymmetrical, i.e. higher from migratory herds than from sedentary herds based on movement rates; and 4) moderate levels of gene flow should explain the observed patterns of differentiation. In this paper, we refer to demographic migration, i.e. the movement of an individual into another population, using the term *immigration*, to distinguish the term with migration, i.e. the periodic and oriented annual movements of caribou from the summer grounds to the wintering grounds and back.

2. MATERIAL AND METHODS

2.1 Characteristics of caribou herds

We studied four sedentary caribou herds inhabiting the boreal forest of Québec and Labrador: the Lac Joseph (LACJ), Mealy Mountains (MEAL), Red Wine Mountains (REDW), and Jamésie (JAME) herds (see Figure 1). The present abundance of the LACJ herd is considerably reduced from historical levels (St-Martin, 1987). Based on classification surveys done each spring from 2000 to 2003, recruitment rate is good and suggests that the herd is now stable or slightly increasing at about 1100 caribou (Couturier *et al.*, 1999; Jung *et al.*, 2000; Schmelzer *et al.*, 2004). The MEAL herd underwent a marked decline between the 1950s and the mid 1970s from a few thousands caribou to only a few hundreds (Otto, 2002; Schmelzer *et al.*, 2004). Following hunting closure, the herd began to recover after the late 1970s. It is now stable or slightly increasing at about 2600 caribou (Otto, 2002; Schmelzer *et al.*, 2004). The REDW herd has sharply declined over the last 20-30 years from 751 caribou in 1981 to about 87 in 2003 (Harrington & Veitch 1991; Schaefer *et al.*, 1999; Jung *et al.*, 2001; Schmelzer *et al.*, 2004). While the parturition rate was still high, the decline was associated with lower recruitment, increased mortality of adult females, and possibly emigration to migratory herds (Schaefer *et al.*, 1999). The JAME herd is estimated at 610 caribou (St-Pierre, D., unpubl. data). The herd discreteness and annual range are unknown and only approximate annual range is shown on Figure 1. The JAME herd shared its winter range with both migratory herds in recent years.

The Torngat Mountains (TORN) herd belongs to the montane ecotype and makes altitudinal migrations. With the Gaspésie Herd studied by Courtois *et al.*, (2003), this is the only other montane ecotype population found in Québec-Labrador. The TORN herd shares most of its range with the migratory Rivière-George Herd (GEOR) (Figure 1). Bélanger & Le Hénaff (1985) suggested that the TORN herd contained approximately 5000 caribou although they mentioned that little information was available. Using

telemetry, Schaefer & Luttich (1998) later confirmed the demographic distinctiveness of the TORN herd which was often confounded with the GEOR herd.

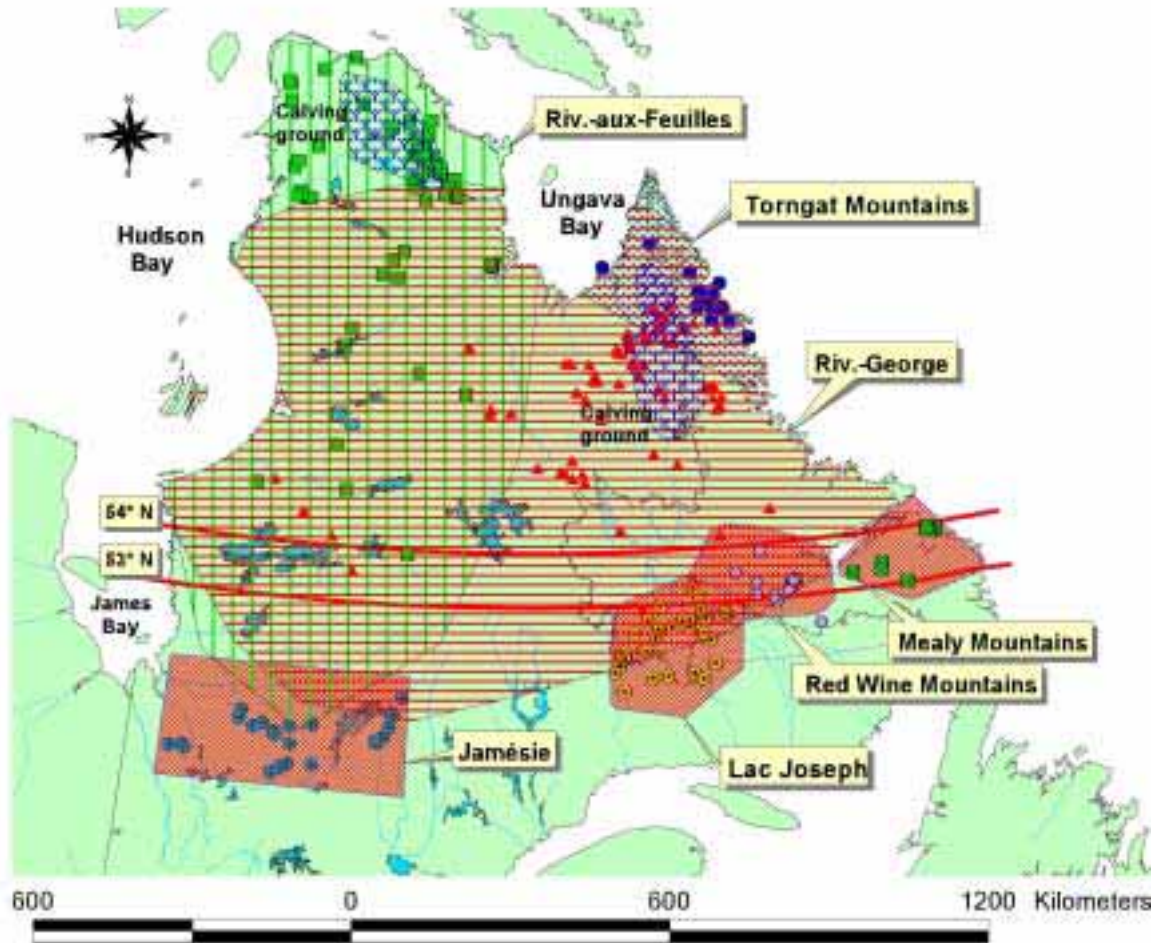


Figure 1. Map of northern Québec and Labrador showing the annual ranges of the migratory Rivière-George herd (horizontal shading, Minimum convex polygon [MCP] area for 1991-2003), migratory Rivière-aux-Feuilles herd (vertical shading, MCP area for 1993-2003), four sedentary caribou herds (Lac Joseph, Mealy Mountains, Red Wine Mountains: following Schmelzer, *et al.*, 2004; Jamésie: approximate annual range), and montane Torngat herd (Schaefer & Luttich, 1998). The calving ground is shown for both migratory herds. The sedentary ecotype range is located south of the 54° N (northern extreme limit) and 53° N (average northern limit). Sample locations for DNA analysis are also shown within each annual range. Only animals of known herd origin were used (i.e. they must have been captured when the migratory herds were clearly separated based on satellite-telemetry).

Finally, our study includes the two migratory herds of caribou of Québec and Labrador (Figure 1). The Rivière-aux-Feuilles (LEAF) herd was first described in June 1975 when Le Hénaff (1976) saw a group of about 20,000 calving females near the Rivière-aux-Feuilles (58 °N 73 °W). Since then, the calving ground has gradually shifted north by about 400 km (Couturier *et al.*, 2003; 61 °N 74 °W, Figure 1). Couturier *et al.*, (2004) have estimated that the LEAF herd size increased from 56,000 caribou in 1975 to 276,000 in 1991. After 25-30 years of steady growth, this herd is now the largest in Québec and included about 628,000 heads in 2001 (Couturier *et al.*, 2004). For more than a century, females of the Rivière-George (GEOR) herd have given birth on the tundra plateaus located near the river of the same name (57 °N 65 °W, Figure 1). After a population peak in the 1890s (Low, 1896; Elton, 1942), the GEOR herd remained extremely low until the 1950s. From as few as 6000 caribou in 1956 (Banfield & Tener, 1958), the GEOR herd increased rapidly to more than 775,000 animals in 1993, then declined to 385,000 in 2001 (Couturier *et al.*, 2004). Due to their different calving grounds, population dynamics and body condition, LEAF and GEOR are presently managed as separate herds although nothing is known about their genetic distinctiveness.

2.2 Satellite-tracking data

Opportunities for gene flow can be detected with satellite-tracking technology given that enough individuals are sampled for an extended period of time. We installed ARGOS satellite-tracking collars (Service ARGOS Inc., Largo, Maryland) to caribou of the GEOR herd (142 animals, from 1986 to 2003) and the LEAF herd (37 animals, from 1993 to 2003). Life expectancy of collar transmitters varied from 1.5 to 3 years and transmitters were periodically replaced to continue monitoring. Thus, the average duration of monitoring for individuals was 2.5 years but some individuals were followed for up to 10 years. In the software Excel (Microsoft, Redmond, Virginia), we developed a customized filtering tool to select a single location per transmission period of 1 to 5 days (i.e. Austin *et al.*, 2003). The algorithm selects locations with the highest accuracy from location quality classes given by Service ARGOS inc. (Largo, Maryland), and later

identifies non-reliable locations based on biologically improbable travel rates (i.e. >50 km/day). We retained 35,554 caribou locations from 1986 to 2003.

2.3 Potential gene flow during the rutting season

In the migratory caribou herds of northern Québec and Labrador, the rutting season is between 18 October and 28 October and peaks on average on 23 October based on field observations collected since 1973. The high synchrony of mating is confirmed by the short length of the calving season, where most of the births occur during a 10-day period centred around 10 June (S. Couturier, unpubl. data). We selected the closest location to 23 October for every satellite-tracked caribou each year. This selection filter applied to the general database provided a total of 444 locations from 1986 to 2003 that were transferred into the Geographic Information System ArcView 3.1 (ESRI inc., Redlands, California).

To estimate the annual overlap of the rutting range between the migratory GEOR and LEAF herds, we first generated a minimum convex polygon (MCP) with all the selected locations of animals of a given herd using the Animal Movement script (Hooge, Eichenlaub, 1996). We used bootstrap simulations to determine the minimum number of satellite-tracked animals required to generate a non-biased MCP and found that a minimum of 12 animals/herd was needed. We excluded years 1993, 2002, and 2003 from analyses because we did not meet the minimal number of animals in the LEAF herd in those years. We then delimited a 50-km-buffer around the MCPs (hereafter MCP₊₅₀) of the LEAF and GEOR herds to account for daily movements of animals around the peak of the rut and extensive areas used by large groups. We calculated the size of the overlap zone MM (in km²) between the LEAF MCP₊₅₀ and the GEOR MCP₊₅₀. We also expressed the MM overlap zone in % = $[\text{MM GEOR and LEAF} / (\text{MCP}_{+50} \text{ GEOR} + \text{MCP}_{+50} \text{ LEAF}) - \text{MM GEOR and LEAF}] \times 100$.

For the rutting range overlap between migratory and sedentary herds (MS), we used the 54° and 53° parallels as the northern extreme limit and the average northern limit of the

sedentary range, respectively (Courtois *et al.*, 2004; see Figure 1). Both limits are approximations that consider contemporary variations in the latitudinal distribution of sedentary herds from east to west. Specifically, MS was calculated as the overlap zone in km^2 between the MCP_{+50} of a migratory herd (LEAF or GEOR) and the range of sedentary herds south of the 54° and 53° parallels.

