Journal of Mammalogy, 86(3):495–505, 2005

VARIATION IN MITOCHONDRIAL DNA AND MICROSATELLITE DNA IN CARIBOU (*RANGIFER TARANDUS*) IN NORTH AMERICA

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Genetic variation of caribou (*Rangifer tarandus*) at 18 microsatellite DNA loci and the cytochrome-*b* gene of mitochondrial DNA (mtDNA) was quantified in 11 herds of 3 North American subspecies: Alaskan barren ground caribou (*R. t. granti*), Canadian barren ground caribou (*R. t. groenlandicus*), and woodland caribou (*R. t. caribou*). Phylogenetic analysis of 1,194 nucleotides of cytochrome-*b* sequence resulted in a clade of 52 genotypes in *R. t. granti*, *R. t. groenlandicus*, and in 1 herd of *R. t. caribou*, and a clade of 7 genotypes in *R. t. caribou*. mtDNA sequence divergence is approximately 1% between these clades and 0.3–0.6% within these clades. The subspecies do not have monophyletic mtDNA, but do have different frequencies of mtDNA genotypes. Microsatellite allele frequencies also are differentiated between the woodland (*R. t. caribou*) and barren ground (*R. t. granti* and *R. t. groenlandicus*) subspecies. An exception is the George River herd in Labrador, which is classified as *R. t. caribou* but has mtDNA and microsatellite allele frequencies intermediate between the other herds of *R. t. caribou* and *R. t. groenlandicus*. Within subspecies, there is relatively low differentiation of microsatellite allele frequencies and mtDNA genotypes among herds of *R. t. granti* and *R. t. groenlandicus*, and relatively high differentiation of microsatellite alleles and mtDNA genotypes among herds of *R. t. caribou* in 4 geographically separate areas in Canada. The extent of differentiation of mtDNA genotype frequencies and microsatellite allele frequencies within and among each subspecies reflects past and present gene flow among herds. Issues related to subspecies, populations, ecotypes, and herds are discussed.

Key words: caribou, genetics, herds, microsatellite DNA, mitochondrial DNA cytochrome-*b* gene, populations, *Rangifer tarandus*, subspecies

Four extant subspecies of caribou (*Rangifer tarandus*) commonly are recognized in North America (Fig. 1): Alaskan barren ground caribou (*R. t granti*), Canadian barren ground caribou (*R. t. groenlandicus*), Peary caribou (*R. t. pearyi*), and woodland caribou (*R. t. caribou*—Banfield 1961; Bergerud 2000; Røed et al. 1991), although other classifications have been suggested (e.g., Geist 1998). Subspecies of caribou have been designated based on variation in morphology, habitat use, and behavior that may reflect adaptation to local conditions, sexual selection, or nongenetic environmental influences on phenotype (Bergerud 2000; Courtois et al. 2003; Cronin et al. 2003a; Geist 1987, 1998; Klein et al. 1987; Reimers 1993). However, it is generally agreed that subspecies designations should be based on phylogenetic relatedness (Avise and Ball 1990; Cronin et al. 2003b), and the phylogenetic relationships of the North American subspecies are not definitive. For example, the barren ground (*R. t. granti* and *R. t. groenlandicus*) and woodland (*R. t. caribou*) subspecies do not have strictly monophyletic mitochondrial deoxyribonucleic acid (mtDNA—Cronin 1992). However, frequencies of mtDNA genotypes and transferrin alleles are differentiated between *R. t. groenlandicus* and *R. t. caribou* (Flagstad and Røed 2003; Gravlund et al. 1998; Røed et al. 1991). Other studies of molecular markers including proteins (Baccus et al. 1983; Røed et al. 1991; Røed and Whitten 1986; Storset et al. 1978), mtDNA (Cronin et al. 1995), nuclear genes (Cronin et al. 1995; Olsaker and Røed 1990), and microsatellite DNA (Côté et al. 2002; Courtois et al. 2003; Engel et al. 1996; Røed and Midthjell 1998; Wilson et al.

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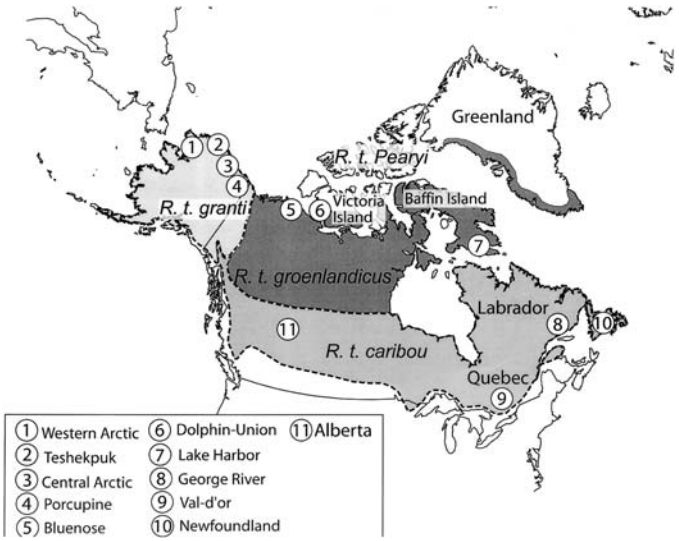

Fig. 1.—Distribution of caribou herds and subspecies in North America. Approximate locations of samples analyzed for mtDNA and microsatellite DNA variation are indicated by numbered circles.

1997; Zittlau et al. 2000) show varying levels of differentiation of subspecies of *Rangifer*.

Within subspecies, caribou occur in herds or populations that have temporally and spatially variable levels of mixing and gene flow. Caribou herds generally are considered groups that share calving or winter ranges (Bergerud 2000; Skoog 1968; Zittlau et al. 2000), and populations are interbreeding groups that have limited gene flow with other groups (Courtois et al. 2003; Cronin et al. 2003b). Overlapping seasonal ranges or dispersal may result in an interbreeding population that consists of >1 herd of caribou (Côté et al. 2002; Courtois et al. 2003; Cronin et al. 2003b; Skoog 1968; Whitten and Cameron 1983). Genetic relationships of caribou herds and populations have been used to identify management and conservation units, and to estimate the extent of immigration and emigration (Courtois et al. 2003; Zittlau et al. 2000). In some cases, there is differentiation of microsatellite DNA allele frequencies over small geographic scales (45–200 km) of herds of woodland caribou in Québec (Courtois et al. 2003) and the Yukon Territory (Zittlau et al. 2000), and reindeer (*R. t. platyrhynchus*) on Svalbard Island, Norway (Côté et al. 2002). In contrast, there is limited differentiation of microsatellite allele frequencies of barren ground caribou (*R. t. granti*) herds across 1,000 km of the North Slope of the Brooks Range of Alaska (Cronin et al. 2003b).

In this paper, we further quantify the genetic relationships of 3 caribou subspecies (*R. t. granti*, *R. t. groenlandicus*, and *R. t. caribou*) including 11 herds in North America with 18 microsatellite loci and sequences of the mtDNA cytochrome-*b* gene. mtDNA is maternally inherited and reflects female-mediated gene flow and phylogeny, and microsatellites are biparentally inherited in the nuclear genome and reflect male- and female-mediated gene flow. Our objectives were to assess the mtDNA phylogeny of the 3 subspecies and to compare frequencies of mtDNA genotypes and microsatellite alleles among the 3 subspecies and among herds within each subspecies in Alaska and Canada.

Table 1.—Measures of genetic variation in 3 subspecies and 11 caribou (*Rangifer tarandus*) herds in North America. Measures of genetic variation include expected heterozygosity (H_E), observed heterozygosity (H_O), average number of alleles per locus (A), and allelic richness. Sample size is indicated as *n*. Numbers in parentheses refer to the sample locations in Fig. 1. The Central Arctic, Porcupine River, Teshekpuk Lake, and Western Arctic herds are in Alaska, and the Dolphin–Union, Victoria Island, Lake Harbor, Baffin Island, and Bluenose herds are in Canada.

