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Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds

MARYLÈNE BOULET,*† SERGE COUTURIER,*†‡ STEEVE D. CÔTÉ,*† ROBERT D. OTTO§¶ and LOUIS BERNATCHEZ*

Département de Biologie, Université Laval, Québec, QC, Canada G1K 7P4, †Centre d'études nordiques, Université Laval, Québec, QC, Canada G1K 7P4, ‡Ministère des Ressources naturelles et de la Faune, Direction de la recherche sur la faune, 880 Ch. Ste-Foy, 2th floor, Québec, QC, Canada G1S 4X4, §Wildlife Division, Department of Environment and Conservation, PO Box 2007, Corner Brook, NL, Canada A2H 7S1

Abstract

Genetic differentiation is generally assumed to be low in highly mobile species, but this simplistic view may obscure the complex conditions and mechanisms allowing genetic exchanges between specific populations. Here, we combined data from satellite-tracked migratory caribou (*Rangifer tarandus*), microsatellite markers, and demographic simulations to investigate gene flow mechanisms between seven caribou herds of eastern Canada. Our study included one montane, two migratory, and four sedentary herds. Satellite-tracking data indicated possibilities of high gene flow between migratory herds: overlap of their rutting ranges averaged 10% across years and 9.4% of females switched calving sites at least once in their lifetime. Some migratory individuals moved into the range of the sedentary herds, suggesting possibilities of gene flow between these herds. Genetic differentiation between herds was weak but significant (F_{ST} = 0.015): migratory and montane herds were not significantly distinct (F_{ST} all ≤ 0.005), whereas sedentary herds were more differentiated (F_{ST} = 0.018–0.048). Geographical distances among sedentary herds limited gene flow. Historical estimates of gene flow were higher from migratory herds into sedentary herds ($4Nm$ all > 9) than vice-versa ($4Nm$ all < 5), which suggests migratory herds had a demographic impact on sedentary herds. Demographic simulations showed that an effective immigration rate of 0.0005 was sufficient to obtain the empirical F_{ST} of 0.015, while a null immigration rate increased the simulated F_{ST} to > 0.6. In conclusion, the weak genetic differentiation between herds cannot be obtained without some genetic exchanges among herds, as demonstrated by genetic and spatial data.

Keywords: caribou, demographic simulations, gene flow, metapopulation, microsatellite, population structure, *Rangifer tarandus*, satellite-tracking

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Introduction

Highly mobile species have the capacity to disperse across large distances. As a consequence, genetic differentiation is assumed to be low within these species, because high rates of gene flow would prevent the accumulation of genetic differences among populations (Wayne & Koepfli 1996). This simplistic view may obscure the more complex ecological conditions and mechanisms that allow genetic exchanges between populations of highly mobile species. For example, habitat barriers and geographical distances are effective mechanisms limiting gene flow in highly mobile terrestrial mammals such as bobcats (*Lynx rufus*, Riley *et al*. 2006), cougars (*Felis concolor*, McRae *et al*. 2005), coyotes (*Canis latrans*, Riley *et al*. 2006), and grey wolves

Correspondence: Marylène Boulet, Department of Biological Anthropology and Anatomy, Box 90383, 08 Bio Science Bldg, Duke University, Durham, NC 27708, USA. Fax: 919-660-7348; E-mail: marylene.boulet@duke.edu

¶Present address: Institute for Biodiversity, Ecosystem Science, and Sustainability, Sir Wilfred Grenfell College, 1 University Drive, Corner Brook, NL, Canada A2H 6P9

(*Canis lupus*, Carmichael *et al*. 2001; Geffen *et al*. 2004; Weckworth *et al*. 2005).

A simple assessment of genetic differentiation or rates of gene flow, by means of genetic markers, cannot always identify the specific mechanisms used by animals to maintain genetic connectivity between groups. This is because genetic markers cannot reveal where individuals have spent portions of their life cycle and when they may have joined other groups. Radio- and satellite-tracking methods can reliably determine the geographical location of large and highly mobile species throughout their annual cycle. These methods can estimate potential for gene flow between groups via the location of individuals during the periods that are critical for genetic exchanges. In migratory or highly mobile ungulates, male and female seasonal ranges are often different and gene flow may include population mixing during the reproduction season or during annual migration, females giving birth on sites different than their natal sites, or dispersion of juveniles in adjacent groups. In contrast, genetic analyses can estimate realized gene flow, that is whether animals have successfully transmitted their genes into a new gene pool, and trace historical formations of populations. While genetic data can test whether groups comprising individuals of one sex are more structured than those of the other sex, spatial data can test whether one sex shows stronger philopatry than the other (Goudet *et al*. 2002; Prugnolle & de Meeus 2002). Genetic and spatial approaches are complementary and studies integrating both approaches are emerging (Bethke & Taylor 1996; Paetkau *et al*. 1999; Taylor *et al*. 2001; Sacks *et al*. 2004; Sacks *et al*. 2005; Cronin *et al*. 2006; Riley *et al*. 2006).

In terrestrial mammals, the caribou (or reindeer in Eurasia, *Rangifer tarandus*) is among the most mobile species. In North America, three ecotypes are present: migratory, montane, and sedentary (Bergerud 2000). The migratory ecotype undertakes long-distance migrations of hundreds of kilometres between summer range in the tundra and winter range in the boreal forest. Migratory females breed in late October during the fall migration. They return to the tundra in spring, aggregate on the way to calving grounds, and in June they calve together on traditional calving grounds (Bergerud 2000). The spring migration to calving grounds at high latitude is thought to reduce predation risk (Bergerud & Page 1987). Females tend to be more philopatric to natal calving grounds than to any other areas used during the annual cycle. Because of this characteristic, biologists identified migratory herds based on geographical features located in the vicinity of calving grounds, such as a river or a lake. Migratory herds can be large and some herds include more than 300 000 individuals (Bergerud 2000). In contrast, the montane ecotype undertakes altitudinal movements associated with food availability and predation avoidance but usually stays in the same alpine area. Montane herds tend to be smaller and most herds have less than 5000 individuals (COSEWIC 2002). Finally, the sedentary ecotype resides in the boreal forest throughout the year and does short-distance migrations (< 100 km) between summer and winter quarters. Sedentary females use a different strategy and tend to disperse from each other during calving season to reduce risks of predation from large carnivores. Sedentary herds typically comprise less than 2000 individuals (COSEWIC 2002).

Mitochondrial (mt) DNA analyses of caribou herds revealed three evolutionary lineages, presumably representing three remnant populations that were isolated during the last Pleistocene glaciation (Flagstad & Røed 2003). Levels of genetic differentiation were usually not concordant with a taxonomic classification of subspecies, which was based on skull characteristics, and suggested that morphological differentiation of subspecies evolved after Pleistocene glaciations (Banfield 1961). Two of these mtDNA lineages are found in North America, the Beringian-Eurasian and the North American lineages, and they mix along a northeast-southwest cline spanning eastern Canada to the Rocky Mountains (Dueck 1998; Flagstad & Røed 2003; Cronin *et al*. 2005). Microsatellite markers confirmed that herds from eastern North America are distinct from herds from western North America and that at least one eastern herd is admixed (Cronin *et al*. 2003; Cronin *et al*. 2005). In the Northwest Territories, differentiation is higher among Arctic island herds (F_{ST} range = 0.005–0.077) than among continental herds (F_{ST} range = 0.0002–0.0083; Zittlau 2004). While continental herds separated by several hundred kilometres may not be significantly different from each other (Zittlau 2004), reindeer from valleys < 50 km apart in Svalbard showed weak (F_{ST} = 0.03), but significant differentiation likely due to genetic drift and philopatry (Côté *et al*. 2002). In conclusion, the high mobility of caribou may not necessarily lead to genetic homogenization of herds because evolutionary history, geographical barriers, and genetic drift can play a role in shaping the genetic structure of herds.

Despite the ability of satellite-tracking to detect small- to large-scale movements of highly mobile species over an extended period of time, very little attention has been given to the genetic consequences of movements undertaken by individuals into the range of other groups. In caribou, for example, we currently do not know whether individuals from large migratory herds contribute to the gene pool of the smaller sedentary or montane herds, and if so, in which circumstances. In addition, we do not know whether those large migratory herds are demographically linked and therefore genetically similar.