The space use pattern of the TORN herd was estimated from the maps presented by Schaefer & Luttich (1998) for the rutting period and from the data that we collected in 1997 and 1998 on four adult females tracked by satellite telemetry. Based on this information, we defined the TORN herd rutting range as the area north of a straight line drawn from Kangiqsualujjuaq to the Okak Bay on the Labrador Coast (57.38° N; 61.86° W; Figure 1).

2.4 Potential gene flow during the calving season

In migratory caribou, females are typically philopatric to their calving site, i.e. they return yearly to the same area to give birth (Skoog, 1968; Miller, 2003). Although there is no spatial overlap in the female calving grounds between the GEOR and the LEAF herds, which are 700 km apart (Figure 1), some females may actually switch calving grounds from one year to another. This would represent possibilities of genetic exchanges among migratory herds, first through the female gene pool if she remains with the new herd and mate with males of this herd the following year and also through her calves if calves learn the location of the calving site from their mother and then remain in the new herd thereafter. To verify the possible occurrence of calving ground switching in the migratory GEOR and LEAF herds, we analysed the locations of 149 satellite-tracked females during June, the month of calving. We scored herd switching as GEOR herd females present on or near the LEAF herd calving ground and LEAF females present on or near the GEOR herd calving ground (see Figure 1 for the recent calving grounds location).

2.5 Sampling and DNA analyses

We collected blood and tissue samples from seven caribou herds of northern Québec and Labrador: LACJ ($n= 37$), MEAL ($n= 12$), REDW ($n= 20$), JAME ($n= 27$), TORN ($n= 24$), LEAF ($n= 115$), and GEOR ($n= 98$) (Figure 1). Samples were obtained from 1995 to 2004, but most of them (~75%) were collected in 2000-2002. Samples were usually collected during the calving and post-calving seasons, but some were obtained in other seasons from radio-tracked animals with confirmed herd identity. For live animals, we used blood aliquots stored in vials (with EDTA, heparin or as is) or spread onto FTA™ GeneCard (Life Technologies, Burlington, Ontario); for dead animals (i.e., First Nations hunting or natural death) we used an ear piece or jaw muscles. All samples were stored at -20°C prior to laboratory analyses. DNA was extracted using QIAamp DNA Blood mini kit (blood), QIAamp DNA micro kit (blood cards), or DNeasy Tissue kit (muscles) (QIAGEN, Valencia, California) following the manufacturer protocol except that samples were eluted in 35-70 µL of double-distilled water. Ear samples were extracted following a modification of the BCA DNA purification protocol using BAC Miniprep kit (Millipore, Billerica, ME). The incubation lysis buffer was composed of Tris-HCL 50mM, EDTA 100mM, SDS 1%, proteinase K (0.1 mg/mL), and water.

We genotyped 333 individuals at eight microsatellite loci: BM4513 (Bishop *et al.*, 1994), RT1, RT5, RT6, RT7, RT9, RT24, and RT27 (Wilson *et al.*, 1997) using PCR reactions described in Courtois *et al.*, (2003). DNA fragments were resolved on an ABI 3100 genetic analyser (Applied Biosystem Inc., Foster City, California) using GeneScan 500 ROX™ as a size standard and scored using GeneScan 3.7 and Genotyper 3.7 software (Applied Biosystem Inc., Foster City, California).

2.6 Genetic diversity and Hardy-Weinberg equilibrium

We measured the level of genetic diversity in the caribou herds by calculating the number of alleles per locus (A), observed heterozygosity (H_o) and unbiased gene diversity (H_e , *sensu* Nei, 1978) using the program Genetix 4.02 (Belkir *et al.*, 2000). Individuals with

incomplete genotypes were not used. We standardized the allelic richness found in each herd for a sample size of 11 using the program FSTAT 2.9.3 (Goudet, 1995) because sample size varied between herds. We verified departures from the Hardy-Weinberg equilibrium for each combination of herd and microsatellite loci, across all loci for each herd and across all herds for each locus using the program Genepop 3.3 (Raymond, Rousset, 1995). The locus BM4513 showed a significant lack of heterozygotes in all herds, probably due to the preferential amplification of small alleles (< 130 bp) versus large alleles (> 150 bp) and was therefore removed from all analyses.

2.7 Genetic population structure

We used the program Genepop 3.3 (Raymond & Rousset, 1995) to determine whether caribou herds had distinctive allele frequencies over all loci following Guo & Thompson (1992). In addition, we determined the level of genetic differentiation in caribou herds by calculating the index of differentiation F_{ST} (i.e., θ_{ST} , Weir & Cockerham, 1984) using FSTAT 2.9.3 (Goudet, 1995). This program calculates 95% confidence intervals around F_{ST} estimates, thus a 95% confidence interval excluding the value zero indicates significant patterns of genetic structure at $\alpha=0.05$. We calculated pairwise F_{ST} estimates between each herd in Arlequin 2.000 (Schneider *et al.*, 2000) and used an α of 0.05 and sequential Bonferroni corrections to avoid type I errors (Rice, 1989).

2.8 Barriers to gene flow

We examined two mechanisms that can reduce or prevent gene flow in caribou: geographic features (large rivers and tree line) and geographic distance between herds. We computed a spatial analysis of molecular variance or SAMOVA (Dupanloup *et al.*, 2002). This method is based on a simulated annealing procedure to maximize differentiation between groups of populations. Because this method integrates the geographical coordinates of populations in the annealing process, it offers the advantage of identifying the location of geographic barriers reducing gene flow between groups (Dupanloup *et al.*, 2002; Pearse & Crandall, 2004). Here, we chose the location of the

traditional calving sites of migratory caribou herds as a proxy for the location of herds, because females migrate to these sites in spring to give birth and tend to be philopatric. For the sedentary and montane herds, we used the centroid of the annual ranges shown on Figure 1. We modelled two to seven groups and recorded the differentiation obtained as well as the resulting barrier to gene flow. We also conducted Mantel tests of isolation-by-distance in IBD 1.52 (Bohonak, 2002) using the log (F_{ST}) and the log (distance in km between herds) to determine to what extent geographic distance between herds was a barrier to gene flow.

2.9 Historical levels of realized gene flow

To determine the extent of realized gene flow between herds, we used the program Migrate (Beerli & Felsenstein, 2001), which is based on a coalescent method, to obtain historical estimates of asymmetric gene flow between herds. We did the following comparisons: 1) GEOR vs. all sedentary herds; 2) LEAF vs. all sedentary herds; and 3) between each of the sedentary herds. To avoid inflating gene flow estimates due to unequal sampling sizes (Austin *et al.*, 2004), we used half of the individuals (those with an even ID number) for the GEOR ($n= 47$) and the LEAF ($n= 61$) herds. We compared gene flow asymmetries using the 95% confidence intervals around gene flow estimates.

2.10 Simulations of levels of gene flow between herds

We simulated different scenarios of population structure between fictive caribou herds using EASYPOP 1.8 (Balloux, 2001). Our objective was to determine whether the system could be near migration-drift equilibrium, i.e. if the observed level of structure could be explained by high levels of gene flow between herds that would counter the effects of drift especially in the small sedentary herds. We simulated five herds with varying population size of reproducing adults and immigration rates (i.e. the probability that an individual moves in a population different from the population where he was born) to mimic gene flow dynamics between herds under study: population A represented a large migratory herd with 100,000 reproducing females (N_{ef}) and 40,000 reproducing males

(N_{em}) broadly equivalent to the GEOR or LEAF herds at intermediate population levels; population B was a large sedentary population of 500 females and 200 males equivalent to the MEAL herd, population C was an intermediate size sedentary herd with 200 females and 80 males equivalent to the LACJ herd, and populations D and E were two small sedentary herds with 100 females and 40 males equivalent to the JAME and REDW herds. A population equivalent to the TORN herd was not included because this herd was not distinct from the migratory herds (see results). These demographic parameters were selected based on observed adult sex ratio in herds of northern Québec and average estimates of herd sizes over several years (Couturier *et al.*, 1990 & 2004). We assumed random mating based on observations of animals during the rut. In the migratory herds, the rut occurs during the fall migration and bulls cannot secure a harem of females due to high densities of migrating individuals (Miller, 2003; S. Couturier, unpubl. data). In sedentary herds in the boreal forest, individuals come in and out of breeding groups and density is low (Bergerud, 1973 & 2000).

Two major caribou evolutionary lineages characterized by distinct mitochondrial DNA clades are present in Canada: a northern lineage mainly present in western Canada and a southern lineage mostly restricted to south eastern Canada (Dueck, 1998; see also Flagstad & Røed, 2003). The Québec – Labrador Peninsula represents an area of secondary contact because the relative frequency of the two lineages in the MEAL, GEOR and the North East Ontario herds are very similar (Dueck, 1998). We simulated a historical scenario covering about 6000 years, which broadly represents the period when central lands of Québec and Labrador became available to caribou herds after the last glaciation (Dyke & Prest, 1987). We postulated that the two lineages merged to form a large panmictic herd from which the actual herds of northern Québec and Labrador could have burgeoned, and we separated our scenarios into two phases. The panmictic phase was characterized by a complete mixing of these two lineages. In EASYPOP, panmixia was simulated with an effective immigration rate M of 0.99 between the herds that will burgeon from the panmictic herd. In this program, immigration rates are probabilities that an individual moves in a population different from the population where he has been born. The fragmentation phase was characterized by the division of the panmictic herd into the

five fictive herds (one migratory and four sedentary herds) during which a significant genetic structure between the five herds could emerge. We used Fisher's Island model with seven microsatellite loci, 10 possible states for microsatellite loci based on the average number of alleles across loci, a mutation rate of 0.0001 (Ellegren, 2000), and a mixed model including single step mutations (SSM, 80%) and random mutations (KAM, 20%) based on the average percentage of non-single step mutations that we found across loci. We assumed a generation time of three years based on productivity data of females of several herds (Couturier *et al.*, 1990; Crête *et al.*, 1996; Adams & Dale, 1998).

We tested four types of scenarios. Scenario A had a panmictic phase of 1000 generations, a fragmentation phase of 1000 generations, and immigration rates between 0 and 0.1 that were not sex-biased. Scenario B had a longer panmictic phase of 1500 generations, a shorter fragmentation phase of 500 generations, and immigration rates between 0.00025 and 0.00075 that were not sex-biased. We performed the scenario B to determine whether differentiation obtained between the herds would be sensitive to variations in length of historical events. Scenario C had a panmictic phase of 1000 generations, a fragmentation phase of 1000 generations, and sex-biased immigration rates ($M_f = 0.00025$ and $M_m = 0.0005$ and vice-versa) to determine whether dispersal differences between sexes could modify the observed level of structure of a given immigration rate. Finally, the historical scenario D also had 1000 generations of panmixia and a fragmentation phase of 1000 generations but included five herds of equal size (20,180 females and 8072 males in each herd) totalling the same number of individuals as in scenario A.

3. RESULTS

3.1 Opportunities for gene flow during the rut

We estimated the overlap between the migratory LEAF and GEOR herds for each rutting season from 1994 to 2001 (Table 1 and Figure 2). The extent of overlap varied from year to year, with no overlap in 1994 and a maximal overlap in 1996 (89,000 km², 34.8% overlap). Overlap of rutting range was observed for seven out of eight years (Table 1).

Between 1991 and 2003, we observed eight instances of migratory caribou moving south of the 54° parallel (the northernmost limit of the sedentary range) and one instance (one male from the GEOR herd in 1993) south of the 53° N (the average northern limit of the sedentary herds) during the rutting period (18 October to 28 October) (Table 1, Figure 2). These movements into the sedentary range tended to be more common and more extended for the GEOR animals ($n=6$ forays over 13 years, average overlap= 7,186 km²) than for those of the LEAF herd ($n=2$ forays over 11 years, average overlap= 152 km²). We recorded two instances of forays (in 1991 and 1998) of GEOR individuals into the TORN range (Table 1, Figure 2).

