

Genetic variation in caribou and reindeer (*Rangifer tarandus*)

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Summary

Genetic variation at seven microsatellite DNA loci was quantified in 19 herds of wild caribou and domestic reindeer (*Rangifer tarandus*) from North America, Scandinavia and Russia. There is an average of 2.0–6.6 alleles per locus and observed individual heterozygosity of 0.33–0.50 in most herds. A herd on Svalbard Island, Scandinavia, is an exception, with relatively few alleles and low heterozygosity. The Central Arctic, Western Arctic and Porcupine River caribou herds in Alaska have similar allele frequencies and comprise one breeding population. Domestic reindeer in Alaska originated from transplants from Siberia, Russia, more than 100 years ago. Reindeer in Alaska and Siberia have different allele frequencies at several loci, but a relatively low level of genetic differentiation. Wild caribou and domestic reindeer in Alaska have significantly different allele frequencies at the seven loci, indicating that gene flow between reindeer and caribou in Alaska has been limited.

Keywords caribou, genetic variation, microsatellite DNA, *Rangifer*, reindeer.

Introduction

Caribou and reindeer (*Rangifer tarandus*) occur across arctic and subarctic North America and Eurasia in wild and domestic populations. In North America, native wild animals are referred to as caribou, and domestic animals, originating from European and Asian stock, are referred to as reindeer. In Eurasia, both wild and domestic *Rangifer* are referred to as reindeer. Several subspecies of reindeer and caribou are recognized (Bergerud 2000), although they are not necessarily monophyletic groups (Cronin 1992; Gravlund *et al.* 1998).

There is considerable natural variation in phenotypic traits among herds of caribou and reindeer. For example, both sexes of *Rangifer* have antlers, but the frequency of antlered and antlerless females varies considerably among herds (Reimers 1993). Other morphological (e.g. body size, proportions, and coloration) and physiological (e.g. timing of

reproduction and parturition) traits also vary among herds (Klein 1980; Klein *et al.* 1987; Bergerud 2000). Caribou are generally larger, have longer legs, are more wary and difficult to handle, and may breed 2–4 weeks later than reindeer (Klein 1980). The environmental and genetic components of these phenotypic differences have not been quantified, although they are probably due in part to local adaptations in wild herds, and selection in domestic herds.

There is interest in the relationship between caribou and reindeer because of the potential influence of domestic stock on the fitness of wild populations and the potential for wild caribou to contribute to the performance of domestic herds. Domestic reindeer occur in either confined herds or free-ranging herds. In western Alaska, for example, reindeer occur on large unfenced ranges where large numbers of reindeer have joined wild herds. There has also been deliberate cross-breeding of wild caribou with domestic reindeer in Alaska. Although there has been ample opportunity for interbreeding, there has apparently been little genetic influence of reindeer on wild caribou in Alaska (Klein 1980; Røed & Whitten 1986; Cronin *et al.* 1995).

There is also interest in the relationship among wild herds for assessment of the effect of immigration and emigration on demography and management (Cronin *et al.* 1998;

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Bergerud 2000). Wild caribou occur in herds that range in size from a few hundred to hundreds of thousands of animals. The numbers of animals in herds may fluctuate dramatically and there may be varying levels of interherd movements and gene flow (Skoog 1968; Bergerud *et al.* 1984; Cronin *et al.* 1998).

The genetic relationships among caribou and reindeer herds have been previously assessed with molecular markers, including transferrin and other proteins (Storset *et al.* 1978; Baccus *et al.* 1983; Røed & Whitten 1986; Røed *et al.* 1991), mitochondrial DNA (mtDNA; Cronin 1992; Cronin *et al.* 1995; Gravlund *et al.* 1998), nuclear genes (Olsaker & Røed 1990; Cronin *et al.* 1995), and microsatellite DNA (Engel *et al.* 1996; Wilson *et al.* 1997; Røed & Midthjell 1998; Zittlau *et al.* 2000). These studies have shown that caribou and reindeer generally have high levels of genetic variation and differentiation among herds.