	Microsatellites				Allelic	mtDNA cytochrome *b*	
Subspecies and herd	*n*	H_E	H_O	A	richness	*n*	No. genotypes
R. t. granti							
Central Arctic, Alaska (3)	47	0.492	0.451	6.61	2.15	31	25
Porcupine River, Alaska (4)	57	0.474	0.458	6.56	2.18	30	20
Teshekpuk Lake, Alaska (2)	12	0.502	0.500	4.17	2.22	12	8
Western Arctic, Alaska (1)	19	0.505	0.462	5.33	2.13	19	14
R. t. groenlandicus							
Dolphin−Union, Victoria Island, Northwest Territories (6)	18	0.472	0.453	4.61	2.01	6	3
Lake Harbor, Baffin Island, Northwest Territories (7)	18	0.431	0.391	4.17	2.24	17	4
Bluenose, Northwest Territories (5)	14	0.507	0.479	5.06	1.63	14	7
R. t. caribou							
Val d'Or, Quebec (9)	6	0.304	0.213	2.22	1.86	6	2
Alberta (11)	3	0.398	0.370	2.11	2.03	3	1
George River, Labrador (8)	9	0.459	0.470	3.33	1.82	7	3
Newfoundland (10)	10	0.398	0.362	2.72	2.22	4	2

Materials and Methods

Tissue (blood, liver, and muscle) samples were collected from caribou in 11 locations in North America (Fig. 1; Table 1). To avoid confusion among terms (i.e., subspecies, ecotype, population, and herd) we will refer to each of the subspecies by its Latin name, and sampling location as herds (Fig. 1), because these names are established in the literature (e.g., Bergerud 2000). Alaskan barren ground caribou (*R. t. granti*) samples were obtained from the Teshekpuk Lake herd, Central Arctic herd, Western Arctic herd, and Porcupine River herd. Canadian barren ground caribou (*R. t. groenlandicus*) samples were obtained from the Bluenose herd at Hope Lake in the Northwest Territories, the Lake Harbor herd on southern Baffin Island, and the Dolphin–Union herd on southern Victoria Island. Woodland caribou (*R. t. caribou*) were obtained from herds in Newfoundland and Alberta, the Val-d'Or herd in Québec, and the George River herd in Labrador, although the inclusion of the George River herd in *R. t. caribou* has been questioned (e.g., Courtois et al. 2003; Geist 1998). The Central Arctic herd, Western Arctic herd,

Porcupine River herd, Lake Harbor herd, Dolphin–Union herd, Newfoundland herd, and George River herd were analyzed previously for 7 microsatellite loci (Cronin et al. 2003b), and the Val-d'Or herd was analyzed previously for 8 microsatellite loci (Courtois et al. 2003). Samples were collected by biologists in research projects except for those from the Teshekpuk Lake herd, which were collected by hunters.

DNA was extracted from tissues with standard methods (Cronin et al. 1995). Genotypes at 18 microsatellite loci were determined with polymerase chain reaction by using primers developed for cattle. These loci include 7 used previously on caribou and reindeer: BM848, BM6438, BMC1009, IGF-1, CRH, CSN10, and RBP3 (Cronin et al. 2003b), and 11 additional loci (BMS574, TGLA44, BMS1788, BMS1315, BMS1247, ILSTS028, ILSTS023, BMS745, BMS468, BMS2270, and CSSM036). Polymerase chain reaction primer sequences and bovine chromosome location for these 18 loci are available from the authors, and in Fries et al. (1993), Barendse et al. (1994), Bishop et al. (1994), Cronin et al. (2003b), and Slate et al. (1998). There is conservation of microsatellite loci between bovids and cervids (Slate et al. 1998; Talbot et al. 1996), although we do not know if these loci occur on homologous chromosomes in both families. In addition, some of these loci are linked to functional genes in the cattle genome (retinol-binding protein 3 interstitial [RBP], corticotropin releasing hormone [CRH], kappa-casein [CSN10], and insulin-like growth factor 1 [IGF-1]), and also may be so linked in the genome of *Rangifer*.

Polymerase chain reactions (15 μl) contained 5–50 ng of DNA in 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 2.5 mM $MgCl_2$, 0.2 mM of each deoxynucleoside triphosphate, 2 μM of each of the 2 primers, and 0.5 units of AmpliTaq DNA polymerase (Perkin Elmer, Norwalk, Connecticut). Reactions were heated to 95°C for 5 min followed by 38 cycles of amplification. Each cycle consisted of denaturation for 45 s at 95°C, annealing for 30 s at 54°C (IGF-1 and CSN10), 60°C (ILSTS023), or 58°C (all other loci), and extension for 1 min at 70°C. Polymerase chain reaction products were run with the 400HD Rox standard (Automated Biosystems Inc., ABI, Foster City, California) on gels formed with Long Ranger Singel packs (BioWhittaker Molecular Applications, Rockland, Maine) on an ABI 377 autosequencer. Genotypes were determined and data tables were created with ABI Genescan 3.1 and Genotyper 1.1.1 software packages.

The mtDNA cytochrome-*b* gene was amplified and sequenced with methods described by Cronin et al. (1999) for 149 caribou. Nucleotide sequence divergences were calculated for all nucleotide sites and for synonymous (ds) and nonsynonymous (dn) substitutions (Jukes and Cantor 1969) with the MEGA computer program (Kumar et al. 1993). We used a *Z*-test in the MEGA program to test the hypothesis that substitutions reflect purifying selection (i.e., ds > dn,). Phylogenetic relationships of the mtDNA sequences were assessed with maximum parsimony with the MEGA program. The cytochrome-*b* sequence of white-tailed deer (*Odocoileus virginianus*) was used as an outgroup. In addition to analysis of mtDNA sequence variation, we compared the distribution of mtDNA genotypes among herds and subspecies with estimates of pairwise F_{st} (Weir and Cockerham 1984) and genetic distances (chord distance—Cavalli-Sforza and Edwards 1967). We used genetic distances to construct a dendrogram using the unweighted pair-group method based on arithmetic averages (UPGMA—Sneath and Sokal 1973).

Microsatellite DNA variation within herds was quantified with the average number of alleles per locus (A), observed heterozygosity (H_O), and expected heterozygosity (H_E) with the Microsatellite Toolkit computer program (Park 2001). Because sample sizes were small for some herds, we also calculated allelic richness (i.e., the numbers of alleles standardized according to sample sizes—El Mousadik and Petit 1996; Petit et al. 1998) with the F-STAT program (Goudet 1995). Mean allelic richness values for all 18 loci were compared among herds with an analysis of variance. We tested among genotypes at each locus for Hardy–Weinberg equilibrium with the BIOSYS computer program (Swofford and Selander 1981). The GENEPOP program (Raymond and Rousset 1995a) was used to test among loci for linkage disequilibrium and differentiation of allele frequencies among herds with pairwise tests of heterogeneity (Raymond and Rousset 1995b). For the Hardy-Weinberg tests and tests of heterogeneity, we compared across 17 polymorphic loci and applied a Bonferroni correction (Rice 1989) to adjust significance values for multiple tests ($P = 0.05/17$ loci $= 0.0029$). We also quantified differentiation of allele frequencies by calculating pairwise F_{st}, genetic distances, and a UPGMA dendrogram as described for the mtDNA genotype frequencies.