3.2 Opportunities for gene flow during the calving seasons

For the calving season, we recorded 14 cases of females switching from one herd to another (9.4% of 149 satellite-tracked females). All but one (female 64) occurred from the GEOR herd to the LEAF herd (Table 2). The satellite-tracking data provided evidence of asymmetric immigration between the two migratory herds on a short-time scale (McNemar's test, $P=0.002$). Statistics based on caribou.year also showed evidence of asymmetric immigration: the 14 females emigrated during 20 caribou.years for the GEOR herd (20/302 or 6.6%) and one caribou.year for the LEAF herd (1/106 or 0.9%) (McNemar's test, $P < 0.001$). Calving ground switches were not always permanent, for example, female 145 was with the GEOR herd in 1998 and 1999, switched to the LEAF herd in 2000, was back with the GEOR herd in 2001, and moved again with the LEAF

herd in 2002 and 2003. In contrast, female 143 used the GEOR calving ground during four years then used the LEAF calving ground for at least four years (Table 2).

Table 1. Opportunities for gene flow based on satellite-tracking data of caribou from northern Québec-Labrador during the rutting season: range overlap between migratory herds, between migratory and sedentary herds, and between the migratory Rivière-George herd and the montane Torngat herd.

Year	MIGR vs. MIGR ^a				MIGR vs. SED			MIGR vs. MON
	GEOR rut range (km ²)	LEAF rut range (km ²)	Overlap range (km ²)	Overlap range (%)	GEOR overlap south of 53° (km ²)	GEOR overlap south of 54° (km ²)	LEAF ^b overlap south of 54° (km ²)	GEOR overlap (km ²)
1991	284,368				0	0		6,697
1992	265,578				0	0		0
1993	440,695				16,885	65,681	0	0
1994	130,397	59,190	0	0	0	15,165	0	0
1995	167,932	103,138	13,701	5.3	0	0	0	0
1996	109,438	235,321	89,035	34.8	0	193	0	0
1997	199,174	96,356	4,058	1.4	0	2,958	0	0
1998	242,193	88,153	17,766	5.7	0	1,046	0	4,371
1999	127,105	116,017	501	0.2	0	0	263	0
2000	292,439	153,798	51,470	13.0	0	0	0	0
2001	160,594	157,077	51,479	19.3	0	0	0	0
2002	192,974				0	8,377	1,404	0
2003	165,215				0	0	0	0

^a Abbreviations are: GEOR= Rivière-George, LEAF= Rivière-aux-Feuilles, MIGR= migratory herd, SED= sedentary herd, and MON= montane herd.

^b No LEAF caribou were observed south of latitude 53° N.

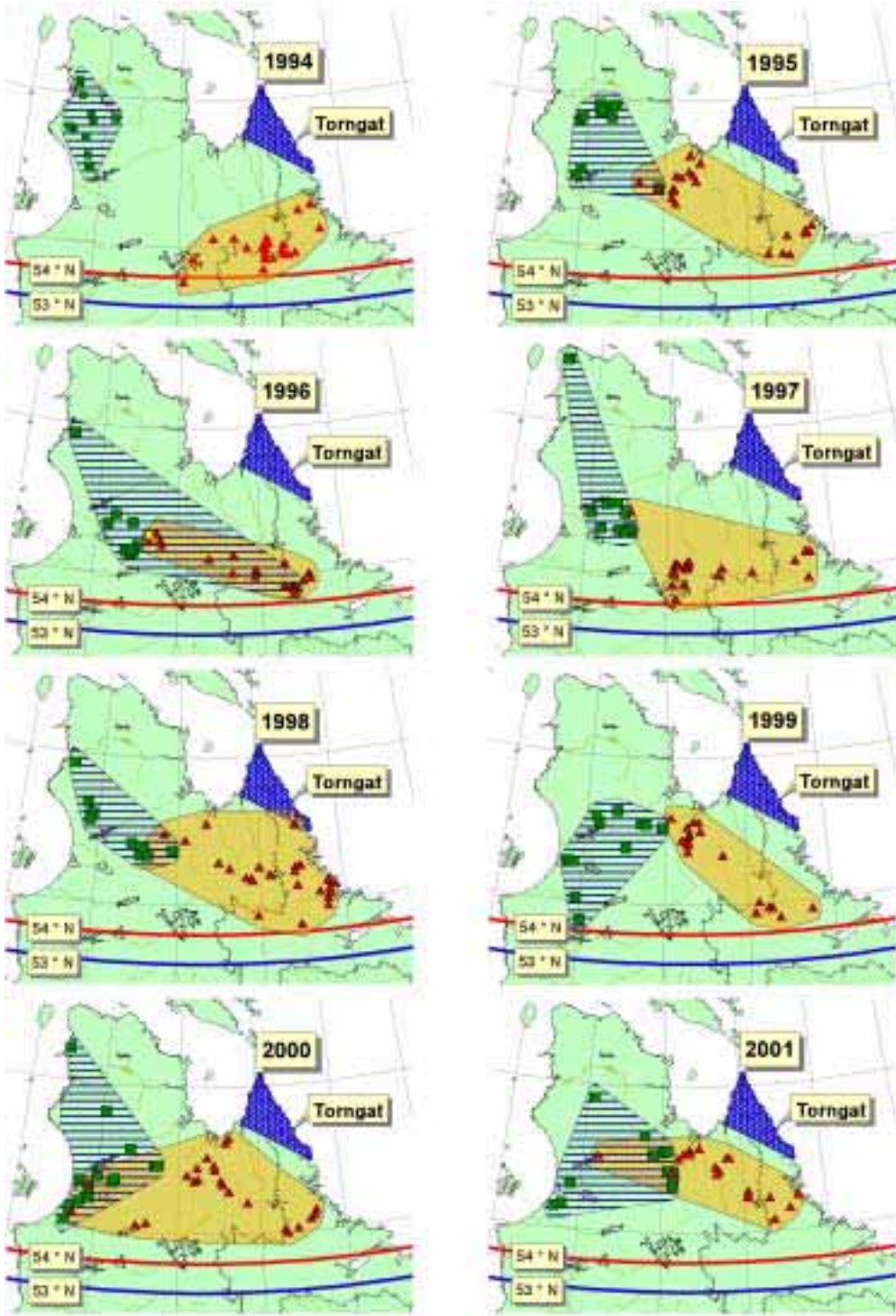


Figure 2. Rutting ranges of migratory caribou Rivière-George herd (light shading located in the south-east portion of the map), migratory Rivière-aux-Feuilles herd (stipped-motif shading located in the north-west) and montane Torngat herd at the peak of the rut (ca. 23 October) from 1994-2001. The sedentary ecotype range is located south of the 54° N.

Table 2. Occurrences of calving site switching by female caribou between migratory Rivière-aux-Feuilles (L) and Rivière-George (G) herds during successive calving seasons (June 1986 to June 2003).

Female ID	Initial Herd ^a	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03
	1	G						G	L										
31	G								L										
64	L									L	L	G							
81	G										G	L							
103	G													L	G	G	G	G	G
119	G													L	G				
137	G															G	G	L	L
139	G															G	G	L	L
141	G															G	G	L	
143	G											G	G	G	G	L	L	L	L
145	G													G	G	L	G	L	L
515	G				G	G	L	G											
519	G						G	L	G	G	G								
572	G															G	G	G	L

^a Initial herd refers to the herd where the female was initially collared.

3.3 Polymorphism and Hardy-Weinberg equilibrium

The number of alleles and the standardized allelic richness per locus tended to be highest in the largest herds: TORN, LEAF and GEOR (Table 3 and Figures 3 A-G). The average number of alleles across all loci in each herd ranged from 5.3 (MEAL) to 10.3 (GEOR) and was within the range of values reported by Courtois *et al.*, (2003) for sedentary, montane and migratory (GEOR) herds of south and central Québec (where A_{mean} across loci ranged from 4.4 to 13.0). Caribou herds did not deviate from the Hardy-Weinberg equilibrium (global test across all herds and loci, $\chi^2 = 111.5$, $df = 96$, $P = 0.13$, Table 3).

Table 3. Number of alleles observed at each locus (A), allelic richness standardized for the smallest sample size with complete scoring ($n= 11$, AR_{11}), observed heterozygosity (Ho), expected heterozygosity (He), and mean number of alleles / loci (A_{mean}) found in the caribou herds of northern Québec and Labrador.

	LACJ ^a ($n= 36$) ^b	MEAL ($n= 12$)	REDW ($n= 20$)	JAME ($n= 27$)	TORN ($n= 24$)	LEAF ($n= 114$)	GEOR ($n= 98$)
RT1							
A	10	7	6	9	9	10	12
AR_{11}	7.153	6.826	5.266	7.069	6.821	7.344	7.701
Ho	0.861	0.667	0.650	0.852	0.833	0.798	0.724
He	0.821	0.804	0.731	0.839	0.778	0.833	0.816
RT5							
A	8	6	7	8	10	13	11
AR_{11}	5.632	5.826	6.062	7.197	7.479	7.782	6.927
Ho	0.806	0.667	0.850	0.885	0.833	0.814	0.732
He	0.784	0.732	0.749	0.864	0.795	0.834	0.828
RT6							
A	6	4	4	5	9	11	11
AR_{11}	4.606	3.917	3.737	4.553	7.298	5.818	5.155
Ho	0.784	0.500	0.400	0.632	0.625	0.637	0.577
He	0.604	0.486	0.426	0.704	0.641	0.613	0.620
RT7							
A	8	7	7	8	10	8	10
AR_{11}	6.630	6.750	6.439	6.297	7.784	6.169	6.711
Ho	0.838	0.833	0.850	0.593	0.833	0.748	0.804
He	0.833	0.819	0.837	0.767	0.804	0.784	0.790
RT9							
A	8	4	7	9	9	11	10
AR_{11}	6.161	4.000	6.204	5.098	6.825	5.426	5.841
Ho	0.784	0.833	1.000	0.519	0.708	0.583	0.745
He	0.768	0.717	0.780	0.601	0.752	0.658	0.727
RT24							
A	9	5	7	9	7	9	10
AR_{11}	6.354	5.000	5.749	6.897	6.326	6.521	6.671
Ho	0.730	0.546	0.684	0.654	0.667	0.763	0.776
He	0.740	0.584	0.634	0.784	0.770	0.748	0.781
RT27							
A	6	4	7	10	6	9	8
AR_{11}	4.555	3.996	6.062	6.922	4.628	5.499	5.031
Ho	0.784	0.583	0.800	0.778	0.625	0.748	0.592
He	0.732	0.583	0.749	0.814	0.725	0.746	0.709
All							
A_{mean}	7.857	5.286	6.429	8.286	8.571	10.143	10.286
Ho	0.798	0.661	0.748	0.702	0.732	0.727	0.707
He	0.755	0.675	0.701	0.768	0.752	0.745	0.753

^a Abbreviations are: LACJ= Lake Joseph, MEAL= Mealy Mountains, REDW= Red Wine Mountains, JAME= Jamésie, TORN= Torngat, LEAF= Rivière-aux-Feuilles, and GEOR= Rivière-George.

^b N refers to sample size.