In a previous assessment, we quantified the differentiation of domestic reindeer and wild caribou in Alaska at two nuclear loci (*CSN10* and a *DQA* locus of the Major Histocompatibility Complex), and the D-loop of mtDNA (Cronin *et al.* 1995). Most alleles for each locus occurred in both caribou and reindeer, although allele frequencies indicated that gene flow between caribou and reindeer in Alaska is limited. In this 1995 study, only Alaska herds were compared. Reindeer in Alaska originated from transplants from Siberia, Russia, in the 1890s, and the extent of genetic differentiation between the Russian and Alaskan reindeer after 100 years of separation has not been quantified. This is of interest because of the potential for hybridization, genetic drift, and selection to have altered the genetic makeup of the Alaskan herds after more than 100 years of domestication and interaction with wild caribou. Cronin *et al.* (1995) also compared several herds of wild caribou, but small sample sizes precluded conclusions about the relationships among herds. Our objective in this paper is to quantify genetic differentiation of wild caribou and domestic reindeer in Alaska and Siberia, Russia, and we include herds from other areas for a broader geographical perspective. We used microsatellite DNA markers from cattle gene maps, as in other studies of genetic variation in cervids (Engel *et al.* 1996; Talbot *et al.* 1996; Slate *et al.* 1998; Cronin *et al.* 2001).

Materials and methods

Blood and muscle samples were obtained from 19 herds of caribou and reindeer (Table 1). Caribou samples included arctic Alaska (Teshekpuk Lake, Central Arctic, Western Arctic and Porcupine River) and Canadian (Alberta, Labrador, Newfoundland, North-west Territories, Baffin Island and Victoria Island) herds. Reindeer samples included

Table 1 Measures of genetic variation of caribou and reindeer herds for seven microsatellite loci.

Population	<i>N</i>	<i>A</i>	<i>H_o</i>	<i>H_e</i>	<i>P</i>
Alaskan caribou					
Teshekpuk Lake Herd	3	2.6	0.476	0.514	71.4
Central Arctic Herd	54	6.6	0.417	0.477	71.4
Western Arctic Herd	14	4.4	0.432	0.508	71.4
Porcupine Caribou Herd	58	6.6	0.480	0.495	71.4
Canadian caribou					
Alberta	3	2.1	0.381	0.448	71.4
Labrador	10	3	0.452	0.436	85.7
Newfoundland	10	2.4	0.471	0.459	100.0
North-west Territory	4	3.4	0.500	0.536	71.4
Baffin Island	6	3	0.405	0.435	71.4
Victoria Island	19	5	0.504	0.519	71.4
Alaskan reindeer					
Hagemeister Island	19	3.1	0.496	0.477	85.7
Tom Gray Herd	23	3.9	0.429	0.492	85.7
Nunivak Island	15	3.3	0.400	0.434	71.4
Eurasian reindeer					
Pevek, Russia	3	2	0.333	0.448	71.4
Wrangel Island, Russia	5	3	0.486	0.510	71.4
Severoevensk, Russia	43	4	0.409	0.476	85.7
Sweden	1	1.7	0.714	0.714	71.4
Norway	11	3	0.416	0.446	71.4
Svalbard Island	7	1.3	0.041	0.041	28.6

N = sample size, *A* = average number of alleles/locus, *H_o* = observed individual heterozygosity, *H_e* = expected individual heterozygosity and *P* = percentage of polymorphic loci.

domestic animals from Alaska (Hagemeister Island, Tom Gray Seward Peninsula herd and Nunivak Island), Siberia, Russia (Wrangel Island, Pevek and Severoevensk), Sweden, Norway and Svalbard Island.

Deoxyribonucleic acid was extracted from tissues with standard methods (Cronin *et al.* 1995). Genotypes at seven microsatellite loci were determined with polymerase chain reaction (PCR) using primers developed in cattle (Table 2).

The PCR reactions (15 µl) contained 5–50 ng DNA in 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 2.5 mM MgCl₂, 0.2 mM of each dNTP, 2 µM of each of the two primers, and 0.45 units of AmpliTaq™ DNA polymerase (Perkin Elmer, Norwalk, CT, USA). Reactions were heated to 95 °C for 5 min followed by 38 cycles of amplification. Each cycle consisted of 45 s at 95 °C, 30 s at 54 °C for *CSN10* and *IGF1* or 58 °C for the other loci, and 1 min at 70 °C. A cocktail of all seven PCR products was run simultaneously using the 400HD Rox standard (ABI, Foster City, CA, USA) on gels formed with Long Ranger Singel™ packs (Bio-Whittaker Molecular Applications, Rockland, ME, USA) on an ABI 377 autosequencer. Genotypes were determined and data tables created using ABI Genescan 3.1 and Genotyper 1.1.1 software packages.