Here, we examine possible gene flow mechanisms between two migratory, one montane, and four sedentary caribou herds of eastern Canada, and we assess genetic connectivity between these herds. The novelty of our

approach is that we combine the use of satellite-tracking technology, genetic analyses, and demographic simulations to understand gene flow mechanisms in an ungulate. Our specific objectives were to: (i) identify potential gene flow mechanisms by analysing movements of satellite-tracked animals during the October rut and June parturition seasons; (ii) assess the genetic structure and identify possible barriers to gene flow using spatial analyses; (iii) quantify historical gene flow between herds; (iv) test for evidence of sex-biased gene flow; and (v) quantify the levels of gene flow required to explain the observed population differentiation among herds by simulating various demographic scenarios. To avoid confusion, we will refer to demographic migration (i.e. permanent movement of adults or dispersal of young into another herd) using the term immigration and restrict the term migration to the periodic and orientated annual movements of migratory caribou between summer and winter ranges. We define gene flow as the inclusion of genes of a population into the gene pool of another population.

Materials and methods

Characteristics of caribou herds

Our study included the only two migratory herds of eastern North America: the Rivière-George (George River, GEOR) and the Rivière-aux-Feuilles (Leaf River, LEAF) herds. Females of the GEOR herd give birth on tundra plateaus (57°N, 65°W, see Fig. 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 5000 caribou in 1956 (Banfield & Tener 1958), the GEOR herd increased rapidly to more than 775 000 individuals in 1993, then declined to 385 000 animals in 2001 (Couturier *et al*. 1990, 2004). The migratory LEAF herd was first described in June 1975 when Le Hénaff (1976) saw a group of about 20 000 calving females near the Leaf River (58°N, 73°W). Since then, the location of the calving ground gradually shifted north by about 400 km (61°N, 74°W, Fig. 1) and the herd reached more than 628 000 individuals in 2001 (Couturier *et al*. 2004). Although nothing is known about their genetic distinctiveness, these migratory herds are presently managed as separate herds because of their different calving grounds and population dynamics.

According to Bélanger & Le Hénaff (1985), the Torngat Mountains (TORN) herd comprises approximately 5000 individuals; however, no recent census has confirmed the current herd size. This herd belongs to the montane ecotype, which performs altitudinal migrations in alpine habitats (Fig. 1). This herd was often confounded with the migratory GEOR herd, whose range partially overlaps with the TORN herd during part of the year (Schaefer & Luttich 1998).

We also included four sedentary caribou herds inhabiting the boreal forest of Québec and Labrador: Lac Joseph (Lake Joseph, LACJ, $n = 1100$ caribou), Mealy Mountains (MEAL, $n = 2600$), Red Wine Mountains (REDW, $n = 87$), and the Jamésie (JAME) herds ($n \approx 600$) (Schaefer *et al*. 1999; Schmelzer *et al*. 2004; and references therein; D. St-Pierre, unpublished data) (Fig. 1). The LACJ, JAME and REDW herds sometimes share their winter ranges with migratory herds (Schaefer *et al*. 1999; D. St-Pierre, unpublished data). These four herds are classified within the woodland caribou boreal populations, which are designated as Threatened in Canada because of a widespread decline throughout their range (COSEWIC 2002).

Satellite-tracking data

To monitor movements of migratory caribou, we installed ARGOS satellite-tracking collars (Service ARGOS Inc.) to 171 caribou of the GEOR herd ($n = 24$ males and 147 females, from 1986 to 2003) and to 42 caribou of the LEAF herd ($n = 8$ males and 34 females, from 1993 to 2003). The average duration of individual monitoring was 2.5 years but some animals were followed for up to 10 years. We used a filtering tool in Excel (Microsoft) to select the most accurate location per transmission period (i.e. one location/animal approximately every 4 or 5 days) and to identify suspicious locations generating travel rates > 50 km/day (see Austin *et al*. 2003 for a similar algorithm). Using this data set of migratory animals, we focused on two possible gene flow mechanisms: overlap of rutting range and calving site switch by females (see below).

Possibilities of gene flow during the rutting season

In migratory herds of eastern Canada, the rutting season lasts about 2 weeks and peaks around 23 October (S. Couturier, unpublished data). We selected the closest location to 23 October for every satellite-tracked caribou each year and obtained 444 locations between 1986 and 2003, which we transferred into a Geographic Information System (ARCVIEW 3.1, ESRI Inc.).

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). Using bootstrap simulations, we determined that a minimum of 12 animals/herd/year were necessary to generate a nonbiased MCP (data not shown). We excluded years 1993, 2002, and 2003 in the LEAF herd because this minimal criterion was not met. We then delimited a 50-km buffer around the MCPs (hereafter MCP_{+50}) of the LEAF and GEOR herds to account for movements of animals around the peak of the rut and extensive areas used by large

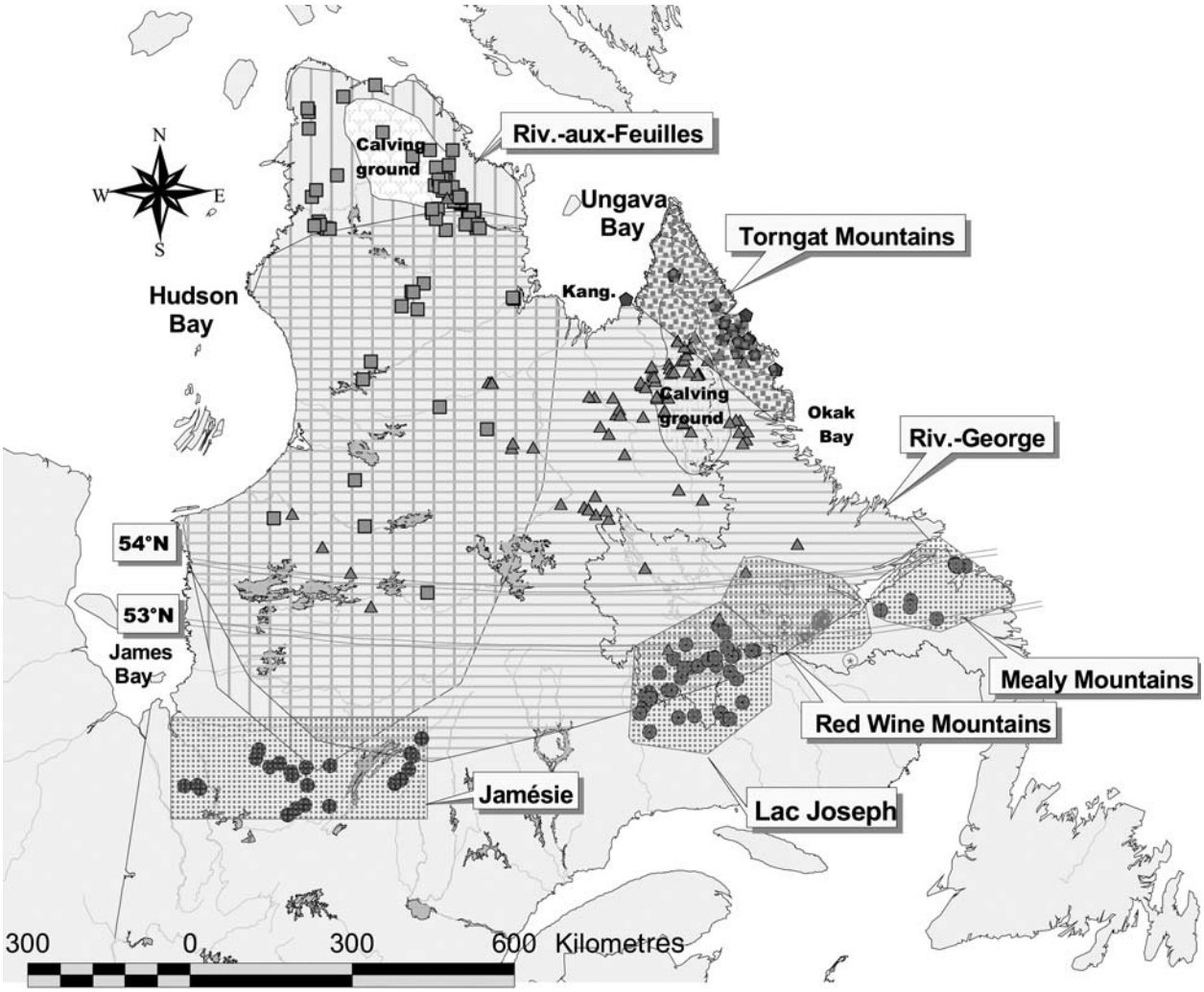

Fig. 1 Distribution of caribou in northern Québec and Labrador showing the annual ranges of the migratory Rivière-George herd (horizontal lines, MCP area for 1991–2003, from satellite locations), migratory Rivière-aux-Feuilles herd (vertical lines, MCP area for 1993–2003, from satellite locations), montane Torngat herd (dotted polygon, range following Schaefer & Luttich 1998; Kang., Kangiqsualujjuaq), and sedentary Lac Joseph, Mealy Mountains, Red Wine Mountains and Jamésie herds: (shaded polygons, range following Schmelzer *et al*. 2004 and references therein; Jamésie, approximate annual range). The calving grounds of migratory herds are delimited by ovals filled with pictograms. The sedentary range is located south of the 54°N (northern extreme limit) and 53°N (average northern limit). Sites where samples for DNA analyses were collected are shown.

groups. We calculated the size of the overlap zone MM (in square kilometres) between the LEAF MCP_{+50} and the GEOR MCP_{+50}. We also expressed the MM overlap zone in percentage = [MM/(MCP_{+50} GEOR + MCP_{+50} LEAF) – MM] × 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 ranges, respectively (Courtois *et al*. 2004; Fig. 1). Both limits are approximations taking into account contemporary variations in the latitudinal distribution of sedentary herds from east to west. Specifically, MS was calculated as the overlap zone in square kilometres 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 (abbreviated to Kang. on Fig. 1) to Okak Bay on the Labrador Coast (57.38°N, 61.86°W).