RESULTS

Mitochondrial DNA.—We obtained 1,194 nucleotides of mtDNA cytochrome-*b* sequence for 149 caribou (Genbank accession numbers AY726672–AY726730). From these data, we identified 59 mtDNA genotypes differing by ≥1 nucleotide substitutions. There were substitutions at 90 different nucleotide positions, and 16 of these substitutions resulted in amino acid substitutions (i.e., nonsynonymous substitutions). There were 81 transitions and 9 transversions. The mean nucleotide sequence divergence distances (Jukes and Cantor 1969) between the caribou genotypes was 0.0074 ($SE = 0.0011$). The rate of synonymous substitutions between genotypes (ds = 0.0284) was significantly greater than the rate of nonsynonymous substitutions (dn = 0.00082) between genotypes ($Z = 6.0494$, $P < 0.0001$). The average sequence divergence between the 59 genotypes of *Rangifer* and the white-tailed deer genotype was 0.1269 ($SE = 0.0002$).

The maximum-parsimony phylogenetic analysis of the mtDNA cytochrome-*b* sequences resulted in 2 primary clades (Fig. 2). A majority-rule consensus tree of 7,221 equally parsimonious trees was generated (62 parsimonious informative sites, 241 steps; consistency index = 0.8382). The proportion of the equally parsimonious trees with a given clade identified is shown at the nodes of the tree. One clade contains 52 genotypes and includes all of the barren ground caribou of Alaska (*R. t. granti*) and Canada (*R. t. groenlandicus*). Both *R. t. granti* and *R. t. groenlandicus* occur together in various clades in Fig. 2. One genotype in this clade (genotype C10) also occurs in *R. t. caribou* in Labrador. In addition, an mtDNA genotype in this clade observed in *R. t. granti* is characteristic of domestic reindeer (*R. t. tarandus*) in Alaska (genotype R1).

A smaller clade in Fig. 2 includes 7 mtDNA genotypes restricted to the herds of *R. t. caribou* in Labrador, Newfoundland, Alberta, and Québec. This clade is identified in 100% of the equally parsimonious trees. Similar phylogenetic trees with 2 primary groups, one containing only genotypes of *R. t. caribou* and another with genotypes of *R. t. granti* and *R. t. groenlandicus*, were obtained with UPGMA and neighbor-joining (Saitou and Nei 1987) analyses of nucleotide sequence Jukes and Cantor distances (data not shown—Jukes and Cantor 1969). Although the subspecies *R. t. caribou* is characterized by phylogenetically distinct mtDNA genotypes, the 3 subspecies do not have strictly monophyletic mtDNA. The *R. t. caribou*

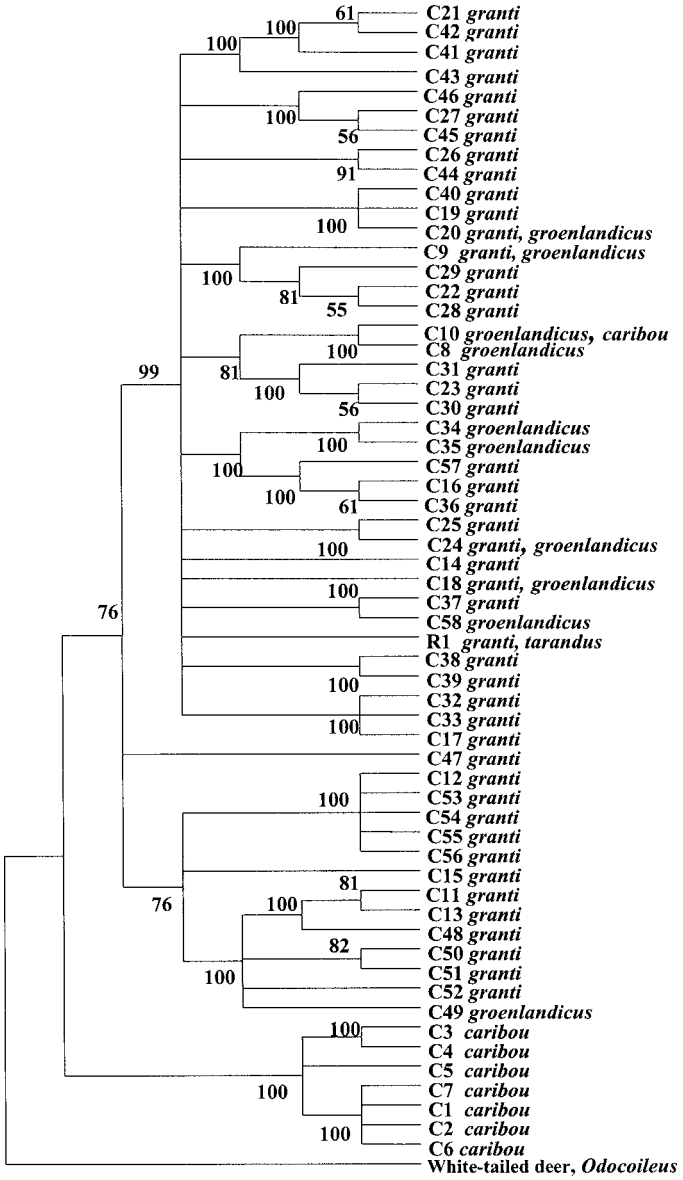

FIG. 2.—Maximum parsimony majority-rule consensus tree of mtDNA cytochrome-*b* genotypes in subspecies of North American caribou. The numbers at nodes are the proportion of the equally parsimonious trees with a given topology. The numbers preceded by a "C" or an "R" represent mtDNA genotypes.

in Labrador share a genotype (C10) with the Canadian *R. t. groenlandicus* on Baffin Island, and 4 genotypes (C9, C18, C20, and C24) are shared by the 2 barren ground subspecies (*R. t. granti* and *R. t. groenlandicus*).

The phylogenetic analysis indicates that most of the mtDNA genotypes found in *R. t. caribou* are differentiated from those of *R. t. granti* and *R. t. groenlandicus*. In contrast, mtDNA genotypes of *R. t. granti* and *R. t. groenlandicus* are not phylogenetically differentiated. However, comparison of the mtDNA genotype distributions (without regard to phylogenetic relatedness of the mtDNA sequences) indicates that different mtDNA genotypes predominate in each subspecies (Table 2). Comparisons of mtDNA genotype frequencies among the subspecies show that *R. t. granti* and *R. t. groenlandicus* are moderately differentiated from each other, whereas these 2 subspecies are highly differentiated from *R. t. caribou*. The herds of *R. t. groenlandicus* shared 4 mtDNA genotypes with the herds of *R. t. granti* (C9, C18, C20, and C24), and the average pairwise F_{st} was 0.1316 between these subspecies. The herds of *R. t. groenlandicus* shared 1 genotype (C10) with the Labrador herd of *R. t. caribou*, whereas the herds of *R. t. granti* shared no genotypes with the herds of *R. t. caribou*. The average pairwise F_{st} estimates are relatively high between *R. t. caribou* and *R. t. groenlandicus* ($F_{st} = 0.3339$), and between *R. t. caribou* and *R. t. granti* ($F_{st} = 0.2197$).

Considerable variation occurred among herds, although these results are tentative because of the large number of mtDNA genotypes and limited sample sizes. Significantly different mtDNA genotype frequencies were found in all of the pairwise tests of heterogeneity between the 11 herds ($P < 0.0009$) except for the Dolphin–Union and Bluenose herds of *R. t. groenlandicus* ($P = 0.09$). Also, the overall F_{st} (0.1267) for the mtDNA genotype frequencies among all 11 herds was relatively high.