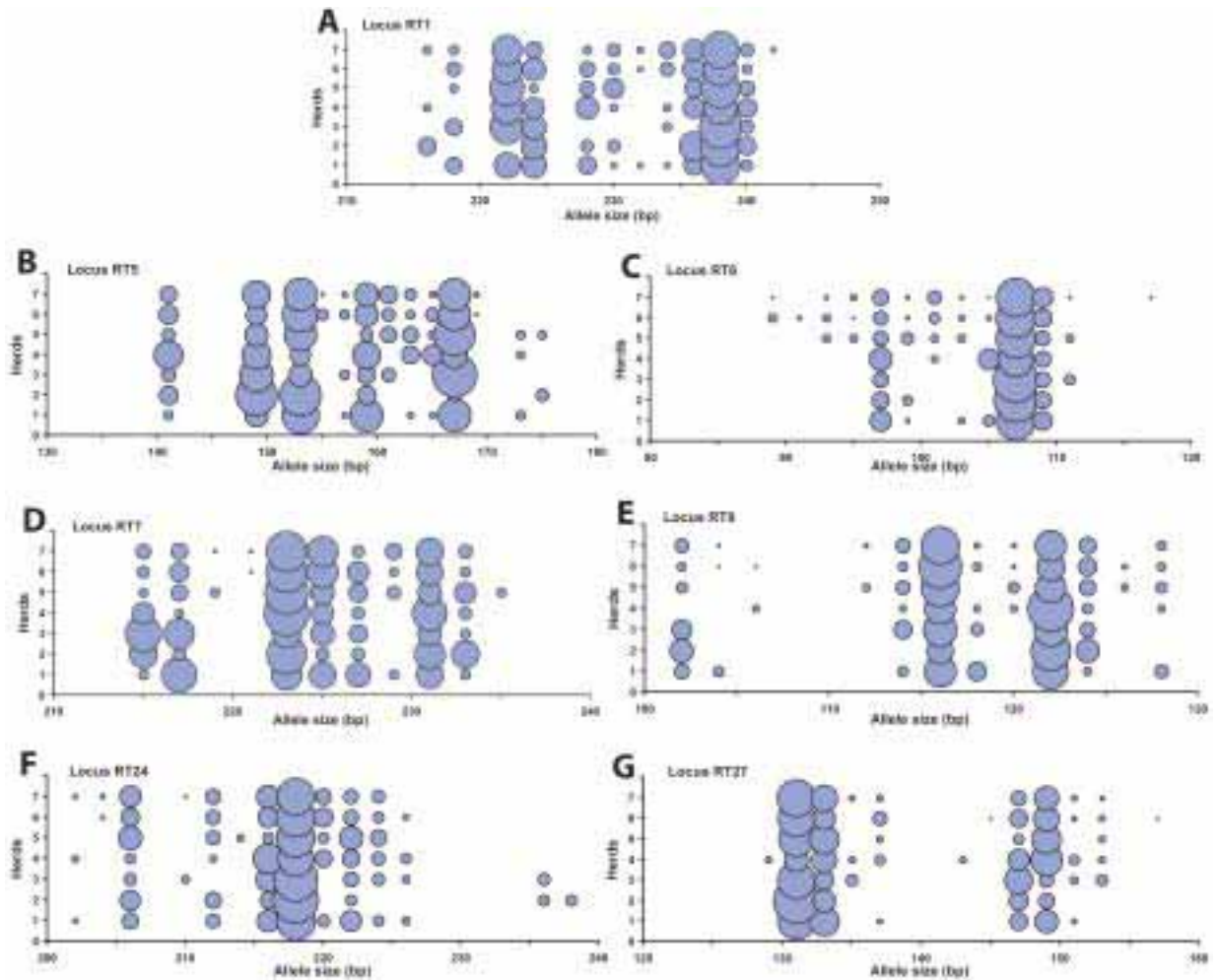


Figure 3. Frequency distribution of alleles present among the seven microsatellite loci analysed for caribou herds of northern Québec and Labrador: A) RT1, B) RT5, C) RT6, D) RT7, E) RT9, F) RT24, and G) RT27. Herds are labelled as follow on the y-axis: #1= Lac Joseph, #2= Mealy Mountains, #3= Red Wine Mountains, #4= Jamésie, #5= Torngat, #6= Rivière-aux-Feuilles, and #7= Rivière-George. Each allele found in a particular herd is represented by a circle proportional to the frequency of this allele within the herd.

3.4 Genetic differentiation between herds

We measured the level of differentiation between herds in two ways. First, allele frequencies across loci significantly differed among herds ($\chi^2 = \text{infinity}$, $df = 14$, $P < 0.001$). Allele frequencies differed in all herd pairs (P 's ≤ 0.005 after sequential Bonferroni adjustments), but GEOR and TORN ($P = 0.30$), GEOR and MEAL ($P = 0.05$), and LEAF and TORN ($P = 0.02$, non significant after sequential Bonferroni adjustments) (Table 4). Differentiation was mostly the result of higher prevalence of rare alleles in the GEOR, LEAF and TORN herds and differences in the frequency of common alleles, especially between the northern herds (i.e., GEOR, LEAF, and TORN) and the four sedentary herds (see Figures 3 A-G). All alleles were either present in the GEOR, LEAF, or TORN herds except alleles 236 ($n = 1$ in REDW and $n = 1$ in MEAL) and 238 ($n = 1$ in MEAL) at locus RT24 and alleles 129 ($n = 1$ in JAME) and 143 ($n = 1$ in JAME) at RT 27. This pattern in the distribution of alleles suggests that the sedentary herds may be subsamples of the large size migratory herds (Figures 3 A-G).

The global pattern of genetic differentiation across all herds was low but highly significant (AMOVA, $\theta = 0.015$, 95% confidence interval = 0.008 to 0.021, $P < 0.001$). Pairwise F_{ST} estimates between herds revealed that most herds significantly differed from each other ($P \leq 0.001$, Table 5). Pairwise F_{ST} estimates between migratory and sedentary herds varied from 0.017 (LEAF vs. LACJ) to 0.038 (LEAF vs. MEAL), whereas estimates between sedentary herds varied from 0.018 (LACJ vs. REDW) to 0.048 (MEAL vs. JAME). In contrast, the migratory herds (LEAF and GEOR) as well as the montane herd (TORN) showed no significant patterns of differentiation (pairwise F_{ST} values ≤ 0.005 , $P \geq 0.07$, Table 5). Thus, the strongest levels of differentiation occurred between sedentary herds separated by large distances (> 1000 km) and between sedentary and migratory herds.

Table 4. Genetic differentiation in allele frequencies between caribou herds of northern Québec and Labrador at seven microsatellite loci. Numbers above the diagonal refer to the number of loci that showed significant differences in allele frequencies, whereas numbers below the diagonal refer to multilocus P -values obtained following Fisher's method (Raymond & Rousset, 1995).

	Sedentary			Montane		Migratory	
	LACJ ^a	MEAL	REDW	JAME	TORN	LEAF	GEOR
LACJ	-	1	0	2	0	2	2
MEAL	0.001* ^b	-	1	0	1	2	0
REDW	< 0.001*	< 0.001*	-	2	1	1	1
JAME	< 0.001*	< 0.001*	< 0.001*	-	0	3	3
TORN	< 0.001*	0.005*	< 0.001*	< 0.001*	-	0	0
LEAF	< 0.001*	< 0.001*	< 0.001*	< 0.001*	0.02	-	0
GEOR	< 0.001*	0.05	< 0.001*	< 0.001*	0.30	0.002*	-

^a Abbreviations are: LACJ= Lake Joseph, MEAL= Mealy Mountains, REDW= Red Wine Mountains, JAME= Jamésie, TORN= Torngat, GEOR= Rivière-George, LEAF= Rivière-aux-Feuilles.

^b P -values significant after sequential Bonferroni adjustments (Rice, 1989) are indicated by an asterisk (*).

Table 5. Pairwise estimates of genetic differentiation (F_{ST}) between caribou herds of northern Québec and Labrador (above diagonal) and corresponding P -values (below diagonal).

	Sedentary			Montane		Migratory	
	LACJ ^a	MEAL	REDW	JAME	TORN	LEAF	GEOR
LACJ	-	0.028	0.018	0.029	0.017	0.017	0.015
MEAL	<0.001* ^b	-	0.037	0.048	0.040	0.038	0.025
REDW	<0.001*	<0.001*	-	0.042	0.022	0.029	0.021
JAME	<0.001*	<0.001*	<0.001*	-	0.027	0.032	0.026
TORN	0.002	<0.001*	<0.001*	<0.001*	-	0.005	-0.001
LEAF	<0.001*	<0.001*	<0.001*	<0.001*	0.11	-	0.002
GEOR	<0.001*	<0.001*	<0.001*	<0.001*	0.66	0.07	-

^a Abbreviations are: LACJ= Lake Joseph, MEAL= Mealy Mountains, REDW= Red Wine Mountains, JAME= Jamésie, TORN= Torngat, GEOR= Rivière-George, LEAF= Rivière-aux-Feuilles.

^b P -values significant after sequential Bonferroni adjustments (Rice, 1989) are indicated by an asterisk (*).

3.5 Barriers to gene flow

In the SAMOVA analysis, the highest F_{ST} value was obtained when the number of groups was fixed to $k=2$ ([MEAL] [all other herds], $F_{ST}=0.051$, $P < 0.001$), suggesting that a barrier prevented or restrained gene flow between the MEAL herd and the other herds (Figure 4). Genetic differentiation between the sedentary herds was influenced by the geographic distance between them ($\log F_{ST}=0.50 \log \text{geographic distance} - 2.88$, $R^2=0.59$, $P=0.04$). However, the addition of the two migratory herds, which were located further away (see Figure 1), did not increase the strength of the isolation-by-distance relationship but reduced it to a great extent ($\log F_{ST}=1.38 \log \text{geographic distance} - 5.6$, $R^2=0.04$, $P=0.25$). This result suggests that the migratory herds had a genetic effect via gene flow on the sedentary herds independently of the geographic distance.

3.6 Historical estimates of gene flow

Historical gene flow estimates were usually high (i.e. Nm was often > 5 migrants per generation) suggesting important historical immigration among herds (Figure 5). The GEOR and the LEAF herds historically tended to be a source of genes for some sedentary herds (Figure 5). However, gene flow between the LEAF and the sedentary herds could have been driven by the GEOR herd, which demographically influenced the LEAF herd based on satellite-tracking data. Within the sedentary herds, gene flow values were variable: whereas the MEAL herd tended to exchange few individuals, especially with the REDW herd ($Nm < 3$ in both directions), exchanges between the other herds were more common (Nm values from 6 to 9). The JAME herd acted as a receiving herd while the REDW was a source herd. In summary, long-term history is characterized by high gene flow among herds that have been mostly driven by the migratory herds.