Opportunities for gene flow during the calving season

We analysed the locations of 149 satellite-tracked females during June (1986–2003) to verify whether GEOR and LEAF females could switch calving grounds from one year to another. We scored herd switching when females were present on or near the calving ground of the neighbouring migratory herd (Fig. 1).

Sampling and DNA analyses

We collected 333 caribou samples, including 37 LACJ, 12 MEAL, 20 REDW, 27 JAME, 24 TORN, 115 LEAF, and 98 GEOR. Migratory herds were more intensively sampled because they are at least 100 times larger than sedentary herds (see section about *Characteristics of caribou herds*). 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 postcalving 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); for dead animals, we used an ear piece or jaw muscle. All samples were stored at –20 °C before laboratory analyses. DNA was extracted using QIAamp DNA Blood mini kit (blood), QIAamp DNA micro kit (blood cards), or DNeasy Tissue kit (muscles) (QIAGEN). Ear samples were extracted following a modification of the BAC DNA purification protocol using BAC Miniprep kit (Millipore). The incubation lysis buffer was composed of Tris-HCL 50 mM, EDTA 100 mM, SDS 1%, proteinase K (0.1 mg/mL), and water.

We genotyped the 333 individuals at seven microsatellite loci: RT1, RT5, RT6, RT7, RT9, RT24, and RT27 (Wilson *et al*. 1997) using polymerase chain reactions (PCR) described in Courtois *et al*. (2003). DNA fragments were resolved on an ABI PRISM 3100 genetic analyser (Applied Biosystems Inc.) using GeneScan-500 ROX as a size standard and scored using GENESCAN 3.7 and GENOTYPER 3.7 software (Applied Biosystems Inc.).

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 (Belkhir *et al*. 2000). Individuals with incomplete genotypes were not discarded. We standardized herd allelic richness for a sample size of 11 (the smallest complete sample in our data set, MEAL herd) using the program FSTAT 2.9.3 (Goudet 1995). 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).

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 (Guo & Thompson 1992). In addition, we calculated the index of differentiation F_{ST} using the program FSTAT 2.9.3 (Goudet 1995). 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 reduce the probability of type I error (Rice 1989). To avoid sample size biases, we did these analyses twice: with all data (n = 333 individuals) and then by reducing the number of migratory individuals by half (individuals with even ID number, GEOR: n = 47; LEAF: n = 61). Because results were the same in all genetic analyses including SAMOVA (see below), we only present data for the complete data set.

Barriers to gene flow

We examined two mechanisms that can reduce or prevent gene flow in caribou. First, we computed a spatial analysis of molecular variance or SAMOVA (Dupanloup *et al*. 2002). This method defines groups of populations that are geographically homogeneous and maximally differentiated from each other. Specifically, it incorporates the geographical coordinates of populations in an annealing procedure to maximize the proportion of total genetic variance due to differences between groups of populations. By doing so, it identifies the location of geographical barriers (e.g. rivers, tree line) reducing gene flow between groups. Contrary to the program STRUCTURE (Pritchard *et al*. 2000), SAMOVA does not classify individuals into distinct groups. We selected the SAMOVA method over the *a-posteriori* method implemented in STRUCTURE, because STRUCTURE did not perform well with our data, which were characterized by low but significant differentiation between herds. Specifically, under different parameters and models, STRUCTURE could not recover the groupings identified by SAMOVA (M. Boulet, unpublished data). At low levels of population structure, tests based on predefined groups may be more powerful than Bayesian analyses implemented in STRUCTURE (Pritchard *et al*. 2007). In addition, STRUCTURE does not perform well in presence of significant isolation-by-distance patterns, a situation we observed between resident herds (see Results).

In the first SAMOVA analysis, we chose the location of the traditional calving sites of migratory caribou herds as a proxy for herd location because (i) females migrate to these sites in spring to give birth and tend to be philopatric to them (Miller 2003); (ii) it is the place of birth more than the

site of breeding that determines herd identity in young caribou; and (iii) the locations of calving sites are more stable through years than the rutting areas (S. Couturier, unpublished data). Since reproduction takes place on the rutting range, we replaced the geographical coordinates of the migratory herd calving grounds by the coordinates of the rutting range in a second series of analyses. For the sedentary and montane herds, we used the centroid of the annual ranges shown on Fig. 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 between calving grounds or rutting range in kilometres) to determine whether large geographical distances impede gene flow between herds.

Historical levels of realized gene flow

We used a coalescent-based model to obtain historical estimates of asymmetric gene flow ($4Nm$) between herds (MIGRATE 2.0.3, Beerli & Felsenstein 2001). The low differentiation observed between herds prevented us from using models of contemporary gene flow based on assignment tests (Piry *et al*. 2004). Because the migratory herds (GEOR and LEAF) were not significantly different, we did the analyses for both herds separately: (i) GEOR and all sedentary herds; (ii) LEAF and all sedentary herds. We used half of the individuals for the GEOR ($n = 47$) and the LEAF ($n = 61$) herds to avoid inflating gene flow estimates because of unequal sample sizes (Austin *et al*. 2004). We applied the following settings: 10 short chains with 50 000 trees sampled, 500 trees recorded, three long chains with 500 000 trees sampled, and 5000 trees recorded. Burn-in was set at 10 000 trees for each chain type. We selected the Brownian motion approximation and assumed equal mutation rates between microsatellite loci. Analyses included nine runs that were replicated four times within a single run. A different random number seed was used each time. For the first run, we estimated θ and $4Nm$ from F_{ST} estimates calculated by MIGRATE 2.0.3. For the subsequent eight runs, we used θ and $4Nm$ values obtained from previous runs. Estimates, which were averaged across the four replicates, were slightly variable after nine runs but showed consistent patterns. We present results from the last (ninth) run only. We compared gene flow asymmetries using the 95% confidence intervals around $4Nm$ estimates. In this study, $4Nm$ values are interpreted as representing historical means of gene flow.

Sex-biased gene flow

We assumed the most dispersing sex would be males, because female caribou are philopatric to calving grounds (Miller 2003). For satellite-tracking data, we tested whether rutting range overlap between migratory herds was mostly driven by the presence of males, as opposed to females, at the limits of the GEOR and LEAF $MCPs_{+50}$. We also tested whether excursions into the domain of sedentary or montane caribou herds were more frequent in males than in females. We scored excursions when migratory males or females were present on the range of other herds, based on their locations obtained from satellite-tracking data. We used one-tailed Fisher's exact tests for both analyses. For microsatellite data, we tested for sex-biased gene flow between the two migratory herds and between all herds. We excluded JAME, REDW, and MEAL herds because no male had been sampled in those herds. We used the F_{ST} test which performs well for species with high dispersal rates (Goudet *et al*. 2002). This test assumes that allele frequencies of individuals of the dispersing sex (here, males) should be more similar than those for individuals of the philopatric sex (here, females). Hence, we expect a lower F_{ST} value for males when compared to females. This test was computed in FSTAT 2.9.3 using 1000 simulations (Goudet 1995).

Simulations of levels of gene flow between herds

We simulated different scenarios of population structure between fictive caribou herds of different effective population sizes. Our objective was to determine whether the observed level of structure, a reference F_{ST} value of 0.015 based on empirical data, could be explained by high levels of gene flow that would counter the effects of genetic drift in small sedentary herds. Simulations were carried out in the program EASYPOP 1.8 (Balloux 2001). The demographic parameters required by the program 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*. 2004). We assumed random mating because (i) in large migratory herds males cannot secure a group of females (Bergerud 2000; Miller 2003); (ii) male-mating effort is high, so that high-ranking males become exhausted before the end of the rutting season (Hirotani 1994); and (iii) paternity analyses showed that a large proportion of males including yearling males can father at least one young (Røed *et al*. 2005).