Table 2 Bovine microsatellite loci, PCR primers and bovine chromosomes analysed in caribou and reindeer.

Locus	Primer sequence	Bovine chromosome	Reference
<i>BM6438</i>	Forward: TTGAGCACAGACACAGACTGG Reverse: ACTGAATGCCTCCTTTGTGC	1	Bishop <i>et al.</i> (1994)
<i>BMC1009</i>	Forward: GCACCAGCAGAGAGGACATT Reverse: ACCGGCTATTGTCCATCTTG	5	Bishop <i>et al.</i> (1994)
<i>IGF1</i> Insulin-like growth factor 1	Forward: GAGGGTATTGCTAGCCAGCTG Reverse: CATATTTTCTGCATAACTTGAACCT	5	Kirkpatrick (1992)
<i>CRH</i> Corticotropin releasing hormone	Forward: CTCGCTCACCTGCAGAAGCACC Reverse: GCTGAGCAGCCGTCTAAGTTGC	14	Moore <i>et al.</i> (1992), Fries <i>et al.</i> (1993)
<i>BM848</i>	Forward: TGGTTGGAAGGAAAACCTGG Reverse: CCTCTGCTCCTCAAGACAC	15	Bishop <i>et al.</i> (1994)
<i>CSN10</i> Casein, Kappa	Forward: ATGCACCCTTAACCTAATCCC Reverse: GCACTTTATAAGCACACAGC	6	Bishop <i>et al.</i> (1994)
<i>RBP3</i> Retinol-binding protein 3, interstitial	Forward: TGTATGATCACCTTCTATGCTTC Reverse: GCTTTAGGTAATCATCAGATAGC	28	Cronin <i>et al.</i> (2001), Moore <i>et al.</i> (1992), Fries <i>et al.</i> (1993)

We quantified genetic variation within herds, including the average number of alleles per locus, observed heterozygosity, and expected heterozygosity with the BIOSYS computer program (Swofford & Selander 1981). We used the GENEPOP program (Raymond & Rousset 1995) to test among loci for linkage disequilibrium, Hardy–Weinberg equilibrium, and differentiation of allele frequencies among herds with pairwise tests of heterogeneity. We also calculated genetic distances (Cavalli-Sforza & Edwards 1967 chord distance) between each pair of herds with sample sizes >5. The genetic distances were used to construct a dendrogram with the neighbour-joining method (Saitou & Nei 1987), using the jumble option of the PHYLIP computer program (Felsenstein 1995). The jumble option randomizes the input order of the herds into the analysis.

Results

In our samples of caribou and reindeer there are two alleles at two loci (*BMC1009*, *CSN10*), five alleles at two loci (*IGF1*, *RBP3*), and eight (*BM6438*), 16 (*CRH*), and 19 (*BM848*) alleles at one locus each (Table 3). Most alleles occurred across herds and geographical regions, but several alleles were restricted to Alaskan caribou: alleles 246, 248, and 262 for locus *BM6438*; alleles 359, 379, 383, 389 and 401 for locus *BM848*; and alleles 253, 257, 259 and 263 for locus *CRH*. In addition, allele 355 for locus *BM848* was restricted to the Norway herd, allele 188 for locus *CSN10* was restricted to the Labrador and Newfoundland herds, and allele 361 for locus *BM848* was restricted to the Victoria Island herd (Table 3).