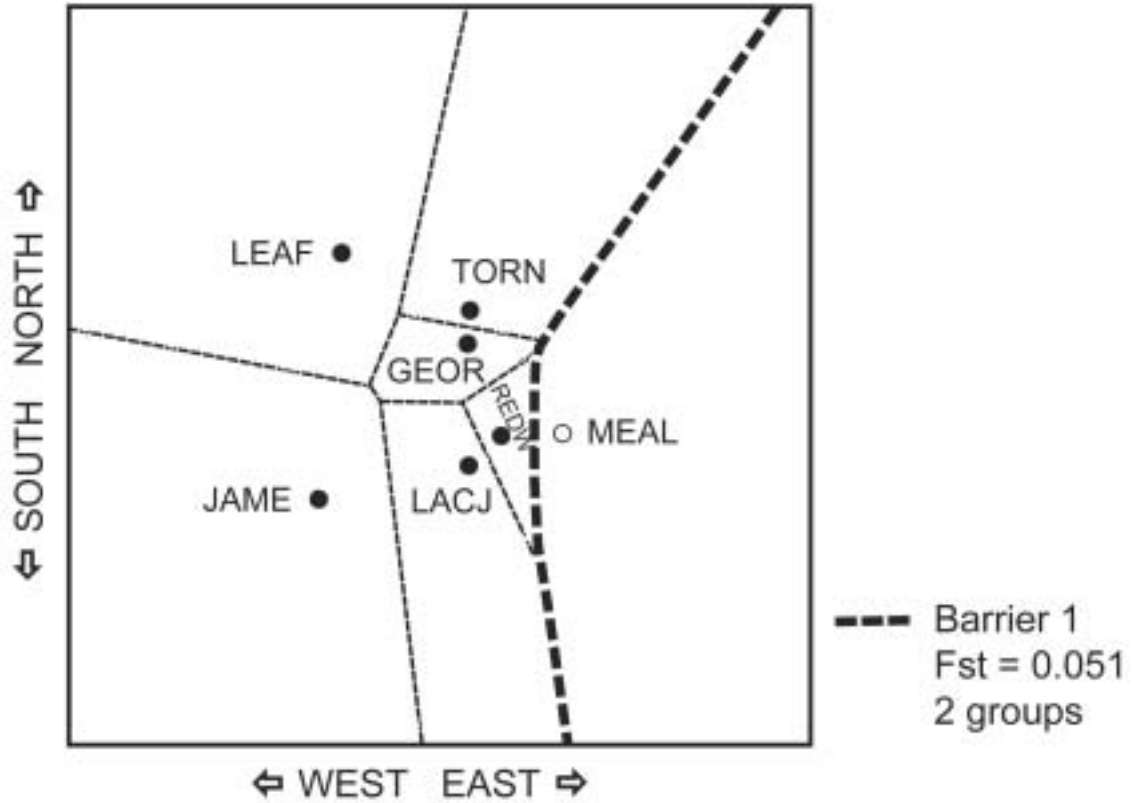


Figure 4. Barriers to gene flow in caribou herds of northern Québec and Labrador identified by the SAMOVA analysis when $k=2$. The barrier suggests that gene flow is lowest between the Mealy Mountains herd and all other herds. Abbreviations are: GEOR= Rivière-George, LEAF= Rivière-aux-Feuilles, LACJ= Lac Joseph, MEAL= Mealy Mountains, REDW= Red Wine Mountains, JAME= Jamésie, and TORN= Torngat.

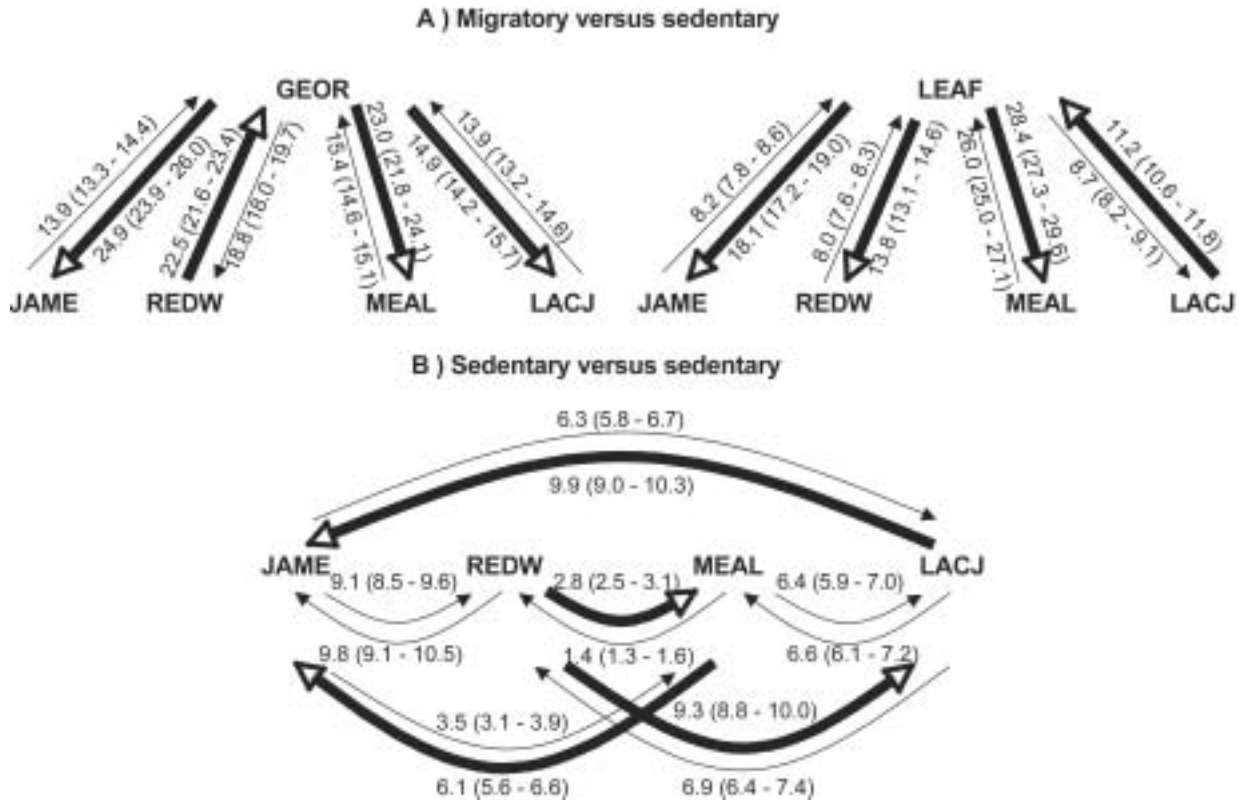


Figure 5. Historical gene flow estimates between (A) the migratory caribou GEOR and LEAF herds versus the sedentary herds, and (B) among all sedentary herds. Numbers refer to the number of immigrants per generation and their respective 95% confidence intervals. Bold arrows represent directions between herd pairs in which the immigration rate was significantly asymmetric. Abbreviations are: GEOR= Rivière-George, LEAF= Rivière-aux-Feuilles, LACJ= Lac Joseph, MEAL= Mealy Mountains, REDW= Red Wine Mountains, JAME= Jamésie, and TORN= Torngat.

3.7 Simulations of historical scenarios

In scenario A (panmixia= 1000 generations or 3000 years, fragmentation= 1000 generations, no sex-biased dispersal), moderate (0.001) to high (0.1) effective immigration rates were sufficient to prevent significant genetic differentiation between herds. These effective immigration rates translated into 101 to 10,090 female immigrants and into 40 to 4036 male immigrants between all pairwise combinations of herds, i.e. represented all the immigrants of the system at a given generation. In contrast, an absence of gene flow ($M= 0$) between all herds raised the F_{ST} value to 0.015 within seven

generations and to 0.66 after 1000 generations (Table 6). An immigration rate of 0.0005 (i.e. 50 immigrant females and 20 immigrant males) led to a F_{ST} value of 0.015 that was relatively stable for more than 1750 generations (5250 years), suggesting that caribou herds behaved like a metapopulation at this level of gene flow. A similar result was obtained with slightly lower values of immigration rate (i.e., 0.00025) with a F_{ST} that stabilized at around 0.03. This suggests that metapopulation dynamics can evolve within a specific range of immigration rates.

This stability in F_{ST} values was also present in scenario B which was characterized by a longer phase of panmixia (1500 generations or 4500 years) and a shorter phase of herd fragmentation (500 generations or 1500 years, Table 6). Similarly, in scenario C, a two-fold sex-biased dispersal in favour of males or females did not prevent the development of a metapopulation dynamics (Table 6). Finally, the historical scenario D, which was characterized by an immigration rate of 0.0005 between five equally-large populations (i.e. a total metapopulation of 100,900 females and 40,360 males), indicated that the genetic structure was possibly due to drift effects in the smaller herds, because the herds were not structured in such a case (global F_{ST} = 0.00087 after 1000 generations).

Table 6. Overall F_{ST} values between all caribou herds for simulations of historical scenarios of fragmentation of an initial herd into five herds of varying size (see parameters below) and varying effective immigration rates.

Immigration ^h	$F_{ST} G1000$ ⁱ	$F_{ST} G1250$	$F_{ST} G1500$	$F_{ST} G1750$	$F_{ST} G2000$	$G_{FST 0,015}$
Historical scenario A ^{a e f h}						
$M_f = 0.1$ $M_m = 0.1$	0.0014	0.0013	0.0009	0.0008	0.0006	DNR ^k
$M_f = 0.05$ $M_m = 0.05$	-0.0003	-0.0002	-0.0001	0.0016	0.0013	DNR
$M_f = 0.01$ $M_m = 0.01$	0.0007	0.0005	0.0008	0.0018	0.0008	DNR
$M_f = 0.005$ $M_m = 0.005$	0.0001	0.0005	0.0015	0.0022	0.0015	DNR
$M_f = 0.001$ $M_m = 0.001$	0.0007	0.0077	0.0067	0.0102	0.0104	DNR
$M_f = 0.00075$ $M_m = 0.00075$	0.0005	0.0081	0.0089	0.0082	0.0089	DNR
$M_f = 0.0005$ $M_m = 0.0005$	0.0013	0.0105	0.0153	0.0133	0.0115	12
$M_f = 0.00025$ $M_m = 0.00025$	0.0001	0.0272	0.0319	0.0277	0.0309	14
$M_f = 0.0001$ $M_m = 0.0001$	-0.0007	0.0591	0.0558	0.0699	0.0827	7
$M_f = 0.0000$ $M_m = 0.0000$	0.0000	0.3820	0.5580	0.6199	0.6581	7
Historical scenario B ^{b e f h}						
$M_f = 0.00075$ $M_m = 0.00075$	N/A ^j	N/A	0.0006	0.0124	0.0078	166
$M_f = 0.0005$ $M_m = 0.0005$	N/A	N/A	0.0008	0.0168	0.0168	15
$M_f = 0.00025$ $M_m = 0.00025$	N/A	N/A	0.0005	0.0225	0.0243	11
Historical scenario C ^{c e f h}						
$M_f = 0.00025$ $M_m = 0.0005$	0.0001	0.0181	0.0166	0.0202	0.0218	19
$M_f = 0.0005$ $M_m = 0.00025$	-0.0005	0.0145	0.0179	0.0199	0.0153	16
Historical scenario D ^{d e g h}						
$M_f = 0.0005$ $M_m = 0.0005$	0.0000	0.0042	0.0067	0.0087	0.0090	DNR

^a Historical scenario A: 1000 generations in panmixia ($M_f = 0.99$ and $M_m = 0.99$) + 1000 generations of structure, no sex-biased dispersal, five herds of unequal sizes.

^b Historical scenario B: 1500 generations in panmixia ($M_f = 0.99$ and $M_m = 0.99$) + 500 generations of structure, no sex-biased dispersal, five herds of unequal sizes.

^c Historical scenario C: 1000 generations in panmixia ($M_f = 0.99$ and $M_m = 0.99$) + 1000 generations of structure, 2-fold difference in sex-biased dispersal, five herds of unequal sizes.

^d Historical scenario D: 1000 generations in panmixia ($M_f = 0.99$ and $M_m = 0.99$) + 1000 generations of structure, no sex-biased dispersal, five herds of equal size.