We simulated a historical scenario covering 2000 generations or about 8000 years if assuming an average generation time of 4 years (Couturier *et al*. 1990; Adams & Dale 1998). This 8000-year period broadly represents the phase when central lands of Québec and Labrador became available to caribou herds after the last glaciation (Dyke & Prest 1987). We postulated that there was a large panmictic herd from which the actual herds of Québec and Labrador could have burgeoned, and we separated our scenarios into two phases. The panmictic phase was characterized by a complete mixing of herds. In EASYPOP, panmixia was simulated with an effective immigration rate m of 0.99 between the

herds that burgeon from the panmictic herd. The fragmentation phase was characterized by the division of the panmictic herd into smaller herds. We used seven microsatellite loci, each with 10 possible states based on the average number of alleles across loci observed in this study. The mutation rate of loci was set to 0.0001 (Ellegren 2000). We used a mutation model that included 80% single-step mutations and 20% random mutations based on mutation types observed in our data.

We tested four types of scenarios. Scenario A started with a panmictic phase of 1000 generations and an immigration rate of 0.99, then continued with a fragmentation phase of 1000 generations and immigration rates between 0 and 0.001 that were not sex-biased. It included five herds of varying sizes to mimic relationships between existing herds: Herd 1 represented a large migratory herd with 100 000 reproducing females (N_{ef}) and 40 000 reproducing males (N_{em}) broadly equivalent to the GEOR and LEAF herds at intermediate sizes; Herd 2 was a large sedentary herd of 500 females and 200 males equivalent to the MEAL herd; Herd 3 was a sedentary herd of intermediate size with 200 females and 80 males equivalent to the LACJ herd; Herd 4 and 5 were two small sedentary herds with 100 females and 40 males each, equivalent to the JAME and REDW herds. The TORN herd was not included because it was not distinct from migratory herds (see results). Scenario B also had 1000 generations of panmixia and 1000 generations of fragmentation, but included five herds of equal size (20 180 females and 8072 males in each herd). In Scenario C, we reduced the size of the migratory herd present in Scenario A down to the size of a sedentary herd, that is 500 females and 200 males. In Scenario D, we included only the four sedentary herds. Scenarios C and D were simulated to determine whether significant genetic population structure could emerge from small herds in absence of a large migratory herd. If so, this would suggest that large migratory herds have an effect on the gene pool of sedentary herds. Results were not modified by a higher mutation rate (0.001), sex-biased dispersal, or variation in the duration of the fragmentation phase (data not shown).

For each scenario, we used a spatial model that took into account the geographical distance between populations. Immigration rate from population i to population j was computed as $\exp^{-r*(di.j)}$ where $di.j$ is the distance between populations and $r = 1/\text{mean dispersal}$ (Balloux 2001). For the large Herd 1, we averaged the geographical coordinates of the GEOR and LEAF calving grounds and we used the geographical coordinates of the MEAL, LACJ, JAME, and REDW for Herds 2–5, respectively. We used the distance between the LEAF and GEOR calving grounds as an estimate of the mean dispersal distance for males and females (659 km). We also repeated these simulations using the geographical coordinates of the rutting ranges because fertilization occurs during rut.

Results

Opportunities for gene flow during the rut

The spatial overlap between the migratory GEOR and LEAF herds during the rut averaged 10%, but varied from year to year. In 1994, overlap was absent, whereas in 1996 overlap was maximal (89 000 km^2, 34.8% overlap; Table 1, Appendix). Between 1991 and 2003, we counted eight instances of migratory caribou moving south of the 54° parallel and one instance of a GEOR male moving south of the 53°N during the rutting period. These movements into the sedentary range tended to be more common and more extended for the GEOR caribou ($n = 6$ excursions over 13 years, average overlap = 7186 km^2) than for the LEAF caribou ($n = 2$ excursions over 11 years, average overlap = 152 km^2). In 1991 and 1998, two GEOR females moved into the TORN range (Table 1, Appendix).

Opportunities for gene flow during the calving seasons

Our extensive satellite-tracking data revealed 14 cases of females switching from one calving site to another at least once in their lifetime. This represents 9.4% of 149 collared females. All switches but one occurred from the GEOR herd to the LEAF herd and this asymmetry in the frequency of calving site switches was highly significant (McNemar's test, $P = 0.002$). In any given year, 6.6% of the GEOR females and 0.9% of the LEAF females changed herd to give birth. Calving site switches were not always permanent, since five females changed calving sites back and forth, but most females that changed calving site remained with their new herd.

Polymorphism and Hardy–Weinberg equilibrium

The number of alleles and the standardized allelic richness per locus tended to be highest in the largest herds: LEAF, GEOR, and TORN (Fig. 2a–g, Table 2). 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 for sedentary, montane and migratory herds of south and central Québec (where A_{mean} across loci ranged from 4.4 to 13.0; Courtois *et al*. 2003). No deviation from the Hardy–Weinberg equilibrium was detected (global test across all herds and loci, $\chi^2 = 111.5$, d.f. = 96, $P = 0.13$).

Genetic differentiation between herds

Allele frequencies across loci differed among herds (χ^2 = infinity, d.f. = 14, $P < 0.001$) because of significant differentiation between most herd pairs (P's ≤ 0.005 after sequential Bonferroni adjustments). The following herd pairs were not distinct: GEOR and TORN ($P = 0.30$), GEOR and

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

	MIGR vs. MIGR				MIGR vs. SED			MIGR vs. MON
Year	GEOR (km²)	LEAF (km²)	Herd overlap range (km²)	Herd overlap range (percentage)	GEOR overlap south of 53° (km²)	GEOR overlap south of 54° (km²)	LEAF overlap south of 54° (km²)*	GEOR overlap (km²)
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

Abbreviations: GEOR, Rivière-George; LEAF, Rivière-aux-Feuilles; MIGR, migratory herd; SED, sedentary herd; and MON, montane herd.
*No LEAF caribou were observed south of latitude 53°N.

MEAL ($P = 0.05$), and LEAF and TORN ($P = 0.02$). The 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 (Fig. 2a–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 RT27.

Heterogeneity in allele frequency distribution among herds translated into a low, albeit highly significant genetic differentiation (AMOVA, $\theta = 0.015$, 95% confidence interval = 0.008–0.021, $P < 0.001$). Pairwise F_{ST} estimates between migratory and sedentary herds varied from 0.015 (GEOR 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 (LEAF and GEOR) and montane (TORN) herds showed no significant patterns of differentiation (pairwise F_{ST} values ≤ 0.005, P's ≥ 0.05, Table 3). In summary, the strongest levels of differentiation occurred between sedentary herds separated by large distances (> 1000 km) and between sedentary and migratory herds.

Barriers to gene flow

In the SAMOVA analysis, differentiation was maximal when the number of groups was set to $k = 2$ groups. The analysis separated the MEAL herd from all other herds no matter whether the geographical coordinates of calving grounds or rutting range were used in the analysis ($F_{ST} = 0.051$, $P < 0.001$ for both analyses, Fig. 3). The F_{ST} dropped to 0.037 ($P < 0.001$) when $k = 3$ and the following groups were formed: MEAL, JAME, and all other herds together. These groupings suggest that a barrier partly isolated the MEAL herd.

Genetic differentiation between sedentary herds was influenced by the geographical distance between them (log $F_{ST} = 0.50$ log geographical distance –2.88, $R^2 = 0.59$, $P = 0.04$). This pattern was not significant when calving grounds of the two migratory herds, which were located further away (GEOR: 57.371 lat, –64.552 long; LEAF: 61.053 lat, –73.624 long), were added to the analysis (log $F_{ST} = 1.38$ log geographical distance –5.56, $R^2 = 0.04$, $P = 0.25$). In contrast, the pattern was significant when rutting ranges of the migratory herds (GEOR: 56.199 lat, –69.614 long; LEAF: 57.752 lat, –72.915 long) were added to the analysis (log $F_{ST} = 1.44$ log geographical distance –5.66, $R^2 = 0.33$, $P = 0.03$).