There is considerable allelic variation in all of the herds except the Svalbard Island reindeer (Table 1). Excluding Svalbard, the percentage of polymorphic loci ranged from

71 to 100%, the average number of alleles per locus ranged from 2.0 to 6.6, and observed heterozygosity ranged from 0.333 to 0.500. The Alaskan caribou had the highest number of alleles/locus (6.6) and relatively high heterozygosity (0.417–0.480). The Alaskan and Russian reindeer had fewer alleles, but similar levels of heterozygosity (0.333–0.496). The Svalbard herd had a relatively low level of variation, particularly heterozygosity, and was fixed for one allele for five of the seven loci. There is a positive relationship between sample size and the numbers of alleles detected ($R^2 = 0.75$, $P = 0.000002$) which may explain the relatively high number of alleles in the Alaskan caribou herds. The numbers of alleles in herds with small sample sizes are probably underestimates and there may be other rare alleles that we did not detect.

Six tests showed significant deviations from Hardy–Weinberg equilibrium ($P < 0.05$): *BM6438* locus for the Severoevensk herd, *CRH* locus for the Western Arctic Herd, and *BM848* locus for the Central Arctic, Tom Gray, Nuni-vak and Severoevensk herds. In all these cases there were fewer observed heterozygotes than expected. All other herd/locus tests were in Hardy–Weinberg equilibrium. Tests of linkage disequilibrium across all herds showed a significant relationship between only the *CRH* and *RBP3* loci ($P = 0.0207$). The *BMC1009* and *IGF1* loci had a relationship that was close to the 0.05 level of significance ($P = 0.0610$). These loci are on the same chromosome in the cattle genome (*BTAS*) and this linkage may also occur in *Rangifer* genome.

The pairwise tests of heterogeneity between the three Alaskan caribou herds with adequate sample sizes (Central Arctic, Western Arctic and Porcupine River) showed no significant differences in allele frequencies between herds for all seven loci combined. Comparisons of individual loci

Table 4 Cavalli-Sforza & Edwards (1967) chord genetic distances between caribou and reindeer herds.

Herd	1	2	3	4	5	6	7	8	9	10	11	12	13
Central Arctic	*****												
Porcupine River	0.125	*****											
Labrador	0.346	0.354	*****										
Newfoundland	0.383	0.396	0.439	*****									
Hagemeister I.	0.329	0.354	0.420	0.344	*****								
Tom Gray Herd	0.281	0.287	0.382	0.364	0.195	*****							
Nunivak I.	0.281	0.314	0.383	0.351	0.176	0.188	*****						
Severoevensk	0.323	0.344	0.475	0.374	0.266	0.217	0.232	*****					
Norway	0.324	0.306	0.400	0.409	0.429	0.378	0.395	0.427	*****				
Svalbard	0.493	0.487	0.592	0.457	0.472	0.513	0.446	0.480	0.493	*****			
Baffin I	0.305	0.312	0.412	0.480	0.388	0.349	0.359	0.398	0.334	0.544	*****		
Western Arctic	0.209	0.213	0.393	0.433	0.399	0.343	0.361	0.399	0.344	0.515	0.375	*****	
Victoria I	0.213	0.214	0.404	0.416	0.364	0.274	0.334	0.310	0.348	0.523	0.301	0.307	*****

between the Alaskan caribou herds indicate a significant difference in allele frequency for only one locus (*IGF1*) between the Western Arctic and Porcupine River herds. There were no significant differences in allele frequency for all seven loci combined, or for any individual locus, between the three Alaskan reindeer herds. Comparisons of the Alaskan caribou with the Alaskan reindeer herds showed highly significant ($P < 0.0001$) allele frequency differences for all seven loci combined, and for 35 of 54 (65%) of the pairwise herd comparisons of individual loci. The Alaskan and Russian reindeer herds also showed highly significant allele frequency differences for all seven loci combined and for 11 of 18 (61%) of the pairwise comparisons of individual loci.

The genetic distances between herds (Table 4) and the neighbour-joining dendrogram resulting from them (Fig. 1) show several important divisions. First, the three Arctic Alaskan caribou herds cluster together, within a larger cluster containing the Victoria Island Arctic Canadian caribou herd. Secondly, the eastern Canadian caribou (Newfoundland and Labrador) occur in separate clusters from the other caribou. Thirdly, the Alaskan and Russian reindeer occur in a cluster, separate from caribou and Scandinavian reindeer. The mean of the pairwise herd genetic distances, D (SE), reflect these clusters: between Alaskan caribou herds $D = 0.1823$ (0.0497); between Alaskan reindeer herds $D = 0.1863$ (0.0096); between Alaskan and Russian reindeer herds $D = 0.2383$ (0.0251); between Alaskan reindeer and Alaskan caribou herds $D = 0.3277$ (0.0408); and between Alaskan caribou and Russian reindeer herds $D = 0.3553$ (0.0392). Although the Alaskan and Russian reindeer have significantly different allele frequencies for several loci, the overall genetic distance is lower than the distance between the Alaskan reindeer and Alaskan caribou.