- ^e Three tryouts were computed for each scenario but since results were very similar, only data for the first tryout are presented.
- ^f Population sizes for scenarios A, B, and C: population A= 100,000 females and 40,000 males, population B= 500 females and 200 males, population C= 200 females and 80 males, population D= 100 females and 40 males, population E= 100 females and 40 males.
- ^g Population sizes for scenario D: 20,180 females and 8072 males in each herd.
- ^h A random mating system, 7 microsatellite loci and a mixed model of molecular evolution have been used.
- ⁱ Abbreviations are: M_f = female effective immigration rate, M_m = male effective immigration rate, F_{ST} _{Gen1000}= overall F_{ST} at generation 1000, and Gen $F_{ST0.015}$ = generation for which the overall F_{ST} between herds reached 0.015.
- ^j N/A= non applicable.
- ^k DNR= did not reach an overall $F_{ST} \geq 0.015$.

4. DISCUSSION

Our primary goals were to assess potential and realised gene flow among caribou herds of northern Québec and Labrador and to model the metapopulation dynamics between these groups. To do so, we used a very unique combination of information: spatial data derived from the most extended data base of satellite-tracked caribou achieved so far, genetic structure among herds, and simulations of historic scenarios. Our main findings were that overlap of rutting ranges and calving site switching were important gene flow mechanisms between migratory herds, whereas forays of migratory individuals into the sedentary range during the rut was a possible gene flow mechanism between the migratory and sedentary ecotypes. In addition, the weak genetic structure observed between herds could be re-obtained by population simulations through a metapopulation dynamics. Below, we discuss the advantages of integrating data from different sources (spatial, genetic, and simulated), we propose a hierarchical metapopulation model that applies to regions where sedentary and migratory herds co-occur during part of their annual cycle, and we discuss the conservation implications of our results for caribou herds and migratory species in general.

4.1 Lessons learned from the integration of data

The global pattern of genetic differentiation we observed was weak but significant ($\theta = 0.015$), and pairwise F_{ST} values among herds ranged from 0 to 0.048. These values were at the lower end of the F_{ST} values observed between caribou herds from southern (Gaspésie montane herd) to central Québec (five sedentary herds) ($F_{ST} = 0.016$ to 0.167, Courtois *et al.*, 2003) and from six forest sedentary herds of Alberta and British Columbia (pairwise $F_{ST} = -0.002$ to 0.082, McLoughlin *et al.*, 2004). However, they were higher than values recorded between eight migratory herds of western Canada (all pairwise $F_{ST} < 0.02$; Zittlau, 2004).

Satellite-telemetry data showed that the migratory herds of Québec and Labrador overlapped during the rutting season in some years. Whether LEAF caribou actually

mated with GEOR caribou, however, is unknown. Nevertheless, we showed that rutting range overlap is spatially extensive and that frequent opportunities for genetic exchanges are possible: 1) the overlap was detected in seven out of eight years with only 12 to 26 satellite-tracked animals per year and herd; 2) the herds were large (see section 2.1) and many more caribou may have intermixed during the rut. In addition, 9.4% of the satellite-tracked females switched calving ground site at least once in their lifetime providing further evidence that the LEAF and GEOR herds are highly demographically connected. This phenomenon was unexpected because most studies of caribou assume that females are philopatric to calving sites (Skoog, 1968; Schaefer *et al.*, 2000; Rettie & Messier, 2001). We suggest that calving site switching may be an important gene-flow mechanism in the LEAF and GEOR herds as well as in other migratory herds of North America.

Alternatively, a recent herd formation may explain the lack of differentiation between the GEOR and the LEAF herds. While historical records for the GEOR herd date from the second part of the 19th century (Low, 1896; Elton, 1942), the records for the LEAF herd are more recent (Le Hénaff, 1976) and the LEAF may have originated from the GEOR herd in the 1970s (Couturier *et al.*, 2003). However, the origin of the LEAF herd could also be more ancient. At the end of the 19th century, Low (1896) reported the presence of Western, Central and Eastern herds in northern Québec and Labrador, which could correspond to the present-day LEAF, GEOR and TORN herds, respectively. Thus, we cannot rule out the possibility that the LEAF herd has been present in northern Québec for at least a century. If we simulate the fragmentation of a large herd (100,000 females and 40,000 males) into two main herds (population A: 20,000 females and 8,000 males; population B: 80,000 females and 32,000 males), differentiation remains extremely low after 10 generations or about 30 years ($F_{ST}= 0.0001$) and even after 100 generations or 300 years ($F_{ST}= 0.0007$). In conclusion, two main factors may explain and maintain the genetic similarity between the GEOR and LEAF herds: the possible recent origin of the LEAF herd from the GEOR and high on-going gene flow between the two herds as revealed by spatial data.

The same factors, i.e. recent herd formation and high gene flow through overlap of rutting range and calving site switching, may explain the weak differentiation in the continental migratory herds of caribou in western Canada. There, the opportunities for gene flow might be even more important because eight migratory herds of 11,000 to 496,000 individuals are present and their respective annual ranges overlap to a large extent: as many as four herds partially overlap in some areas (Zittlau, 2004). However, these spatial data from western herds are based on satellite-tracked females only. Very little is known about the fidelity of males to rutting areas and herds in general. If males are not philopatric to rutting sites, this behaviour could further contribute to genetic homogenisation of western migratory herds (Zittlau, 2004).

Given that migratory caribou can move large distances, we cannot rule out the possibility that other gene flow mechanisms such as dispersal of yearlings and 2-year-olds or immigration occur between the GEOR and LEAF herds and in other migratory herds of western Canada. Natal dispersal has already been suggested as the main gene flow mechanism in sedentary caribou herds (Courtois *et al.*, 2003). Future studies should examine dispersal movements of young individuals and focus more on male movements to better understand the gene flow mechanisms between migratory and sedentary caribou herds.

Another unique phenomenon that was revealed by our extensive satellite-telemetry data base was the presence of forays undertaken by migratory individuals into the sedentary range. Densities of sedentary herds are usually very low (0.008 – 0.029 caribou/ km², Jung *et al.*, 2000 & 2001; Otto, 2002; Schmelzer *et al.*, 2004) and the chances that a migratory individual encounter a sedentary individual of the opposite sex in October may be weak. On the other hand, if migratory males are successful in mating females of sedentary herds, these forays may translate into an input of new or uncommon alleles in the small herds. Asymmetric estimates of gene flow were concordant with these field observations: gene flow was more important from the GEOR herd into three sedentary herds than vice versa (Figure 5).

Alternatively, permanent immigration of caribou into a herd of a different ecotype may be an additional gene flow mechanism that can explain the high estimates between the sedentary and migratory herds, especially the high gene flow observed from the REDW into the GEOR (Figure 5). We currently do not have firm evidence of permanent immigration and reproduction with our satellite-tracking data. However, Schaefer *et al.*, (1999) reported that emigration to the GEOR herd was likely a determining factor in the decline of the REDW herd in the 1990s because five out of 36 VHF radio-collared females moved to the GEOR herd in fall. Whereas one of these females returned to the REDW range six months later, the other females probably died on the GEOR range before the calving season. This result demonstrates that movements of sedentary individuals into the migratory herds are possible. It also stresses the importance of acquiring additional information on annual movements of sedentary herds, especially when these herds are declining, to evaluate how frequently emigration events involving several animals may occur.

On a broader perspective, our study has implications for other organisms and systems. The integration of several data types may be crucial in understanding gene flow dynamics of migratory species such as marine turtles, whales, wolves, or migratory birds. Techniques such as the monitoring of spatial movements have a lot to offer: 1) they may help disentangling the factors explaining weak genetic structure (recent population expansion and/or high contemporary gene flow) by providing estimates of present-day gene-flow via movements of individuals among populations; 2) they may confirm patterns found using an independent marker. This was nicely exemplified in the polar bear studies by Bethke & Taylor (1996), Paetkau *et al.*, (1999) and Taylor *et al.*, (2001). To delineate management units in polar bear populations over the circumpolar range, they used cluster analysis of female movements to quantify potential gene flow and they assessed population structure and long- short-term gene flow using microsatellite genetic markers. The direct comparison of movement data and genetic distances showed a strong correlation ($r_s = -0.60$) between the two techniques (Paetkau *et al.*, 1999). In addition, the extended survey of animal movements revealed six management units, a result that was

concordant with the genetic information (with the exception of one pair of populations), mark-recapture data, and traditional knowledge of Inuit hunters (Taylor *et al.*, 2001).

4.2 Gene flow dynamics between herds: a hierarchical metapopulation?

A metapopulation is defined as a set of populations within a larger area where immigration from one local population to at least some other patches is possible (Hanski & Simberloff, 1997). For gregarious species such as caribou, a more accurate definition could be a set of herds within a large region, where gene flow from one herd to at least some other herds is possible. In addition, because of the movement capabilities of caribou, members of a herd under difficult conditions (e.g. due to degrading or harsh environmental conditions, predation by wolves, or competition for forage) may leave this herd to join another herd or to form a new herd. Thus, the classical source-sink metapopulation model (Hanski & Simberloff, 1997) cannot be applied directly to caribou herds. In addition, the annual cycle of the migratory caribou add a complicating level to the metapopulation concept because reproduction and parturition are separated in time (by eight months) and space (500-1000 km). Below, we propose a hierarchical model that could explain the relationships among migratory herds between each other, sedentary herds between each other, and finally migratory herds versus sedentary herds.

In northern Québec and Labrador, the GEOR and the LEAF herds may interact as “communicating vessels” where high exchanges may mostly occur during years of high overlap of rutting ranges and via calving site switching. Such phenomenon would prevent the establishment of significant genetic structure between the two herds. The GEOR and LEAF herds have also tended to show lagged population fluctuations in recent decades (Couturier *et al.*, 1996 & 2004). It is thus possible that high levels of gene flow occur between the migratory herds in these situations and that even new herds may be created during population peaks. Within the last decade, the LEAF herd has surpassed the GEOR herd in numbers (Couturier *et al.*, 2004). The observation that calving site switches were more common for GEOR females than for LEAF females supports the idea of a contemporary transfer of GEOR individuals into the LEAF herd. The extreme westerly

longitudes of two GEOR females during the rutting seasons of 2000 and one GEOR female in 2001 are also concordant with this idea (Figure 2). In addition, the genetic similarity between the TORN herd and the migratory herds suggests that the TORN herd, which does altitudinal migration in the Torngat Mountains, is a bud of the adjacent GEOR herd. Additional long-term satellite-tracking data during a period of herd fluctuations would be necessary to determine whether the GEOR, LEAF, and TORN herd dynamics behave as proposed. Our present-day extensive spatial data and the lack of genetic differentiation between these herds clearly demonstrate that they are tightly linked.

For the sedentary herds, our data indicate that they are genetically distinct from each other, but levels of gene flow between these herds is variable and influenced by geographic distance (i.e., isolation-by-distance pattern) between herds. Spatial data and observations of a sedentary female collared in the REDW herd that moved to the LACJ herd confirms that contemporary gene flow does occur between the herds: this old and experienced female moved to the LACJ herd, successfully reproduced in the LACJ herd, and then moved back to the REDW herd (R. Otto and T. Chubbs, unpubl. data). Among sedentary herds, isolation-by-distance could be partly driven by the more pronounced differentiation of the easterly MEAL herd versus others. Although we cannot exclude that the differentiation of the MEAL herd might have been influenced by the lower number of samples analysed in this herd, it is possible that Lake Melville in eastern Labrador acted as a barrier reducing gene flow between the MEAL herd and other sedentary herds or the migratory GEOR herd. Interestingly, McLoughin *et al.*, (2004) suggested that a physical obstacle, the Peace River in the Northwest Territories, was responsible for the genetic differentiation observed between sedentary caribou herds and Courtois *et al.*, (2003) showed that large geographic distances between ranges restricted gene flow between herds of southern and north central Québec.