Comparison of herds within subspecies shows that the 4 Alaskan herds of *R. t. granti* have 8–24 mtDNA genotypes each, and several genotypes occur in >1 herd. All 4 Alaskan herds share 3 genotypes (C12, C13, and C15), and 3 herds share 2 other genotypes (C14 and C16). Additional genotypes were shared by 2 of the 4 herds: Central Arctic and Porcupine River herds (C11, C17, C19, C21, and C26), Central Arctic and Teshekpuk Lake herds (C27), Porcupine River and Western Arctic herds (C22), and Central Arctic and Western Arctic herds (R1, the reindeer genotype noted above). Twenty-seven additional mtDNA genotypes occurred in only 1 of the Alaskan herds of *R. t. granti* (12 in the Central Arctic herd, 6 in the Porcupine River herd, 2 in the Teshekpuk Lake herd, and 7 in the Western Arctic herd). The 4 Alaskan herds have a relatively low level of differentiation of mtDNA genotype frequencies, as shown by the pairwise F_{st} estimates among the herds (Table 3) and an average F_{st} of 0.0200.

The 3 Canadian herds of *R. t. groenlandicus* had fewer mtDNA genotypes (i.e., 3–7 genotypes per herd) than the Alaskan herds of *R. t. granti*. All 3 herds of *R. t. groenlandicus* shared 2 genotypes (C8 and C9) that were absent or rare in the other subspecies. Four other mtDNA genotypes (C34, C35, C49, and C58) occurred only in the Bluenose herd of *R. t. groenlandicus*. Differentiation of mtDNA genotype frequencies among the 3 herds of *R. t. groenlandicus* is higher than among the 4 herds of *R. t. granti*, as shown by the pairwise F_{st} estimates among the herds (Table 3) and an average F_{st} of 0.0326.

The herds of *R. t. caribou* each had unique mtDNA genotypes, as described in the phylogenetic analysis. Two genotypes occurred only in Newfoundland (C1 and C2), 2 genotypes occurred only in Labrador (C3 and C4), 2 genotypes occurred only in Québec (C6 and C7), and 1 genotype occurred only in Alberta (C5). The lack of shared mtDNA genotypes among the herds of *R. t. caribou* are reflected in the high pairwise F_{st} values (Table 3) and an average F_{st} of 0.5096.

These intra- and intersubspecies comparisons of mtDNA genotype frequencies are summarized in the genetic distance

TABLE 2.—Numbers of mtDNA genotypes in North American caribou (*Rangifer tarandus*) herds and subspecies.[a] Numbers in bold represent genotypes characteristic of each subspecies. Numbers in italics indicate genotypes shared by different subspecies.

	R. t. granti				*R. t. groenlandicus*			*R. t. caribou*			
Genotype	Central Arctic, Alaska	Porcupine River, Alaska	Teshekpuk Lake, Alaska	Western Arctic, Alaska	Dolphin–Union, Victoria Island, Northwest Territories	Lake Harbor, Baffin Island, Northwest Territories	Bluenose, Northwest Territories	Alberta	George River, Labrador	Newfound-land	Val d'Or, Quebec
C1										**3**	
C2										**1**	
C3									**4**		
C4									**1**		
C5								**3**			
C6											**3**
C7											**3**
C8					**3**	**5**	**6**				
C9	***1***				***1***	***4***	***3***				
C10						***6***			***2***		
C11	**1**	**5**									
C12	**3**	**2**	**1**	**5**							
C13	**1**	**2**	**3**	**1**							
C14	**4**	**1**	**1**								
C15	**1**	**1**	**1**	**2**							
C16	**1**	**3**		**1**							
C17	1	2									
C18				*1*		*2*					
C19	1	1									
C20		*1*			*2*						
C21	1	1									
C22		1		1							
C24		*1*					*1*				
C25		2									
C26	1	1									
C27	1		1								
C45			3								
R1	1			1							

[a] Additional genotypes that occur once in a herd are as follows. Central Arctic: C30, C32, C40, C41, C43, C44, C46, C47, C50, C52, C53, and C57; Porcupine River: C28, C36, C38, C39, C42, and C51; Teshekpuk Lake: C23 and C37; Western Arctic: C29, C31, C33, C48, C54, C55, and C56; and Bluenose: C34, C35, C49, and C58.

estimates (Table 4) and UPGMA dendrogram (Fig. 3). In the dendrogram, the herds of *R. t. granti* and *R. t. groenlandicus* each form separate clusters. Within the cluster of *R. t. granti*, the Central Arctic and Porcupine herds occur together in a smaller cluster. The sharing of 1 mtDNA genotype resulted in the Labrador herd of *R. t. caribou* clustering with the herds of *R. t. groenlandicus*, separate from the other herds of *R. t. caribou*. The lack of shared mtDNA genotypes among the herds of *R. t. caribou* resulted in each herd on a separate branch of the dendrogram.

Microsatellites.—We determined genotypes and allele frequencies (available from authors) for 213 caribou at 18 microsatellite loci. Results for 7 of these loci were reported previously for the Central Arctic, Western Arctic, Porcupine River, Bluenose (Victoria Island), Lake Harbor (Baffin Island), Newfoundland, and George River (Labrador) herds (Cronin et al. 2003b). Most loci are highly polymorphic, although 1 was monomorphic (ILSTS023) and 3 (BMC1009, CSN10, and BMS574) had only 2 alleles. The average numbers of alleles per locus ranged from 2.1 to 6.6 among the herds (Table 1). A significant relationship was found between sample size and average number of alleles per locus ($R^2 = 0.762$, $P = 0.0004$), so this parameter is not a good indicator of relative genetic variation in our samples. Allelic richness values considering sample size varied from 1.6 to 2.24 (Table 1), and were not significantly different ($P = 0.437$). The average observed heterozygosity ranged from 0.21 to 0.50, and average expected heterozygosity ranged from 0.30 to 0.51 among the herds (Table 1). Although a significant relationship was not found between sample size and H_O ($R^2 = 0.1285$, $P = 0.279$) or H_E ($R^2 = 0.1839$, $P = 0.1882$), the smallest sample sizes had the lowest heterozygosities, so this must be considered in comparisons among herds.

Of 187 tests (11 herds for 17 polymorphic loci), 3 had significant ($P < 0.0029$) deviations from Hardy–Weinberg equilibrium, with fewer heterozygotes observed than expected. There were 8 observed and 15 expected heterozygotes for the CSSMO36 locus in the Central Arctic herd of *R. t. granti*, 1 observed and 4.5 expected heterozygotes for the CSSMO36 locus in the Western Arctic herd of *R. t. granti*, and 0 observed and 4 expected heterozygotes for the BMS1788 locus in the

TABLE 3.—Pairwise F_{st} values for mtDNA genotypes (above diagonal) and for 18 microsatellite loci (below diagonal) between 11 caribou (*Rangifer tarandus*) herds in North America.

Subspecies and herd	Central Arctic	Porcupine River	Teshekpuk Lake	Western Arctic	Dolphin–Union, Victoria Island	Lake Harbor, Baffin Island	Bluenose, Northwest Territories	Val d'Or, Quebec	Alberta	George River, Labrador	Newfound-land
R. t. granti											
Central Arctic		0.002	0.023	0.007	0.114	0.112	0.097	0.166	0.281	0.147	0.181
Porcupine River	0.002		0.037	0.019	0.120	0.128	0.110	0.177	0.292	0.157	0.192
Teshekpuk Lake	0.018	0.032		0.035	0.167	0.167	0.146	0.222	0.355	0.199	0.240
Western Arctic	0.009	0.014	0.007		0.147	0.143	0.129	0.197	0.319	0.177	0.214
R. t. groenlandicus											
Dolphin–Union, Victoria Island	0.045	0.045	0.047	0.033		0.077	−0.028	0.333	0.518	0.302	0.366
Lake Harbor, Baffin Island	0.069	0.080	0.087	0.058	0.075		0.049	0.298	0.427	0.195	0.321
Bluenose, Northwest Territories	0.045	0.067	0.078	0.059	0.070	0.089		0.279	0.412	0.255	0.301
R. t. caribou											
Val d'Or, Quebec	0.194	0.219	0.207	0.194	0.263	0.332	0.250		0.600	0.365	0.442
Alberta	0.023	0.021	0.049	0.025	0.098	0.122	0.076	0.308		0.544	0.707
George River, Labrador	0.059	0.070	0.057	0.052	0.099	0.127	0.104	0.234	0.086		0.400
Newfoundland	0.180	0.189	0.169	0.180	0.204	0.241	0.206	0.346	0.231	0.167	

Québec herd of *R. t. caribou*. Because the other herds were in Hardy–Weinberg equilibrium for these loci, we retained them in our analyses. Eight pairs of loci had significant nonrandom associations of genotypes, suggesting possible linkage. Seven of these pairs involved 2 loci, BMS1788 and ILSTS028. The BMS1788 locus was nonrandomly associated with the CRH, BMS745, and TGLA44 loci; and the ILSTS028 locus was nonrandomly associated with the IGF1, BM848, BMS1788, and BMS468 loci. The TGLA44 and BMS2270 loci also had nonrandom association of genotypes.