Historical estimates of gene flow

The GEOR had a major demographic impact on three sedentary herds, gene flow estimates from the GEOR into most herds were ≥ 16.8 (Fig. 4a). The demographic impact of the GEOR on the MEAL herd was not as high ($4Nm = 9.3$). In contrast, gene flow estimates from sedentary herds into the GEOR were much lower (all ≤ 2.0). The LEAF also had an important demographic effect on the

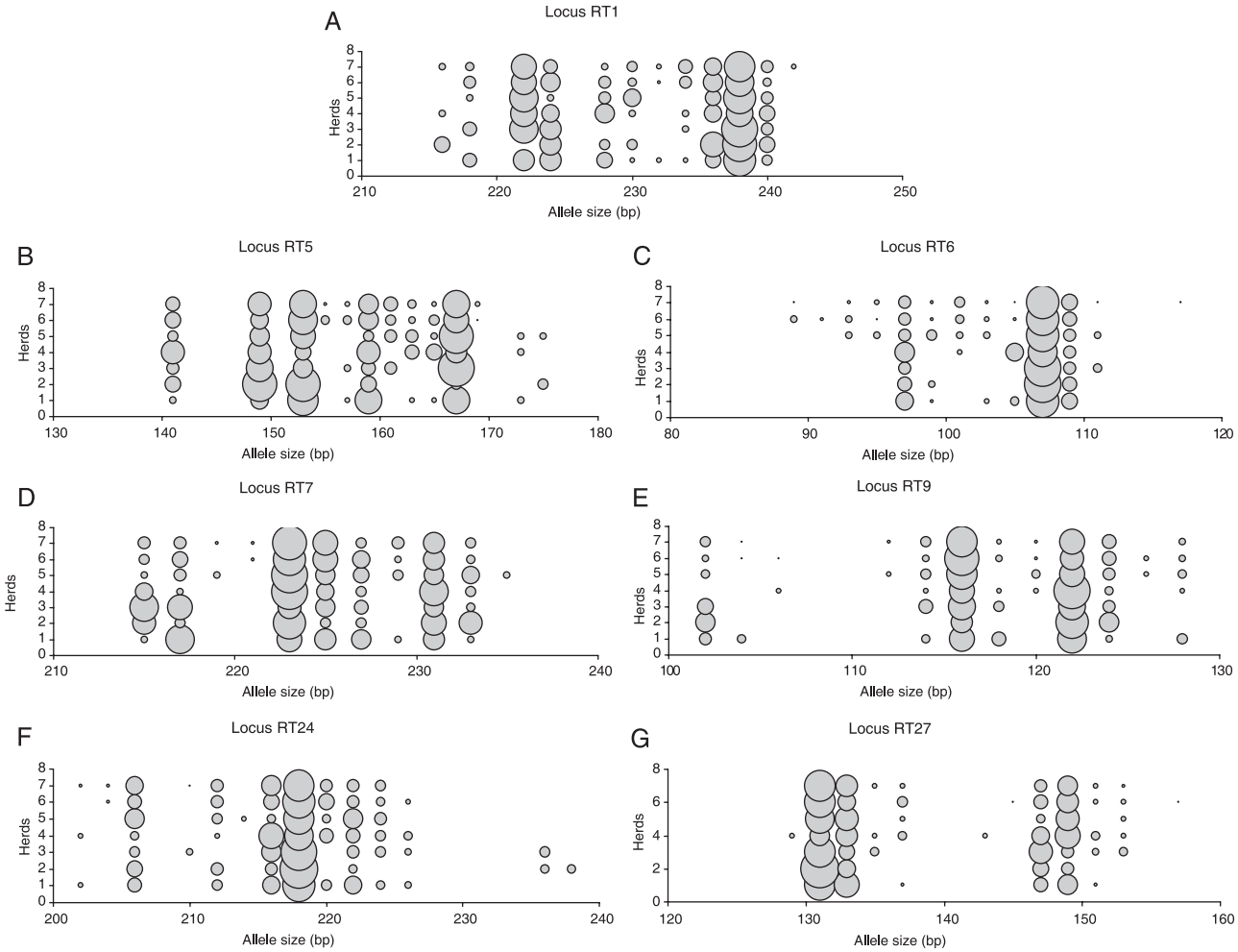

Fig. 2 (A)–(G) Frequency distribution of alleles present among the seven microsatellite loci: (a) RT1 (b) RT5 (c) RT6 (d) RT7 (e) RT9 (f) RT24, and (g) RT27 analysed for caribou herds of northern Québec and Labrador. Herds are labelled as follow: #1, Lac Joseph (LACJ); #2, Mealy Mountains (MEAL); #3, Red Wine Mountains (REDW); #4, Jamésie (JAME); #5, Torngat (TORN); #6, Rivière-aux-Feuilles (LEAF); and #7, Rivière-George (GEOR). Each allele found in a particular herd is represented by a circle proportional to the frequency of this allele within the herd.

sedentary herds, since all gene flow estimates from the LEAF into the sedentary herds were ≥ 17.5 and gene flow estimates from the sedentary herds into the LEAF were ≤ 4.4 (Fig. 4b). Among sedentary herds, gene flow values were generally ≤ 4.0 (Fig. 4). Two exceptions were noticed, gene flow estimates from the LACJ into the JAME (in both GEOR and LEAF analyses) and from the LACJ into REDW (GEOR analyses) were ≥ 10.7. This suggests the LACJ tended to be a source of individuals for other sedentary herds.

Sex-biased gene flow

Males were not more common than females in the overlap zone of the rutting range of migratory herds: 15.6% (5/32) of collared males were observed in that area vs. 17.1% (31/181) of collared females (one-tailed Fisher's exact test, $P = 0.54$). There was no evidence that the frequency of excursions into the domain of the sedentary or montane herds was more common in males than in females: 15.6% of satellite-tracked males undertook such excursions vs. 6.6% of satellite-tracked females (one-tailed Fisher's exact test, $P = 0.15$). In addition, comparing the extent of genetic differentiation (F_{ST} estimate) between males and females, we found no evidence that gene flow was male-biased in migratory LEAF and GEOR herds (male $F_{ST} = 0.0048$, female $F_{ST} = 0.0029$, simulation test: $P = 0.79$) or in LEAF, GEOR, TORN and LACJ herds pooled together (male $F_{ST} = 0.0081$, female $F_{ST} = 0.0078$, simulation test: $P = 0.53$).

Simulations of historical scenarios

In scenario A (panmixia = 1000 generations or 4000 years, fragmentation = 1000 generations, 1 large migratory herd, 4 small sedentary herds), effective immigration rates of

Table 2 Number of alleles observed at each locus (A), allelic richness standardized for the smallest sample size with complete scoring (n = 11, AR11), 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 (LACJ, Lac Joseph; MEAL, Mealy Mountains; REDW, Red Wine Mountains; JAME, Jamésie; TORN, Torngat; LEAF, Rivière-aux-Feuilles; and GEOR, Rivière-George). n refers to sample sizes

	LACJ (n = 36)	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
H_O	0.861	0.667	0.650	0.852	0.833	0.798	0.724
H_E	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
H_O	0.806	0.667	0.850	0.885	0.833	0.814	0.732
H_E	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
H_O	0.784	0.500	0.400	0.632	0.625	0.637	0.577
H_E	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
H_O	0.838	0.833	0.850	0.593	0.833	0.748	0.804
H_E	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
H_O	0.784	0.833	1.000	0.519	0.708	0.583	0.745
H_E	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
H_O	0.730	0.546	0.684	0.654	0.667	0.763	0.776
H_E	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
H_O	0.784	0.583	0.800	0.778	0.625	0.748	0.592
H_E	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
H_O	0.798	0.661	0.748	0.702	0.732	0.727	0.707
H_E	0.755	0.675	0.701	0.768	0.752	0.745	0.753

0.001 were sufficient to prevent significant genetic differentiation between herds (Table 4). In contrast, in absence of gene flow (m = 0) between all herds, the simulated F_{ST} value reached the reference F_{ST} (0.015) within seven generations and culminated around 0.67 after 1000 generations of fragmentation. An immigration rate of 0.0005 led to simulated F_{ST} values that oscillated around reference F_{ST} (0.015) during at least 750 generations of fragmentation. This suggests that caribou herds in northern Québec and Labrador may behave as a metapopulation within a specific range of immigration rates. Finally, the spatial location of the migratory herd (calving or rutting ranges) did not modify the patterns of herd structure.

In scenario B, we set the immigration rate at 0.0005 between five equally large herds. Under these parameters, simulated F_{ST} values never reached the reference F_{ST} value of 0.015 (Table 4). In contrast, scenarios C and D allowed simulated F_{ST} values to reach the reference F_{ST} (0.015) within only six or seven generations of fragmentation. High simulated F_{ST} values (F_{ST} = 0.272) were observed after 250 generations of structure. These results suggest that the effects of genetic drift obtained in small herds

Table 3 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	MEAL	REDW	JAME	TORN	LEAF	GEOR
LACJ	—	0.028	0.018	0.029	0.017	0.017	0.015
MEAL	0.002*	—	0.037	0.048	0.040	0.038	0.025
REDW	0.002*	0.002*	—	0.042	0.022	0.029	0.021
JAME	< 0.001*	< 0.001*	< 0.001*	—	0.027	0.032	0.026
TORN	< 0.001*	< 0.001*	< 0.001*	< 0.001*	—	0.005	–0.001
LEAF	< 0.001*	< 0.001*	< 0.001*	< 0.001*	0.121	—	0.002
GEOR	< 0.001*	< 0.001*	0.002*	< 0.001*	0.681	0.089	—

Abbreviations: LACJ, Lac Joseph; MEAL, Mealy Mountains; REDW, Red Wine Mountains; JAME, Jamésie; TORN, Torngat; GEOR, Rivière-George; LEAF, Rivière-aux-Feuilles.
**P* values significant after sequential Bonferroni adjustments of significance threshold.