When the migratory herds were added to the analysis of isolation-by-distance, the relationship between genetic differentiation and geographic distance was no longer significant although the GEOR and especially the LEAF herds were very distant from the

sedentary herds. The long-term estimates of gene flow between the GEOR and three sedentary herds suggest that the GEOR herd has been a source of caribou for at least three sedentary herds (Figure 5). However, contrary to our hypothesis, the migratory herds may also act as recipient herds for sedentary herds, as demonstrated by significant incoming gene flow from specific sedentary herds into the LEAF or GEOR herds. No matter the direction of gene flow, the migratory herds interact with the sedentary herds and partially blend the gene flow pool of both ecotypes. We propose that the migratory herds (and especially the GEOR herd) may act as generators of gene flow exchanges and that the direction of gene flow may vary throughout the history of the herds depending on the demography of the herds or the environmental conditions prevailing in the area.

4.3 Limitations: the difficulty of assessing gene flow

We used seven microsatellite loci to document gene flow dynamics between seven caribou herds that were not strongly differentiated. Low differentiation and relatively high possibilities for gene flow, as established by field data, prevented us from measuring contemporary gene flow via assignment tests (Austin *et al.*, 2004; Piry *et al.*, 2004) or Bayesian inferences (Wilson & Rannala, 2003). For example, the F_{ST} value between the two migratory herds was only 0.002 and the use of any method estimating gene flow would have been questionable. Because the assessment of realistic estimates of gene flow may be crucial for establishing adequate management plans, especially in declining or harvested populations (Fraser & Bernatchez, 2004), we suggest that other natural markers such as trace elements or stable isotope ratio measurements (Hobson, 1999; Hobson & Wassenaar, 2001) on tissue produced on calving sites could complement the genetic and satellite-tracking data for delineating populations.

4.4 Conservation implications

Based on our findings, we propose that the migratory and sedentary caribou herds of northern Québec and Labrador form a hierarchical metapopulation. Most of these herds are exploited either for recreational or traditional hunting. Management plans of caribou in northern Québec and Labrador should take into account the hierarchy in the possibilities of gene flow, i.e. higher between migratory herds and lower between sedentary herds. More specifically, we suggest that management plans consider two levels: 1) a fine-scale level for the sedentary herds, which are genetically distinct from each other and qualify as management units (Moritz *et al.*, 1995); and 2) a large-scale level to maintain the gene flow between the two migratory herds but also between the migratory and sedentary herds. The fine-scale level would focus at maintaining gene flow between herds, especially sedentary ones. This implies, for example, adjusting the size and spatial distribution of clearcuts in the boreal forests to maintain habitat connectivity (see also Courtois *et al.*, 2003). In contrast, the large-scale approach would be essential to maintain gene flow and high genetic diversity and to avoid inbreeding depression within the small sedentary herds which usually include only a few hundred individuals (COSEWIC, 2002). Our results also stress the importance of accurately delineating populations and knowing more precisely the patterns of space use of populations throughout their annual cycle to assess the migratory connectivity of populations (Webster *et al.*, 2002). This approach may be essential to identify the specific areas used at a given time of the year and the possible threats at each phase of the life cycle (Webster *et al.*, 2002). While this can be achieved relatively easily in medium and large-sized mammals via satellite-tracking methods, other techniques can be used in smaller migratory species (Boulet, 2004).

ACKNOWLEDGEMENTS

We thank D. St-Pierre, S. Rivard, J. Brunelle, D. Jean, B. Baron, M. Kooktook, F. Phillips, and J.A. Schaefer for assistance during sampling collections. We also thank R. St-Laurent and L. Papillon for help with laboratory work, D. Fraser, S. Rogers, M. Hansen, and J. Huot for comments and stimulating discussions, and D. Cooper and J. Bouchard for editing this report. This project was primarily funded by the Institute for Environmental Monitoring and Research in Goose Bay (Newfoundland & Labrador), by the Ministère des Ressources naturelles et de la Faune du Québec (Québec Government) and by the Wildlife Division, Department of Environment and Conservation (Newfoundland & Labrador Government). The *Fondation de la faune du Québec (Fonds pour les espèces nordiques)*, the Natural Sciences and Engineering Research Council of Canada, Université Laval and Caribou Québec also provided funding. The ARGOS satellite telemetry collars were maintained by the governments of Québec and Newfoundland & Labrador, with close cooperation from the Department of National Defence (Canada). The following corporations also participated in the satellite monitoring program: Hydro-Québec (1991-1999), Makivik Corporation (1997-1999) and TVA International (1998-2001).

REFERENCES

- ADAMS, L.G. and DALE, B.W. 1998. Reproductive performance of female Alaskan caribou. *Journal of Wildlife Management* 62, 1184-1195.
- AUSTIN, J.D., LOUGHEED, S.C. and BOAG, P.T. 2004. Controlling for the effects of history and nonequilibrium conditions in gene flow estimates in Northern Bullfrog (*Rana catesbeiana*) populations. *Genetics* 168, 1491-1506.
- AUSTIN, D., McMILLAN, J.I. and BOWEN, W.D. 2003. A three stage algorithm for filtering erroneous ARGOS satellite locations. *Marine Mammal Science* 19, 371-383.
- AVISE, J.C. 2004. Molecular Markers, Natural History, and Evolution. Blackwell Science, London, UK.
- BALLOUX, F. 2001. EASYPOP (version 1.7). A computer program for the simulation of population genetics. *Journal of Heredity* 92, 301-302.
- BANFIELD, A.W.F. and TENER, J.S. 1958. A preliminary study of the Ungava caribou. *Journal of Mammalogy* 39, 560-573.
- BEERLI, P. and FELSENSTEIN, J. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences USA* 98, 4563-4568.
- BÉLANGER, M. and LE HÉNAFF, D. 1985. Distribution, abundance and regulation of caribou hunting in Québec. Proceedings of the Second North American Caribou Workshop, Val Morin, Québec. *McGill Subarctic Research Paper* 40, 3-13.
- BELKIR, K., BORSA, P., CHIKHI, L., RAUFASTE, N. and BONHOEMME, F. 2000. Genetix 4.02, logiciel sous Windows pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000. Université de Montpellier, Montpellier, France.
- BENSCH, S., ANDERSSON, T. and AKESSON, S. 1999. Morphological and molecular variation across a migratory divide in willow warblers, *Phyloscopus trochilus*. *Evolution* 53, 1925-1935.
- BERGERUD, A.T. 1973. Movements and rutting behaviour of caribou (*Rangifer tarandus*) at Mount Albert. *Canadian Field-Naturalist* 87, 357-367.

- BERGERUD, A.T. 2000. Caribou. In: Ecology and Management of large Mammals in North America (eds. Demarais S, Krausman PR) pp 658-693. Prentice Hall, Upper Saddle River, New Jersey.
- BERGERUD, A.T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Proceeding of the Sixth North American Caribou Workshop, 1994. *Rangifer* Special Issue 9, 95-116.
- BERGMAN, C.M., SCHAEFER, J.A. and LUTTICH, S.N. 2000. Caribou movements as a correlated random walk. *Oecologia* 123, 364-374.
- BETHKE, R. and TAYLOR, M.K. 1996. Population delineation of polar bears using satellite collar data. *Ecological Applications* 6, 311-317.
- BISHOP, M.D., KAPPES, S.M., KEELE, J.W., STONE, R.T., SUNDEN, S.F.L., HAWKINS, G.A., SOLINAS, S., FRIES, T.R., GROSZ, M.D., YOO, J. AND BEATTIE, C.W. 1994. A genetic linkage map for cattle. *Genetics* 136, 619-639.
- BLOUIN-DEMERS, G. and WEATHERHEAD, P.J. 2002. Implications of movement patterns for gene flow in black rat snakes (*Elaphe obsoleta*). *Canadian Journal of Zoology* 80, 1162-1172.
- BOHONAK, A.J. 2002. IBD (Isolation by distance): a program for the analyses of isolation by distance. *Journal of Heredity* 93, 153-154.
- BOULANGER, J., HIMMER, S. and SWAN, C. 2004. Monitoring of grizzly bear population trends and demography using DNA mark-recapture methods in the Owikeno Lake area of British Columbia. *Canadian Journal of Zoology* 82, 1267-1277.
- BOULET, M. 2004. Evolutionary and migration patterns in the yellow warbler (*Dendroica petechia*). Ph. D. Thesis, Department of Biology, McMaster University, Hamilton, Ontario.
- COSEWIC. 2002. COSEWIC assessment and update report on the woodland caribou *Rangifer tarandus caribou* in Canada, pp. xi + 1-98. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario.
- CÔTÉ, S.D., DALLAS, J.F., MARSHALL, F., IRVINE, R.J., LANGVATN, R. and ALBON, S.D. 2002. Microsatellite DNA evidence for genetic drift and philopatry in Svalbard reindeer. *Molecular Ecology* 11, 1923-1930.

- COURTOIS, R., BERNATCHEZ, L., OUELLET, J.-P., BRETON, L., DUSSAULT, C., BRETON, L. and MALTAIS, J. 2003. Significance of caribou (*Rangifer tarandus*) ecotypes from a molecular genetics viewpoint. *Conservation Genetics* 4, 393-404.
- COURTOIS, R., OUELLET, J.-P., GINGRAS, A., DUSSAULT, C., BRETON, L. and MALTAIS, J. 2004. Historical changes and current distribution of caribou, *Rangifer tarandus*, in Québec. *Canadian Field-Naturalist* 117, 399-414.
- COUTURIER, S., BRUNELLE, J., VANDAL, D. and ST-MARTIN, G. 1990. Changes in the population dynamics of the George River caribou herd, 1976-87. *Arctic* 43, 9-20.
- COUTURIER, S., OTTO, R., HUOT, J., VAN GINHOVEN, Q. and PHILLIPS, F. 1999. Progress report on the Lac Joseph caribou telemetry program 1998-1999. Unpublished report. Science Division Library. Goose Bay, Newfoundland and Labrador.
- COUTURIER, S., OTTO, R., HUOT, J., VAN GINHOVEN, Q., DOUCET, G.J., CHUBBS, T.E., LAMOTHE, P. and JEAN, D. 2003. Is the metapopulation theory useful in caribou herds conservation? – A test with the Québec-Labrador caribou. Proceedings of the Ninth North American Caribou Workshop. *Rangifer* Special Issue 14, 329.
- COUTURIER, S., JEAN, D., OTTO, R. and RIVARD, S. 2004. Demography of the migratory tundra caribou (*Rangifer tarandus*) of the Nord-du-Québec region and Labrador. Ministère des Ressources naturelles, de la Faune et des Parcs, Québec ISBN: 2-550-43725-X. 66 p.
- CRÊTE, M., COUTURIER, S., HEARN, B.J. and CHUBBS, T.E. 1996. Relative contribution of decrease productivity and survival to recent changes in the demographic trend of the Rivière George Caribou Herd. Proceedings of the Sixth North American Caribou Workshop. *Rangifer* Special Issue 9, 27-36.
- CRONIN, M.A., PATTON, J.C., BALMYSHEVA, N. and MacNEIL, M.D. 2003. Genetic variation in caribou and reindeer (*Rangifer tarandus*). *Animal Genetics* 34, 33-41.