The distribution of microsatellite alleles shows that most alleles are shared among the caribou subspecies and herds. No fixed allelic differences were found among the herds, but it is notable that the 188 allele at the CSN10 locus was observed in Newfoundland and Labrador at a frequency of about 0.30, and this allele did not occur in the other locations. The overall F_{st} among the 11 herds ranged from −0.0105 to 0.3135 (average $F_{st} = 0.1277$) among the 17 polymorphic loci.

To assess genetic differentiation of microsatellite allele frequencies, we conducted pairwise tests of heterogeneity and calculated pairwise (17 polymorphic loci average) F_{st} between herds (Table 3). Within subspecies, a low level of genetic differentiation was found among the 4 herds of *R. t. granti* relative to differentiation of the herds of the other 2 subspecies. The pairwise F_{st} values between the herds of *R. t. granti* ranged from 0.002 to 0.032 (average $F_{st} = 0.0135$). Five (5%) of 102 pairwise tests of heterogeneity between the herds of *R. t. granti* indicated significantly different ($P < 0.0029$) allele frequencies

TABLE 4.—Genetic (chord) distances (Cavalli-Sforza and Edwards 1967) for mtDNA genotypes (above diagonal) and microsatellites (below diagonal) between 11 caribou (*Rangifer tarandus*) herds in North America.

Subspecies and herd	Central Arctic	Porcupine River	Teshekpuk Lake	Western Arctic	Dolphin–Union, Victoria Island	Lake Harbor, Baffin Island	Bluenose, Northwest Territories	Val d'Or, Quebec	Alberta	George River, Labrador	Newfound-land
R. t. granti											
Central Arctic		0.569	0.648	0.651	0.858	0.813	0.852	0.900	0.900	0.900	0.900
Porcupine River	0.151		0.728	0.664	0.846	0.868	0.875	0.900	0.900	0.900	0.900
Teshekpuk Lake	0.271	0.276		0.722	0.900	0.900	0.900	0.900	0.900	0.900	0.900
Western Arctic	0.218	0.219	0.283		0.900	0.864	0.900	0.900	0.900	0.900	0.900
R. t. groenlandicus											
Dolphin–Union, Victoria Island	0.289	0.281	0.348	0.293		0.582	0.531	0.900	0.900	0.900	0.900
Lake Harbor, Baffin Island	0.339	0.354	0.395	0.360	0.353		0.584	0.900	0.900	0.744	0.900
Bluenose, Northwest Territories	0.271	0.287	0.357	0.315	0.315	0.365		0.900	0.900	0.900	0.900
R. t. caribou											
Val d'Or, Quebec	0.427	0.440	0.450	0.428	0.481	0.525	0.455		0.900	0.900	0.900
Alberta	0.375	0.366	0.397	0.394	0.432	0.464	0.420	0.473		0.900	0.900
George River, Labrador	0.336	0.337	0.352	0.355	0.397	0.416	0.388	0.450	0.422		0.900
Newfoundland	0.418	0.415	0.427	0.438	0.447	0.461	0.458	0.501	0.479	0.388	

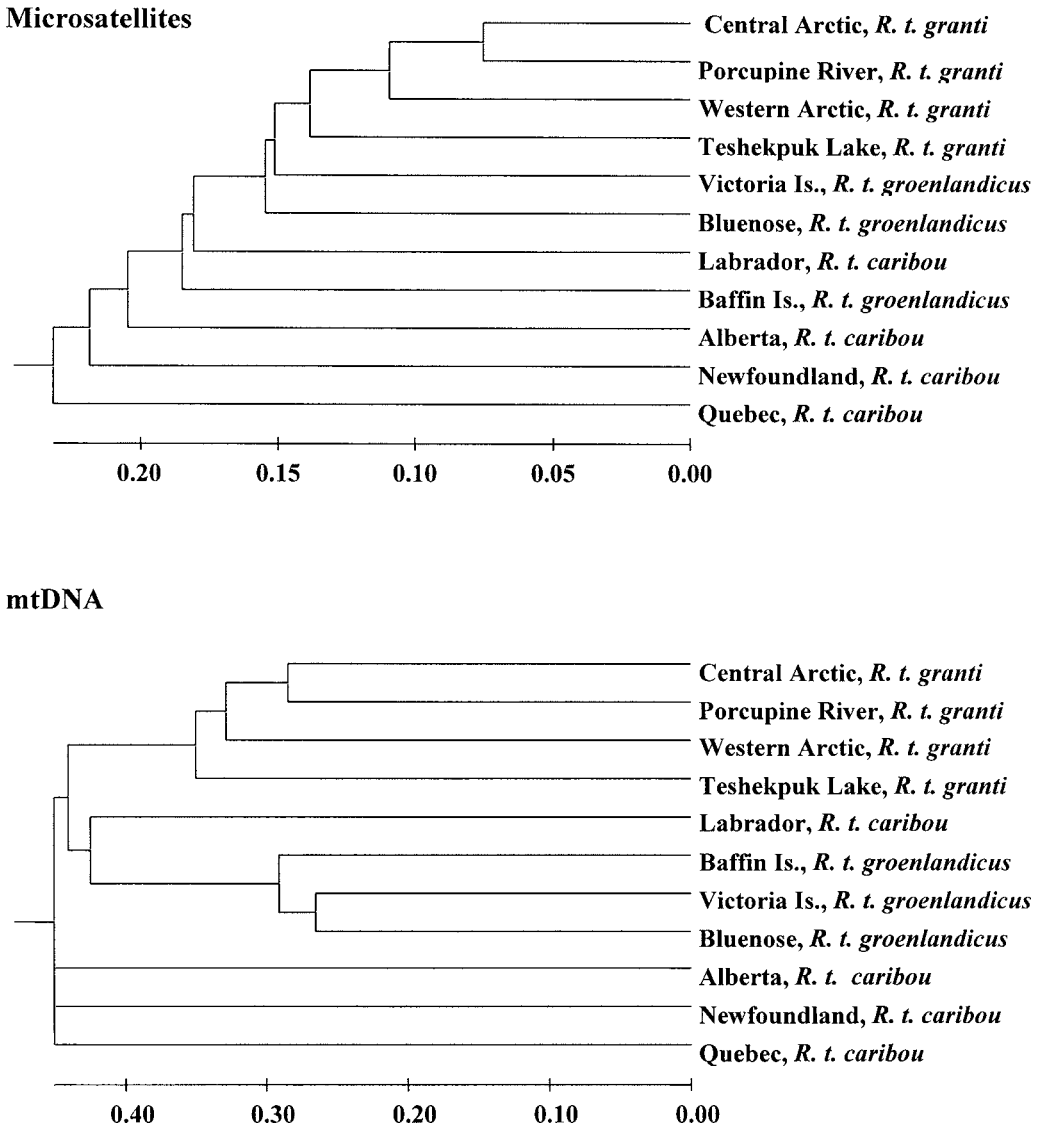

FIG. 3.—Unweighted pair-group method with arithmetic average (UPGMA) dendrograms of North American caribou herds and subspecies constructed with genetic distances (Cavalli-Sforza and Edwards 1967) for 18 microsatellite DNA loci and mtDNA cytochrome-*b* genotypes. Note the different scales on each dendrogram.

between herds. The Central Arctic herd and Porcupine River herd had especially low differentiation, with no significant differences in allele frequencies for any locus and the lowest F_{st} observed ($F_{st} = 0.002$).