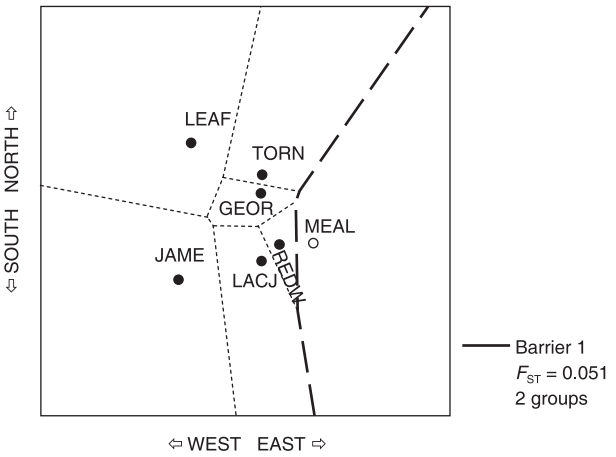

Fig. 3 Barrier to gene flow identified by the SAMOVA analysis when $k = 2$ for caribou herds of northern Québec and Labrador. Abbreviations are: LACJ, Lac Joseph; MEAL, Mealy Mountains; REDW, Red Wine Mountains; JAME, Jamésie; TORN, Torngat; GEOR, Rivière-George; LEAF, Rivière-aux-Feuilles.

(scenarios C and D) could be counteracted by immigration of individuals from larger herds (scenarios A and B).

Discussion

Our primary goals were to identify possible gene flow mechanisms and examine genetic connectivity between caribou herds using complementary approaches. Spatial data revealed evidence for three mechanisms of gene exchanges: (i) range overlap during the rut in migratory herds; (ii) switching of calving sites by migratory females that remained in their new herd; (iii) and excursions by migratory individuals into the ranges of sedentary and montane caribou during the rut. The weak genetic structure (F_{ST} = 0.015) observed between herds was concordant with caribou movements. In addition, this empirical level of structure could be simulated through a metapopulation scenario with an immigration rate of 0.0005 between herds. Below, we discuss the possible factors contributing to genetic connectivity and structure among caribou herds and other highly mobile species; we address the limitations in quantifying gene flow; and we propose a metapopulation model that may apply to species where sedentary and migratory groups co-occur during periods of their annual cycle.

Factors contributing to genetic connectivity and structure

Global genetic differentiation was weak (empirical F_{ST} = 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 to central Québec (one montane and five sedentary herds, F_{ST} = 0.016–0.167, Courtois *et al*. 2003) and from Alberta and British Columbia (six sedentary herds, pairwise F_{ST} = 0–0.082, McLoughin *et al*. 2004). However, they were higher than values recorded between eight migratory herds of northwest Canada (all pairwise $F_{ST} < 0.02$, Zittlau 2004).

Our satellite-telemetry data showed that rutting range overlap is spatially extensive and that frequent opportunities for genetic exchanges exist. First, range overlap was detected in 7 out of 8 years with only 12–26 satellite-tracked animals surveyed per year and herd. Second, the herds were large 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. This phenomenon was unexpected because most studies of *Rangifer* have assumed or shown that females are philopatric to calving sites (Rettie & Messier 2001; Côté *et al*. 2002). We suggest that rutting range overlap and

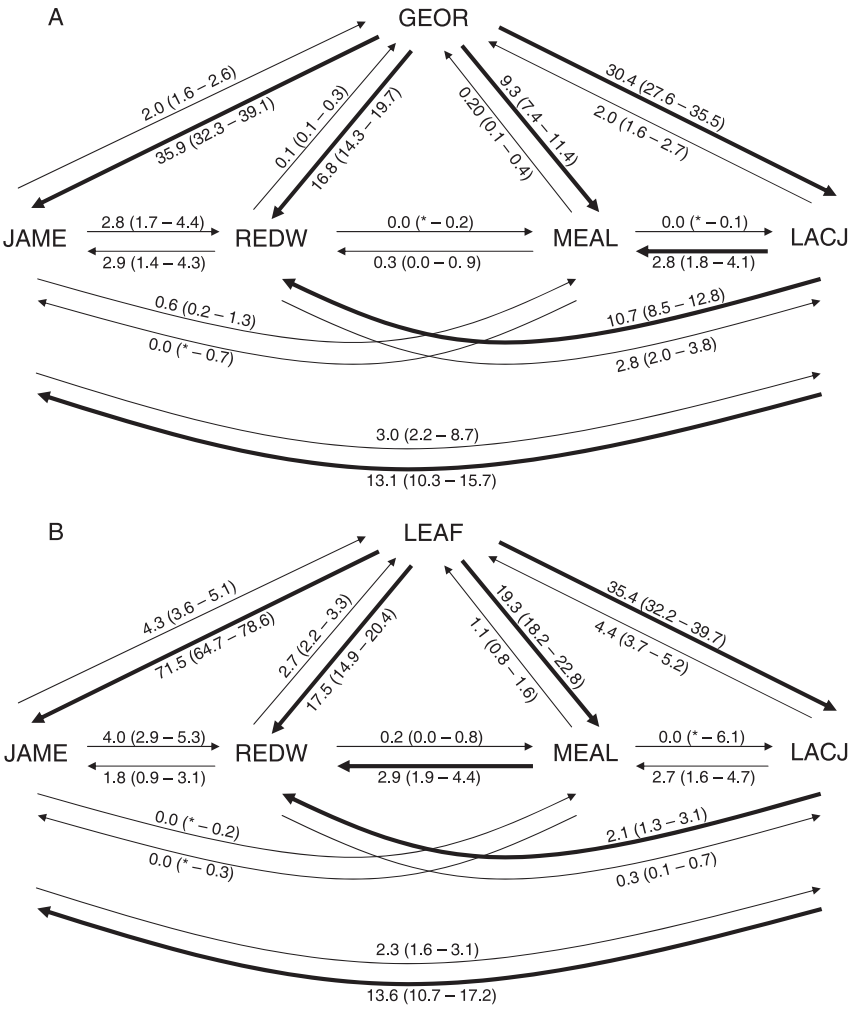

Fig. 4 (a)–(b) Historical gene flow estimates ($4Nm$) between (a) migratory GEOR herd and four sedentary caribou herds of northern Québec and Labrador, and (b) migratory LEAF herd and the same four sedentary herds. Numbers refer to gene flow estimates ($4Nm$) and their respective 95% confidence intervals. The symbol * refers to cases where convergence to percentile value of confidence intervals failed. Bold arrows indicate gene flow estimates that were significantly higher from herd x to herd y than from herd y to herd x. Abbreviations are: LACJ, Lac Joseph; MEAL, Mealy Mountains; REDW, Red Wine Mountains; JAME, Jamésie; TORN, Torngat; GEOR, Rivière-George; LEAF, Rivière-aux-Feuilles.

calving site switching are important mechanisms of genetic connectivity between the GEOR and LEAF herds. The same mechanisms may explain the weak genetic differentiation observed in other continental migratory herds of caribou in northwest Canada (Zittlau 2004). There, the opportunities for gene flow might be even more important, because annual ranges of herds overlap extensively (Zittlau 2004). Both calving site switching and overlap of ranges during the fall have been observed in two caribou herds of Alaska (Hinkes *et al*. 2005). Similar gene flow mechanisms have been observed in other highly mobile species. For example, calving ground switching possibly play a role in genetic exchanges of two chiru (*Pantholops hodgsonii*) herds in Tibet (Ruan *et al*. 2005), range overlap may explain the lack of differentiation between two Alaskan polar bear (*Ursus maritimus*) populations (Cronin *et al*. 2006), and mixing of Natterer's bats (*Myotis nattereri*) at swarming sites during mating period may explain the low genetic differentiation (F_{ST} = 0.017) between isolated summer colonies (Rivers *et al*. 2005).