Discussion

There is considerable allelic diversity and heterozygosity in *Rangifer* at the seven loci we studied, as there is at other microsatellite loci (Engel *et al.* 1996; Wilson *et al.* 1997; Røed & Midthjell 1998; Zittlau *et al.* 2000). We observed a positive relationship between sample size and the average number of alleles/locus in a herd suggesting that estimates of genetic variation should include adequate sampling (approximately $n = 50$ /herd) to detect rare alleles.

Assessments of genetic relationships between populations often include the assumptions that genetic drift and migration are the primary factors affecting allele frequencies, and all alleles are selectively neutral. However, some of the loci we analysed are linked to functional genes in the cattle genome, and it is possible they are also linked to the same loci in *Rangifer*. The tests for linkage disequilibrium indicate that the *BMC1009* and *IGF1* loci may be linked on the same chromosome in reindeer and caribou, as in cattle. Of the loci we analysed, *BM6438* is linked to the polled locus (Schmutz *et al.* 1995), and *CSN10* and *IGF1* have been associated with performance traits in cattle (Moody *et al.* 1996). Given these considerations, there may be selective constraints on linked loci that influence the microsatellite allele frequencies, although if selection acts equally on a locus in each population, it will not affect the relationships inferred from allele frequencies (Cavalli-Sforza & Edwards 1967). The clustering of the Russian/Alaskan reindeer, separate from the Alaskan caribou (Fig. 1), may reflect both genetic drift and selection on the loci we studied, but we have no data relating genotypes and performance traits with which to assess this.

The same microsatellite alleles occur across the range of *Rangifer* suggesting there are no major phylogenetic divisions within the species, although there is differentiation of

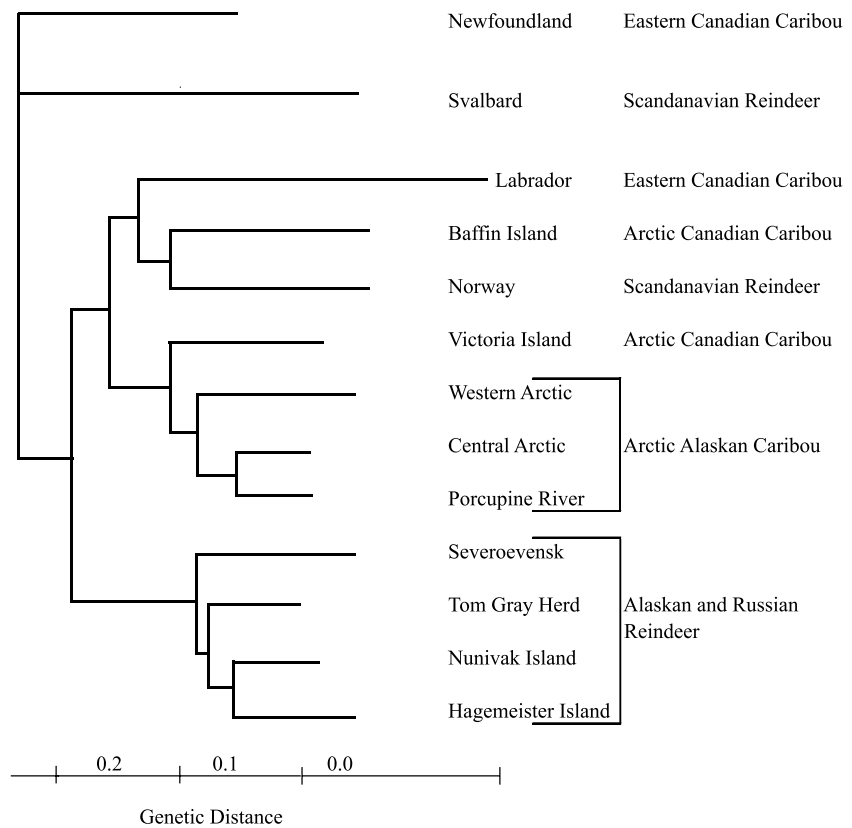


Figure 1 Dendrogram showing the relationships among caribou and reindeer herds. The dendrogram was constructed with the neighbour-joining method (Saitou & Nei 1987) using genetic distances from seven micro-satellite loci.