Differentiation of the 3 herds of *R. t. groenlandicus* is greater than that between the herds of *R. t. granti* (Table 3). F_{st} values ranged from 0.070 to 0.089 (average $F_{st} = 0.0782$). Fourteen (27%) of 51 pairwise comparisons indicated significant differences in allele frequencies between herds. Differentiation of the herds of *R. t. caribou* was higher than that between the herds of either *R. t. granti* or *R. t. groenlandicus*. Pairwise F_{st} values ranged from 0.086 to 0.346 (average $F_{st} = 0.2288$) between the herds of *R. t. caribou*. Twenty (20%) of 102 pairwise comparisons indicated significant differences in allele frequencies between the herds of *R. t. caribou*.

Comparisons among the subspecies showed that *R. t. granti* and *R. t. groenlandicus* were less differentiated from each other than either was to *R. t. caribou*. The average pairwise F_{st} between the herds of *R. t. granti* and herds of *R. t. groenlandicus* (average $F_{st} = 0.0625$) is considerably lower than that between the herds of *R. t. granti* and *R. t. caribou* (average $F_{st} = 0.1200$), and between the herds of *R. t. groenlandicus* and the herds of *R. t. caribou* (average $F_{st} = 0.1620$).

These relationships are reflected in the genetic distances (Table 4) and the UPGMA dendrogram (Fig. 3). The dendrogram reflects the relatively low level of differentiation among the herds of *R. t. granti* and among the herds of *R. t. groenlandicus*, and relatively high levels of differentiation among the herds of *R. t. caribou*. The Central Arctic and Porcupine River herds cluster together in a larger cluster containing all 4 herds of *R. t. granti*, as in the mtDNA UPGMA dendrogram (Fig. 3). The 3 herds of *R. t. groenlandicus* and the Labrador herd of *R. t. caribou* cluster together, and the Alberta, Newfoundland, and Québec herds of *R. t. caribou* cluster

outside this group. The topology of the dendrogram reflects the close relationships of the herds of *R. t. granti*, the close relationship of the herds of *R. t. groenlandicus* with each other and the Labrador herd of *R. t. caribou*, and the high level of differentiation of the 2 barren ground subspecies and the woodland subspecies (*R. t. caribou*).

Discussion

Several patterns of differentiation of mtDNA cytochrome *b* and microsatellite loci are apparent in North American caribou, and consistent with studies of other loci (Courtois et al. 2003; Flagstad and Røed 2003; Gravlund et al. 1998; Røed et al. 1991; Zittlau et al. 2000). First, there is limited genetic differentiation of the 4 herds of *R. t. granti* in northern Alaska. The Central Arctic herd and Porcupine River herd have a particularly low level of differentiation for both mtDNA and microsatellites (Fig. 3). F_{st} is related to the effective number of migrants between populations (N_em) as $F_{st} = 1/(1 + 4N_em$—Wright 1969). N_em between the Alaskan herds of *R. t. granti*, calculated from F_{st} values for microsatellites, range from 8 (between the Porcupine and Teshekpuk herds) to 138 (between the Central Arctic and Porcupine herds). This suggests that there is gene flow among these herds (Cronin et al. 2003b; Skoog 1968; Whitten and Cameron 1983). The Alaskan herds have different calving ranges but their breeding and winter ranges may overlap and there may be movement of individuals between herds (Bergerud et al. 1984; Skoog 1968). Telemetry data indicate high fidelity of female caribou to herds (Whitten and Cameron 1983), but there is little information on movements of males. Males of other mammal species have larger home ranges and disperse more than females, so male-mediated gene flow may be substantial in the Alaskan caribou herds. It is important to note that molecular genetic data such as ours give indirect long-term estimates of gene flow, whereas field observations of movements give direct, short-term estimates of gene flow (Avise 2000:78; Slatkin 1987).

An additional observation is the occurrence in *R. t. granti* of an mtDNA genotype that is characteristic of domestic reindeer (*R. t. tarandus*) in Alaska (genotype R1). Reindeer were introduced to Alaska from Eurasia and the occurrence of this genotype in caribou probably reflects introgressive hybridization from domestic reindeer into wild caribou (Cronin et al. 1995, 2003b). A close phylogenetic relationship of mtDNA in Eurasian *R. t. tarandus* and North American *R. t. granti* and *R. t. groenlandicus* has been reported previously (Flagstad and Røed 2003; Gravlund et al. 1998).

The 2nd pattern is an intermediate level of differentiation of the 3 herds of *R. t. groenlandicus*. These herds cluster together, but are in a group including the Labrador herd of *R. t. caribou* in the microsatellite and mtDNA UPGMA dendrograms (Fig. 3). These herds do not have contiguous ranges, and differences of microsatellite allele frequencies and mtDNA genotype frequencies probably reflect isolation by distance.

A 3rd pattern is the limited differentiation of the barren ground subspecies (*R. t. groenlandicus* and *R. t. granti*) indicated by lack of phylogenetic differentiation of mtDNA genotypes (Fig. 2) and relatively low level of differentiation of microsatellite allele frequencies (Fig. 3). This probably reflects occupation of a common Beringian glacial refugium and some recent gene flow as observed with other genetic markers (Flagstad and Røed 2003; Gravlund et al. 1998; Røed et al. 1991) and morphology (Geist 1998).

The 4th pattern is the high level of differentiation of mtDNA genotype and microsatellite allele frequencies among the woodland (*R. t. caribou*) herds. This probably reflects limited gene flow because of a discontinuous geographic distribution and relatively small herd sizes. This pattern has been reported previously for herds of *R. t. caribou* (Courtois et al. 2003; Zittlau et al. 2000). The extent of female-mediated gene flow is particularly low because the herds of *R. t. caribou* share no mtDNA genotypes (Table 2).

The 5th pattern is the high level of differentiation of the woodland (*R. t. caribou*) and barren ground (*R. t. granti* and *R. t. groenlandicus*) subspecies. This relationship is reflected in the mtDNA sequence phylogeny (Fig. 2) as well as the mtDNA genotype and microsatellite allele frequencies (Fig. 3). Differentiation of the barren ground and woodland subspecies has been observed previously with mtDNA and protein analyses, and probably reflects the isolation of ancestors of *R. t. caribou* south of, and *R. t. granti* and *R. t. groenlandicus* north of the Pleistocene continental glaciers (Flagstad and Røed 2003; Gravlund et al. 1998; Røed et al. 1991). The previous mtDNA analyses included 203 nucleotides (Gravlund et al. 1998) and 470 nucleotides (Flagstad and Røed 2003) of the mtDNA control region. However, 1 of the herds of *R. t. caribou* (Labrador) and the herds of *R. t. groenlandicus* share mtDNA cytochrome-*b* genotype C10 (Table 2; Fig. 2) and have similar microsatellite frequencies (Fig. 3). In our results and those of others (Cronin 1992; Flagstad and Røed 2003) the frequency of the mtDNA genotypes in the Labrador herd that are phylogenetically related to the other genotypes of *R. t. caribou* (genotypes C3 and C4 in our results) is higher than the frequency of the genotypes shared with *R. t. groenlandicus* (genotype C10 in our results). This suggests a higher degree of maternal ancestry of the Labrador herd with *R. t. caribou* than with *R. t. groenlandicus*. However, overall genetic similarity suggests there has been postglacial gene flow between the Labrador herd and the herds of *R. t. groenlandicus* (Røed et al. 1991).