- CRONIN, M.A., RENECKER, L., PIERSON, B.J., PATTON, J.C. and McKENDRICK, J.D. 1995. Genetic variation in domestic reindeer and wild caribou in Alaska. *Animal Genetics* 26, 427-434.
- DUECK, G.S. 1998. *Genetic relations and phylogeography of woodland and barren-ground caribou*. M. Sc. Thesis. Department of Biological Sciences, University of Alberta, Edmonton, Alberta.
- DUPANLOUP, I., SCHNEIDER, S. and EXCOFFIER, L. 2002. A simulated approach to define the genetic structure of populations. *Molecular Ecology* 11, 2571-2581.
- DYKE, A.S. and PREST, V.K. 1987. Late Wisconsin and Holocene history of the Laurentide Ice Sheet. *Géographie Physique et Quaternaire* 41, 237-263.
- ELLEGREN, H. 2000. Microsatellite mutations in the germline: implications for evolutionary inferences. *Trends in Genetics* 16, 551-558.
- ELTON, C.S. 1942. Voles, mice and lemmings: Problems in population dynamics. Oxford University Press, Oxford, UK.
- FLAGSTAD, Ø. and RØED, K.H. 2003. Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. *Evolution* 57, 658-670.
- FRASER, D. and BERTNATCHEZ, L. 2004. An integrative examination of asymmetric migration, sex-biased dispersal and resulting population structure in lacustrine brook charr (*Salvelinus fontinalis* Mitchill). *Molecular Ecology* 13, 67-80.
- GOUDET, J. 1995. FSTAT (version 1.2): A computer program to calculate F- statistics. *Journal of Heredity* 86, 485-486.
- GRAVLUND, P., MELDGAARD, M., PÄÄBO, S. and ARCTANDER, P. 1998. Polyphyletic origin of the small-bodied, high-Arctic subspecies of tundra reindeer (*Rangifer tarandus*). *Molecular Biology and Evolution* 10, 151-159.
- GUO, S.W. and THOMPSON, E.A. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics* 48, 361-372.
- HANSKI, I. and GAGGIOTTI, O.E. 2004. Ecology, Genetics, and Evolution of metapopulations. Elsevier Academic Press, Burlington, New York.

- HANSKI, I., and SIMBERLOFF, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. *In: Metapopulation Biology, Ecology, Genetics, and Evolution* (eds. Hanski I, Gilpin ME), pp. 5-26. Academic Press, San Diego, California.
- HARRINGTON, F. and VEITCH, A.M. 1991. Short-term impacts of low-level jet fighter training on caribou in Labrador. *Arctic* 44, 318-327.
- HOBSON, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314-328.
- HOBSON, K.A. and WASSENAAR, L.I. 2001. Isotopic delineation of North American migratory wildlife populations: loggerhead shrikes. *Ecological Applications* 11, 1545-1553.
- HOOGE, P. and EICHENLAUB, B. 1996. ArcView animal movement extension, Alaska Biological Research Station, Alaska.
- IBARGÜEN, S.B. 2004. Population connectivity: combining methods for estimating avian dispersal and migratory linkages. Ph. D. Thesis. Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, Ohio.
- JEPSEN, B.I., SIEFGISMUND, H.R. and FREDHOLM, M. 2002 Population genetics of the native caribou (*Rangifer tarandus groenlandicus*) and the semi-domestic reindeer (*Rangifer tarandus tarandus*) in Southwestern Greenland: evidence of introgression. *Conservation Genetics* 3, 401-409.
- JOHNSON, C.J., PARKER, K.L., HEARD, D.C. and GILLIGHAM, M.P. 2002. A multiscale behavioral approach to understand the movements of woodland caribou. *Ecological Applications* 12, 1840-1860.
- JUNG, T.S., CHUBBS, T.E., OTTO, R. and JONES, C. 2000. Population status and distribution of woodland caribou of the Lac Joseph herd in western Labrador. Unpublished report. Science Division Library. Goose Bay, Newfoundland and Labrador, Canada.
- JUNG, T.S., CHUBBS, T.E., OTTO, R. and PHILLIPS, F.R. 2001. Population status and distribution of woodland caribou of the Red Wine Mountains herd in central Labrador. Unpublished report. Institute for Environmental Monitoring and Research. Goose Bay, Newfoundland and Labrador, Canada.

- LE HÉNAFF, D. 1976. Inventaire aérien des terrains de vêlage du caribou dans la région nord et au nord du territoire de la municipalité de la Baie James (mai-juin 1975). Service de la recherche biologique, Ministère du Tourisme, de la Chasse et de la Pêche. Québec. 28 p.
- LOW, A.P. 1896. Report on explorations in the Labrador Peninsula along the Eastmain, Koksoak, Hamilton, Manicouagan, and portions of others rivers, in 1892-95. *Geological Survey of Canada* 8, 1-387.
- McLOUGHIN, P., PAETKAU, D., DUDA, M. and BOUTIN, S. 2004. Genetic diversity and relatedness of boreal caribou populations in western Canada. *Biological Conservation* 118, 593-598.
- MALLORY, F.F. and HILLIS, T.L. 1998. Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints, releases, and population dynamics. Seventh North American Caribou Conference. *Rangifer* Special Issue 10, 49-60.
- MILLER, F.L. 2003. Caribou. *In: Wild Mammals of North America* (eds. Feldhamer GA, Thompson BC, Chapman JA), pp. 965-997. Johns Hopkins University Press, Baltimore.
- MORITZ, C., LAVERY, S. and SLADE, R. 1995. Using allele frequency and phylogeny to define units for conservation management. *American Fisheries Society Symposium* 17, 249-262.
- NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89, 583-590.
- OTTO, R.D. 2002. Density distribution survey and population estimate Mealy Mountain caribou herd, 2002. Unpublished report. Science Division Library. Goose Bay, Newfoundland and Labrador.
- PAETKAU, D., AMSTRUP, S.C., BORN, E.W., CALVERT, W., DEROCHE, A.E., GARNER, G.W., MESSIER, F., STIRLING, I., TAYLOR, M.K., WIIG, Ø. and STROBECK, C. 1999. Genetic structure of the world's polar bear populations. *Molecular Ecology* 8, 1571-1584.
- PEARSE, D.E., and CRANDALL, K.A. 2004. Beyond F_{ST} : Analysis of population genetic data for conservation. *Conservation Genetics* 5, 585-602.

- PIRY, S., ALAPETITE, A., CORNUET, J.-M., PAETKAU, D., BAUDOUIN, L. and ESTOUP, A. 2004. GeneClass2: A Software for Genetic Assignment and First-Generation Migrant Detection. *Journal of Heredity* 95, 536-539.
- PROCTOR, M.F., McLELLAN, B.N., STROBECK, C. and BARCLAY, R.M.R. 2004. Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Canadian Journal of Zoology* 82, 1108-1118.
- RAYMOND, M. and ROUSSET, F. 1995. GENEPOP Version 1.2: Population genetics software for exact test and ecumenism. *Journal of Heredity* 86, 248-249.
- RETTIE, W.J. and MESSIER, F. 2001. Range use and movement rates of woodland caribou in Saskatchewan. *Canadian Journal of Zoology* 79, 1933-1940.
- RICE, W.R. 1989. Analysing tables of statistical tests. *Evolution* 43, 223-225.
- RØED, K.H. 1998. Microsatellite variation in Scandinavian Cervidae using primers derived from bovidae. *Hereditas* 129, 19-25.
- RØED, K.H., FERGUSON, M.A.D., CRÊTE, M. and BERGERUD, T.A. 1991. Genetic variation in transferrin as a predictor for differentiation and evolution of caribou from eastern Canada. *Rangifer* 11, 65-74.
- RØED, K.H. and MIDTHJELL, L. 1998. Microsatellite in reindeer, *Rangifer tarandus*, and their use in other cervids. *Molecular Ecology* 7, 1771-1788.
- RØED, K.H. and WHITTEN, K.R. 1986. Transferrin variation and evolution of Alaskan reindeer and caribou, *Rangifer tarandus*, L. *Rangifer* 1, 247-251.
- SCHAEFER, J.A., BERGMAN, C.M. and LUTTICH, S.N. 2000. Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology* 15, 731-739.
- SCHAEFER, J.A. and LUTTICH, S.N. 1998. Movements and activity of caribou, *Rangifer tarandus caribou*, of the Torngat Mountains, northern Labrador and Québec. *Canadian Field-Naturalist* 112, 486-490.
- SCHAEFER, J.A., VEITCH, A.M., BROWN, W.K., HARRINGTON, F.B., THEBERGE, J.B. and LUTTICH, S.N. 1999. Demography of decline of the Red Wine Mountains caribou herd. *Journal of Wildlife Management* 63, 580-587.

- SCHMELZER, I., BRAZIL, J., CHUBBS, T., FRENCH, S., HEARN, B., JEFFERY, R., LeDREW, L., MARTIN, H., McNEILL, A., NUNA, R., OTTO, R., PHILLIPS, F., MITCHELL, G., PITTMAN, G., SIMON, N. and YETMAN, G. 2004. Recovery strategy for three woodland caribou herds (*Rangifer tarandus caribou*; Boreal population) in Labrador. Dept. of Environment and Conservation, Gov. of Newfoundland and Labrador, Corner Brook. Newfoundland and Labrador, 51 p.
- SCHNEIDER, S., ROESSLI, D. and EXCOFFIER, L. 2000. Arlequin Version 2.000; a Software for Population Genetic Data Analysis Genetics and biometry Laboratory, University of Geneva, Geneva.
- SKOOG, R.O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph. D. Thesis. Department of Zoology, California University, Berkeley, California.
- ST-MARTIN, G. 1987. The ecology of the East-Central Québec and western Labrador caribou population as it relates to a proposed road development. M. A. Thesis, Department of Regional Planning and Resource Management, University of Waterloo, Waterloo, Ontario.
- TAYLOR, M.K., AKEEAGOK, S., ANDRIASHEK, D., BARBOUR, W., BORN, E.W., CALVERT, W., CLUFF, H.D., FERGUSON, S., LAAKE, J., ROSING-ASVID, A., STIRLING, I. and MESSIER, F. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. *Canadian Journal of Zoology* **79**, 690-709.
- WEBSTER, M.S., MARRA, P.P., HAIG, S.M., BENSCH, S. and HOLMES, R.T. 2002. Links between worlds: unravelling migratory connectivity. *Trends in Ecology and Evolution* **17**, 76-83.
- WEIR, B.S. and COCKERHAM, C.C. 1984. Estimating F statistics for the analysis of population structure. *Evolution* **38**, 1358-1370.
- WILSON, G.A. and RANNALA, B. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* **150**, 499-510.
- WILSON, G.A., STROBECK, C., WU, L. and COFFIN, J.W. 1997. Characterization of microsatellite loci in caribou *Rangifer tarandus*, and their use in other artiodactyls. *Molecular Ecology* **6**, 697-699.

- WITTEVEEN, B.H., STRALEY, J.M., VON ZIEGESAR, O., STEEL, D. and BAKER, C.S. 2004. Abundance and mtDNA differentiation of humpback whales (*Megaptera novaeangliae*) in the Shumagin Islands, Alaska. *Canadian Journal of Zoology* **82**, 1352-1359.
- ZITTLAU, K.A. 2004. Population genetic analyses of North American Caribou (*Rangifer tarandus*). Ph. D. Thesis, Department of Biological Sciences, University of Alberta, Edmonton, Alberta.