Alternatively, recent herd split may explain the lack of differentiation between the GEOR and 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 herd may have originated from the GEOR herd. There are, however, some indications that the LEAF herd could 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. These herds could correspond to the present-day LEAF, GEOR and TORN herds, respectively. If we simulate the fragmentation of a large herd (100 000 females and 40 000 males) into two main herds (Herd 1: 20 000 females and 8000 males; Herd 2: 80 000 females and 32 000 males), genetic differentiation is extremely low (simulated F_{ST} = 0.0001) after 10 generations, or about 40 years, and remains low (simulated F_{ST} = 0.0007) after 100 generations. In summary, three non-exclusive factors may contribute to the genetic similarity between the GEOR and LEAF herds: a possible recent split

Table 4 Overall simulated F_{ST} values between caribou herds obtained from simulating different demographic scenarios. Number of generations required to reach the empirical reference F_{ST} value of 0.015

Immigration	Location of gene exchange	Simulated $F_{ST\ G1000}$	Simulated $F_{ST\ G1250}$	Simulated $F_{ST\ G1500}$	Simulated $F_{ST\ G1750}$	Simulated $F_{ST\ G2000}$	$G_{F_{ST0.015}}$
Scenario A*							
$m_f = m_m = 0.001$	Calving¶	0.0001	0.0078	0.0062	0.0092	0.0079	DNR
$m_f = m_m = 0.001$	Rut	0.0003	0.0097	0.0066	0.0060	0.0077	DNR
$m_f = m_m = 0.00075$	Calving	0.0003	0.0108	0.0086	0.0116	0.0081	DNR
$m_f = m_m = 0.00075$	Rut	0.0007	0.0090	0.0081	0.0131	0.0126	1995
$m_f = m_m = 0.0005$	Calving	–0.0003	0.0123	0.0171	0.0121	0.0151	31
$m_f = m_m = 0.0005$	Rut	0.0001	0.0151	0.0137	0.0093	0.0129	37
$m_f = m_m = 0.00025$	Calving	0.0001	0.0354	0.0270	0.0280	0.0291	17
$m_f = m_m = 0.00025$	Rut	0.0005	0.0238	0.0234	0.0257	0.0260	15
$m_f = m_m = 0.0001$	Calving	0.0001	0.0721	0.0715	0.0584	0.0624	12
$m_f = m_m = 0.0001$	Rut	–0.0002	0.0744	0.0581	0.0570	0.0734	8
$m_f = m_m = 0.0000$	Calving	–0.0003	0.3598	0.5583	0.5971	0.6779	7
$m_f = m_m = 0.0000$	Rut	0.0011	0.4616	0.5421	0.6130	0.6724	7
Scenario B†							
$m_f = m_m = 0.0005$	Calving	0.0000	0.0041	0.0064	0.0088	0.0103	DNR
$m_f = m_m = 0.0005$	Rut	–0.0000	0.0041	0.0066	0.0084	0.0093	DNR
Scenario C‡							
$m_f = m_m = 0.0005$	Calving	–0.0009	0.3216	0.3359	0.3493	0.4406	7
$m_f = m_m = 0.0005$	Rut	–0.0008	0.3500	0.4516	0.4321	0.5462	6
Scenario D§							
$m_f = m_m = 0.0005$	Calving = rut	0.0050	0.2725	0.3505	0.2662	0.3390	7

*Scenario A: 1000 generations of panmixia ($m_f = m_m = 0.99$) +1000 generations of fragmentation ($m_f = m_m = 0.0000$–0.001), one large migratory herd and four small sedentary herds. Effective population sizes: herd 1, 100 000 females and 40 000 males; herd 2, 500 females and 200 males; herd 3, 200 females and 80 males; herd 4, 100 females and 40 males; herd 5, 100 females and 40 males. Total of 100 900 females and 40 360 males across all herds.

†Scenario B: 1000 generations of panmixia ($m_f = m_m = 0.99$) +1000 generations of fragmentation ($m_f = m_m = 0.0005$), five herds of equal sizes. Effective population sizes: 20 180 females and 8072 males in each herd (same total number of individuals as in scenario A).

‡Scenario C: 1000 generations of panmixia ($m_f = m_m = 0.99$) +1000 generations of fragmentation ($m_f = m_m = 0.0005$), one small migratory herd and four small sedentary herds. Effective population sizes: herd 1, 500 females and 200 females; herds 2–5, as in scenario A.

§Scenario D: 1000 generations of panmixia ($m_f = m_m = 0.99$) +1000 generations of fragmentation ($m_f = m_m = 0.0005$), no migratory herd, four small sedentary herds. Effective population sizes: herds 2–5, as in scenario A.

¶For the migratory herd, calving refers to simulation models where the geographical coordinates of calving grounds were used, whereas rut refers to simulation models where the geographical coordinates of rutting ranges of the herd were used. Geographical coordinates of calving and rutting range were the same for sedentary herds.

Acronyms: $F_{ST\ G1000}$, simulated F_{ST} value after 1000 generations of structure; $F_{ST\ G1250}$, simulated F_{ST} value after 1250 generations of structure; $F_{ST\ G1750}$, simulated F_{ST} value after 1750 generations of structure; $F_{ST\ G2000}$, simulated F_{ST} value after 2000 generations of structure; $G_{F_{ST0.015}}$, number of generations required to reach the empirical reference F_{ST} value of 0.015; DNR (did not reach) refers to runs where the reference F_{ST} value (0.015) was not reached.

of the LEAF herd from the GEOR herd, on-going gene flow between the herds via rutting range overlap, and on-going gene flow via calving site switching.

Another unique observation revealed by satellite-tracking data was the occurrence of excursions undertaken by migratory individuals into the sedentary range. Densities in sedentary herds are usually very low (0.008–0.029 caribou/km^2, Schmelzer *et al*. 2004 and references therein). Hence, the chance that a migratory individual would encounter a sedentary individual of the opposite sex in October may be very low. On the other hand, if migratory individuals are successful in mating with those of sedentary herds, these excursions may translate into an input of new or uncommon genes into the small herds. Two types of genetic analyses suggested a demographic effect of the migratory herds on sedentary herds. First, isolation-by-distance pattern was no longer significant when calving grounds of migratory herds were included in the analysis. This result suggests that the migratory herds had a demographic effect on sedentary herds, because calving grounds of migratory herds were located the furthest and their inclusion in the analysis did not improve the strength of the relationship between geographical distance and genetic distance. Second, estimates of gene flow showed that

migratory herds had a major demographic impact on sedentary ones (Fig. 4). Another mechanism that could explain the highly asymmetric gene flow patterns between migratory and sedentary herds is permanent immigration of migratory individuals into sedentary herds. In Alaska, the sedentary Kilbuck herd suddenly increased from about 4220–10 416 caribou because of a massive immigration event of caribou from the migratory Mulchatna herd (Hinkes *et al*. 2005). Most of the radio-tracked Kilbuck females adopted the migratory behaviour of the Mulchatna females and migrated to the Mutchatna calving ground in spring. In addition, Schaefer *et al*. (1999) reported that emigration to the GEOR herd may have been 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.

Our data indicated that gene flow was limited by the geographical distance separating sedentary herds (see also Courtois *et al*. 2003), as observed also in other north temperate ungulates, such as moose (*Alces alces,* Broders *et al*. 1999), roe deer (*Capreolus capreolus,* Zannèse *et al*. 2006), red deer (*Cervus elaphus,* Hmwe *et al*. 2006), and white-tailed deer (*Odocoileus virginianus,* Comer *et al*. 2005). This significant isolation-by-distance pattern could be partly driven by the more pronounced differentiation of the easterly MEAL herd compared to others. We cannot exclude a bias related to the small sample size of this herd to explain its distinctiveness. However, similar results were obtained when we repeated the SAMOVA analysis with fewer migratory individuals (GEOR: $n = 47$; LEAF: $n = 61$; $F_{ST} = 0.054$ with $k = 2$). We suggest Lake Melville in eastern Labrador may act as a barrier partly isolating the MEAL herd from other herds. In western Canada, the Peace River appears to reduce gene flow between sedentary herds living across that river (McLoughin *et al*. 2004), whereas the Mackenzie River and Amundsen Gulf possibly diminish gene flow between grey wolf populations living across these barriers (Carmichael *et al*. 2001).

The genetic interaction of sedentary herds with the migratory herds may explain why our paiwise F_{ST} values were on average lower than those found by Courtois *et al*. (2003). The caribou described in Courtois *et al*. (2003) were from southern herds that have not been recently in contact with the migratory herds and that are more physically isolated from each other. In that study, natal dispersal was the mechanism suggested to explain gene flow between sedentary herds (Courtois *et al*. 2003). In addition, historical events may have played an important role in the differentiation of these herds. Some herds of Québec and Ontario are probably within a secondary contact zone between two mtDNA caribou lineages (Dueck 1998; Flagstad & Røed 2003; Cronin *et al*. 2005). Therefore, allele frequencies may change abruptly across the cline.