Several factors potentially influence these patterns of differentiation. First, we have small sample sizes relative to the numbers of animals in the herds. For example, we had only 12–57 samples from herds of *R. t. granti*, which consist of 30,000–450,000 animals each. Larger sample sizes could show different patterns than we observed. Other microsatellite studies of North American caribou had sample sizes comparable to ours ($n = 14$–58 per population—Courtois et al. 2003; Cronin et al. 2003b; Zittlau et al. 2000). In addition, our analysis of 18 loci includes a small proportion of the nuclear genome, although it is an increase over these previous studies that employed only 7 or 8 loci.

Another important factor is that although patterns of differentiation generally are concordant between mtDNA and microsatellites (Fig. 3), the magnitude of differentiation is

greater for mtDNA. The pairwise F_{st} and genetic distances are generally higher for mtDNA than microsatellites (Tables 3 and 4), no mtDNA genotypes are shared among the herds of *R. t. caribou*, and only 1 mtDNA genotype is shared between *R. t. caribou* and *R. t. groenlandicus* (Table 3). In contrast, all of the herds sampled shared several microsatellite alleles, although at different frequencies. mtDNA is maternally and clonally inherited, so the greater differentiation may reflect lower levels of female-mediated than male-mediated gene flow, or genetic drift due to lower effective mitochondrial gene number than nuclear gene number. However, the patterns of differentiation of mtDNA and microsatellites are not directly comparable because of different levels of resolution of alleles and genotypes. Variation in mtDNA was detected from DNA sequences, whereas variation in microsatellites is detected from size differences of DNA fragments.

The polymerase chain reaction primers for the microsatellite loci we employed were developed in cattle, and there is the potential for null alleles (i.e., nonamplifying alleles) when used in a different species (Engel et al. 1996). However, the relatively small number of loci and herds that were not in Hardy–Weinberg equilibrium suggests that null alleles did not occur in our analysis. In addition, 8 pairs of loci had nonrandom association of genotypes, which may indicate linkage. However, whether these loci actually are linked is questionable. First, none of these pairs of loci are on the same chromosome in the cattle genome (Barendse et al. 1994; Bishop et al. 1994; Fries et al. 1993; Slate et al. 1998). Second, the BMS1788 and ILSTS028 loci are nonrandomly associated, but the 3 loci potentially linked to BMS1788 (CRH, BMS745, and TGLA44) and the 4 loci potentially linked to ILSTS028 (IGF1, BM848, BMS1788, and BMS468) are not linked to each other, as might be expected. More detailed linkage analyses involving known families are required to verify the physical relationships of these loci in the genome of *Rangifer*. We also observed evidence of purifying selection of the mtDNA sequences, which had a significantly higher synonymous than nonsynonymous substitution rate. This reflects possible selection on mtDNA sequences for *Rangifer* as a whole, but not necessarily among the subspecies or herds. Some of the microsatellite loci also could be associated with fitness differences (MacNeil and Grosz 2002), but we cannot assess the potential for selection influencing the genotype or allele frequencies among herds because we lack data for fitness-related traits in individual animals.

The patterns of genetic differentiation of *Rangifer* we present provide some insights for intraspecific taxonomy of *Rangifer*. First, *R. t. granti* and *R. t. groenlandicus* have somewhat differentiated microsatellite and mtDNA genotype frequencies (Fig. 3), but do not have phylogenetically distinct mtDNA (Fig. 2). Both of these subspecies are considerably more differentiated from the woodland subspecies (*R. t. caribou*) for both microsatellite allele and mtDNA genotype frequencies (Fig. 3) and mtDNA sequence phylogeny (Fig. 2). This suggests that *R. t. granti* and *R. t. groenlandicus* appropriately could be placed into 1 subspecies, and *R. t. caribou* could be maintained as a separate subspecies. This is consistent with the classification of Geist (1998), based on morphology. In addition, as described previously, the sharing of an mtDNA genotype and similar microsatellite allele frequencies between the *R. t. caribou* in Labrador and *R. t. groenlandicus* indicate that there is not absolute differentiation of these subspecies as currently designated. These genetic data reflect the inconsistent subspecific designations of caribou in Labrador (e.g., Banfield 1961; Bergerud 2000; Courtois et al. 2003; Geist 1998). Indeed, Geist (1998) considers caribou in Labrador and Newfoundland as 2 additional subspecies (*R. t. caboti* and *R. t. terraenovae*, respectively). Regardless, examination of the genetic data indicates that the Labrador caribou have ancestry with both *R. t. caribou* and *R. t. groenlandicus* and subspecies designations are necessarily indefinite because of gene flow and paraphyletic or polyphyletic intraspecific phylogenies.

We also note that intraspecific classification of *Rangifer* has been complicated by the designation of ecotypes, which are populations with convergent morphological, demographic, and behavioral adaptations to similar ecological conditions (Banfield 1961; Bergerud 2000; Courtois et al. 2003). Ecotypes of *Rangifer* include a small-bodied high-arctic form, a barren ground tundra-dwelling form, a mountain form, and a forest-dwelling woodland form (Bergerud 2000; Courtois et al. 2003; Flagstad and Røed 2003; Gravlund et al. 1998). The potential for confusion between subspecies and ecotype designations is exemplified by the Labrador George River herd, which is of the subspecies *R. t. caribou*, but the barren ground ecotype (Bergerud 2000; Courtois et al. 2003). Both designations are supported by our data, because most mtDNA genotypes in the Labrador herd are phylogenetically like those in the subspecies *R. t. caribou* (Fig. 2), whereas the microsatellite allele and mtDNA genotype frequencies indicate a degree of similarity with the barren ground *R. t. groenlandicus* (Fig. 3).

The overlap of the subspecific and ecotypic designations indicate that it is important to differentiate groups defined by genetic criteria from those defined by ecological criteria. In the case of *Rangifer*, subspecies and populations are defined primarily by genetic criteria whereas ecotypes and herds are defined by ecological criteria. It generally is accepted that subspecies are phylogenetically distinct groups (e.g., Avise and Ball 1990), populations are interbreeding groups with limited gene flow with other populations (Mayr 1963), ecotypes are conspecific groups with similar ecological adaptations regardless of genealogical relationship (Courtois et al. 2003), and herds are groups with common calving grounds or other seasonal ranges (Bergerud 2000). Each of these terms has utility, but it is important to define and use them consistently. Opinions over the level of differentiation needed to distinguish such groups will vary, but agreement on the type of data used (i.e., genetic versus ecological) is a necessary 1st step toward more consistent classifications.

ACKNOWLEDGMENTS

Funding for this paper was provided by BP Exploration (Alaska) Inc. and the United States Department of Agriculture. Samples were obtained from K. Gerhart, C. George, C. MacDonald, G. Finstad, A. Gunne, S. Luttich, S. Mahoney, R. McClymont, W. Wishart, S. Fancy, S. Pitcher, R. Courtois, and M. Crête. L. French conducted many of

the microsatellite laboratory analyses; G. Durner, L. Noel, and S. C. Amstrup helped produce figures; and W. Streever, R. Bradley, and 2 anonymous reviewers provided helpful comments on the manuscript.

Literature Cited

Avise, J. C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, Massachusetts.

Avise, J. C., and R. M. Ball, Jr. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Survey of Evolutionary Biology 7:45–67.

Baccus, R., N. Ryman, M. H. Smith, C. Reuterwall, and D. G. Cameron. 1983. Genetic variability and differentiation of large grazing mammals. Journal of Mammology 64:109–120.

Banfield, A. W. F. 1961. A revision of the reindeer and caribou genus *Rangifer*. Biological Series 66. National Museum of Canada Bulletin. Vol. 177.