allele frequencies between herds of caribou and reindeer. Previous studies suggest the genetic relationships of caribou and reindeer herds may reflect isolation in different regions during glacial periods, and genetic drift and gene flow after the glacial periods in prehistoric populations (Røed *et al.* 1991; Cronin 1992; Gravlund *et al.* 1998). Domestication by man has subsequently resulted in transplantations and selection of reindeer that has affected the distribution of genetic variation in the species. Because our sample sizes, sampling locations and number of loci are limited, the relationships among herds inferred from our data should be considered tentative, although they are in general agreement with previous analyses. For example, we observed different allele frequencies between Newfoundland and Labrador, a unique *CSN10* allele only in Newfoundland and Labrador, and different allele frequencies between these eastern Canadian herds and Alaska, as did Røed *et al.* (1991) who studied serum transferrin protein polymorphisms and Cronin (1992) who studied mtDNA variation. We also observed fixed alleles and different frequencies in Svalbard reindeer compared with Norway reindeer, as did Storset *et al.* (1978) for transferrin.

The Central Arctic, Western Arctic and Porcupine River Alaskan caribou herds are not genetically differentiated from each other (Fig. 1). Although studies of marked

females indicate that the herds are generally segregated on calving ranges (Whitten & Cameron 1983; Cameron *et al.* 1986), the herds frequently mix on breeding and winter ranges (Bergerud *et al.* 1984; Carruthers *et al.* 1987; Bergerud 2000). The genetic data are consistent with field observations that suggest there is interbreeding of animals from different calving ranges (i.e. herds) and that the herds collectively comprise one breeding population (Skoog 1968; Cronin *et al.* 1998). Male caribou may move more extensively than females, and it is probable that male-mediated gene flow also maintains genetic homogeneity among the herds. From a management standpoint, herds can be considered as geographic management units, defined by calving area, and the breeding population consists of animals from different calving herds that have overlapping fall and winter ranges. The situation is different in the southern Yukon Territory, Canada, where caribou herds are segregated on winter ranges and are genetically differentiated (Zittlau *et al.* 2000).

The microsatellite loci we studied have significantly different allele frequencies in Alaskan reindeer and caribou. This pattern was also observed in previous analyses of mtDNA and two nuclear loci (Cronin *et al.* 1995) and transferrin protein polymorphisms (Røed & Whitten 1986). Our data suggest that there may have been a low level of

introgression, but the two forms have maintained different allele frequencies over the 110 years since the introduction of reindeer to Alaska. These observations are consistent with those of Klein (1980) that gene flow between wild caribou and domestic Alaskan reindeer has been limited. It is possible that there has been little interbreeding, or that there has been interbreeding but selection against the hybrid progeny resulted in little introgression in either direction. Reindeer have smaller size, less wariness of predators, different foraging habits, a breeding season beginning 2–4 weeks earlier in the fall, and a lower propensity to migrate than caribou. These characteristics could result in relatively low fitness of reindeer that join wild caribou herds and limit successful interbreeding. In domestic reindeer herds there has been deliberate crossbreeding with wild caribou resulting in increased calf weights, but the loss of traits selected previously, such as docility, may have negative consequences (Klein 1980).

Our data also show that Alaskan and Siberian reindeer have different allele frequencies at several loci, but the genetic distances are small enough that they cluster together in Fig. 1. The Alaskan reindeer originated from Siberian stock, and although we do not know if the Siberian herds we sampled descended from the same stock that was brought to Alaska, the small genetic distances may reflect common ancestry. Analysis of additional loci and comparisons of morphological and physiological phenotypic traits will improve our understanding of the relationship between caribou and reindeer from Siberia and Alaska.

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