Limitations: the difficulty of assessing gene flow

Individual genotype information can be used for quantifying short-term dispersal using population assignment (Austin *et al*. 2004; Piry *et al*. 2004) or *a-posteriori* population delineation tests such as those implemented in STRUCTURE (Pritchard *et al*. 2000). Unfortunately, these approaches suffer from a lack of power when dealing with low population differentiation as it was the case here (Waples & Gaggiotti 2006). We therefore delimited caribou groups *a-priori* based on the current management definition of herds and decades of knowledge of herd space use. A herd is defined as a group of caribou using a distinct calving ground regularly over several years (Bergerud 2000). In practice, herd delineation is based on radio-telemetry and satellite-tracking data. While imperfect because of the possibility that some groups may not be demographically independent, the *a-priori* option directly assessed whether herds delineated by current management definitions were distinct or not. A recent study of the same caribou herds confirmed that individuals from all herds and the three ecotypes were different in terms of body size, confirming the population and ecotype definitions we used here (S. Couturier R. D. Otto, S. D. Côté, G. Luther, S. P. Mahoney, J. Huot, unpublished data). Additional microsatellite or amplified fragment length polymorphism (AFLP) markers could potentially help increasing power and allow the use of assignment-based methods in this specific system.

In mammals, field observations revealed that males usually disperse more than females (Greenwood 1980). Higher gene flow (or less genetic structure) is expected between populations if biparentally inherited markers are used as opposed to maternally inherited markers like mtDNA (Avise 2004). We used microsatellite markers, which are biparentally inherited and therefore blend male and female gene flow. Microsatellite and space use data did not demonstrate sex differences in gene flow, suggesting that female caribou are less philopatric and move more extensively than previously thought (see also Hinkes *et al*. 2005).

Cronin *et al*. (2005) examined genetic differentiation between 11 North American herds using mtDNA and microsatellite markers. Patterns of divergence were generally concordant, although differentiation was higher in mtDNA (range of F_{ST} values: 0–0.707) than in microsatellites (0–0.346). This was partly due to the different mode of inheritance of markers: in theory, F_{ST} values in mtDNA should be four times higher than F_{ST} values in biparentally inherited nuclear markers because of smaller effective population size of the uniparentally inherited marker. Comparisons of mtDNA and nuclear markers may be problematic because these markers have different mutation rates (Balloux *et al*. 2000). Differences in effective population sizes (e.g. higher number of mature females

than mature males) and breeding systems (random mating in large herds vs. polygyny in very small herds) can also bias the expected ratio between markers of different inheritance modes. In highly polygynous systems, the effective number of breeding males is reduced, thus the expected differences in population structure between mtDNA and microsatellite markers is diminished. A Y chromosome marker would be particularly useful for comparing population structure between polygynous vs. random mating systems and for clarifying the role of male gene flow in shaping genetic structure of populations. Additional studies are required to better understand sex-specific immigration and demographic processes in highly mobile species. It would be interesting to compare genetic structure of herds using additional markers such as mtDNA and Y chromosome sequence data, or even XY homologous markers (Prugnolle & de Meeus 2002; Balaresque *et al*. 2006). Few highly mobile terrestrial species other than humans have been surveyed at mtDNA and Y markers to estimate female and male gene flow between populations (but see Sundqvist *et al*. 2001 for a wolf example).

Gene flow dynamics between herds and metapopulation

Migratory caribou travel extensively and may interact with individuals of other herds during periods that are critical for genetic exchanges. Members of a herd experiencing harsh conditions (e.g. degraded environment or competition for forage) may also join another herd or split to form a new herd (Hinkes *et al*. 2005). Thus, a key element of exchanges between populations relates to the demographic and genetic effects of new individuals in the receiving herd. Frequent exchanges between populations at large spatial scales may also partly explain why *Rangifer* tend to be more genetically diversified than other ungulates (Røed & Midthjell 1998; Røed 1998; Wilson & Strobeck 1999; Polziehn *et al*. 2000), even when considering isolated island populations (Côté *et al*. 2002).

We propose that the GEOR and the LEAF herds interact as a metapopulation where genetic exchanges occur via overlap in rutting ranges and calving site switching. High gene flow possibly occurs during population peaks and range expansions and can also lead to herd split or mixing (Hinkes *et al*. 2005). In addition, the genetic similarity between the TORN herd and the migratory herds suggests that the TORN herd is a bud of the adjacent GEOR herd. Additional satellite-tracking data covering periods of herd fluctuations are necessary to determine whether the GEOR, LEAF, and TORN herd demographically behave as a metapopulation. However, spatial and genetic data clearly demonstrate that these herds are tightly linked. Demographic simulations, isolation-by-distance analyses, and long-term estimates of gene flow between the migratory and sedentary herds suggest that the migratory herds have been an important source of genes for sedentary herds (Fig. 4). Migratory herds may therefore mediate gene flow and their influence may vary through time depending on the demography and environmental conditions. The migratory Mulchatna caribou herd in Alaska seems to play a similar role: this large herd of more than 200 000 individuals expanded into the range of smaller sedentary herds and mixed with at least one sedentary herd (Hinkes *et al*. 2005). Finally, gene flow between sedentary herds appears to be limited by geographical distance and barriers. In summary, we suggest that there are three levels of demographic interactions in the northern Québec and Labrador migratory–sedentary caribou herd system: high exchanges between migratory herds, asymmetric exchanges between migratory and sedentary herds, and exchanges limited by distance and barriers between sedentary herds. The combined use of genetic markers, spatial data on marked animals, and population simulations allowed us to better understand the ecological mechanisms that links populations. The role of large migratory groups in generating genetic connectivity between populations should be examined in other systems of caribou herds and other mammal species.

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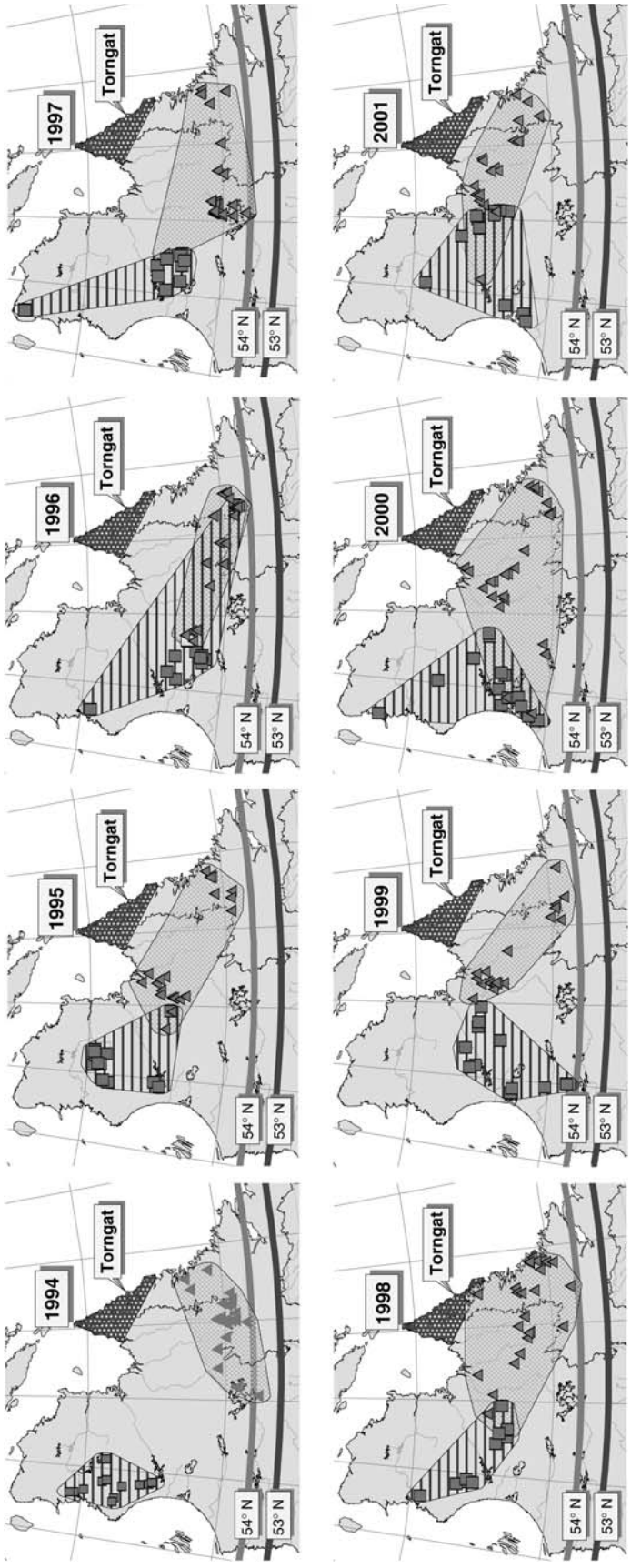

Appendix Rutting ranges of migratory caribou GEOR herd, migratory LEAF herd, montane TORN herd at the peak of the rut (*c.* 23 October) from 1994 to 2001. The sedentary ecotype range is located south of the 54°N