Barendse, W., et al. 1994. A genetic linkage map of the bovine genome. Nature Genetics 6:227–235.

Bergerud, A. T. 2000. Caribou. Pp. 658–693 in Ecology and management of large mammals in North America (S. Demarais and P. R. Krausman, eds.). Prentice-Hall, Inc., Upper Saddle River, New Jersey.

Bergerud, A. T., R. D. Jakimchuk, and D. R. Carruthers. 1984. The buffalo of the north: caribou (*Rangifer tarandus*) and human developments. Arctic 37:7–22.

Bishop, M. D., et al. 1994. A genetic linkage map for cattle. Genetics 136:619–639.

Cavalli-Sforza, L. L., and A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. American Journal of Human Genetics 19:233–257.

Côté, S. D., J. F. Dallas, F. Marshall, R. J. Irvine, R. Langvatn, and S. D. Albon. 2002. Microsatellite DNA evidence for genetic drift and philopatry in Svalbard reindeer. Molecular Ecology 11: 1923–1930.

Courtois, R., L. Bernatchez, J. P. Ouellet, and L. Breton. 2003. Significance of caribou (*Rangifer tarandus*) ecotypes from a molecular genetics viewpoint. Conservation Genetics 4:393–404.

Cronin, M. A. 1992. Intraspecific variation in mitochondrial DNA of North American cervids. Journal of Mammology 73:70–82.

Cronin, M. A., S. P. Haskell, and W. B. Ballard. 2003a. The frequency of antlerless female caribou and reindeer in Alaska. Rangifer 23:67–70.

Cronin, M. A., J. C. Patton, N. Balmysheva, and M. D. MacNeil. 2003b. Genetic variation in caribou and reindeer (*Rangifer tarandus*). Animal Genetics 34:33–41.

Cronin, M. A., L. Renecker, B. J. Pierson, and J. C. Patton. 1995. Genetic variation in domestic reindeer and wild caribou in Alaska. Animal Genetics 26:427–434.

Cronin, M. A., R. Shideler, J. Hechtel, C. Strobeck, and D. Paetkau. 1999. Genetic relationships of grizzly bears in the Prudhoe Bay region of Alaska: inference from microsatellite DNA, mitochondrial DNA, and field observations. Journal of Heredity 90:622–628.

El Mousadik, A., and R. J. Petit. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic of Morocco. Theoretical and Applied Genetics 92:832–839.

Engel, S. R., R. A. Linn, J. F. Taylor, and S. K. Davis. 1996. Conservation of microsatellite loci across species of artiodactyls: implications for population studies. Journal of Mammalogy 77: 504–518.

Flagstad, O., and K. H. Røed. 2003. Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. Evolution 57:658–670.

Fries, R., A. Eggen, and J. E. Womack. 1993. The bovine genome map. Mammalian Genome 4:405–428.

Geist, V. 1987. On speciation in Ice Age mammals, with special reference to cervids and caprids. Canadian Journal of Zoology 65: 1067–1084.

Geist, V. 1998. Deer of the world: their evolution, behavior, and ecology. Stackpole Books, Mechanicsburg, Pennsylvania.

Goudet, J. 1995. FSTAT (version 1.2): a computer program to calculate *F*-statistics. Journal of Heredity 86:485–486.

Gravlund, P., M. Meldgaard, S. Pääbo, and P. Arctander. 1998. Polyphyletic origin of the small-bodied, high-arctic subspecies of tundra reindeer (*Rangifer tarandus*). Molecular Phylogenetics and Evolution 10:151–159.

Jukes, T. H., and C. R. Cantor. 1969. Evolution of protein molecules. Pp. 21–132 in Mammalian protein metabolism (H. N. Munro, ed.) Academic Press, New York.

Klein, D. R., M. Meldgaard, and S. G. Fancy. 1987. Factors determining leg length in *Rangifer tarandus*. Journal of Mammalogy 68:642–655.

Kumar, S., K. Tamura, and N. Nei. 1993. MEGA: molecular evolutionary genetics analysis. Pennsylvania State University, University Park.

MacNeil, M. D., and M. D. Grosz. 2002. Genome-wide scans for QTL affecting carcass traits in Hereford × composite double backcross populations. Journal of Animal Science 80:2316–2324.

Mayr, E. 1963. Populations, species, and evolution. Harvard University Press, Cambridge, Massachusetts.

Olsaker, I., and K. H. Røed. 1990. The major histocompatibility complex of reindeer. Rangifer 3:369–372.

Park, S. D. E. 2001. Trypanotolerance in West African cattle and the population genetic effects of selection. Ph.D. dissertation, University of Dublin, Dublin, Ireland.

Petit, R., A. El Mousadik, and O. Pons. 1998. Identifying population conservation on the basis of genetic markers. Conservation Biology 12:844–855.

Raymond, M., and F. Rousset. 1995a. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Raymond, M., and F. Rousset. 1995b. An exact test for population differentiation. Evolution 49:1280–1283.

Reimers, E. 1993. Antlerless females among reindeer and caribou. Canadian Journal of Zoology 71:1319–1325.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 248–249.

Røed, K. H., M. A. D. Ferguson, M. Crête, and T. A. Bergerud. 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 L. Midthjell. 1998. Microsatellites in reindeer, *Rangifer tarandus*, and their use in other cervids. Molecular Ecology 7:1771–1788.

Røed, K. H., and K. R. Whitten. 1986. Transferrin variation and evolution of Alaskan reindeer and caribou, *Rangifer tarandus* L. Rangifer 1:247–251.

Saitou, N., and M. Nei. 1987. The nieghbor-joining method: a new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4:406–425.

Skoog, R. O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. dissertation, University of California, Berkeley.

SLATE, J., D. W. COLTMAN, S. J. GOODMAN, I. MACLEAN, J. L. PEMBERTON, AND J. L. WILLIAMS. 1998. Bovine microsatellite loci are highly conserved in red deer (*Cervus elaphus*), sika deer (*Cervus nippon*) and Soay sheep (*Ovis aries*). Animal Genetics 29:307–315.

SLATKIN, M. 1987. Gene flow and the geographic structure of natural populations. Science 236:787–792.

SNEATH, P. H., AND R. R. SOKAL. 1973. Numerical taxonomy: the principles and practice of numerical classification. W. H. Freeman & Company, San Francisco, California.

STORSET, A., B. OSAISEN, M. WIKA, AND R. BJARGHOV. 1978. Genetic markers in the Spitsbergen reindeer. Hereditas 88:113–115.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS-1: a FORTRAN program for comprehensive analysis of electrophoretic data in population genetics and systematics. Journal of Heredity 72:281–283.

TALBOT, J., J. HAIGH, AND Y. PLANTE. 1996. A parentage evaluation test in North American elk (wapiti) using microsatellites of ovine and bovine origin. Animal Genetics 27:117–119.

WEIR, B. S., AND C. C. COCKERHAM. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370.

WHITTEN, K. R., AND R. D. CAMERON. 1983. Movements of collared caribou, *Rangifer tarandus*, in relation to petroleum development on the Arctic Slope of Alaska. Canadian Field-Naturalist 97: 143–146.

WILSON, G. A., C. STROBECK, L. WU, AND J. W. COFFIN. 1997. Characterization of microsatellite loci in caribou *Rangifer tarandus*, and their use in other artiodactyls. Molecular Ecology 6:697–699.

WRIGHT, S. 1969. Evolution and genetics of populations. The theory of gene frequencies. Univerisity of Chicago Press, Chicago, Illinois. Volume 2.

ZITTLAU, K., J. COFFIN, R. FARNELL, G. KUZYK, AND C. STROBECK. 2000. Genetic relationships of three Yukon caribou herds determined by DNA typing. Rangifer Special Issue 12:59–62.

Submitted 17 March 2004. Accepted 23 August 2004.

Associate Editor was Robert D. Bradley.