

Genetic variation in transferrin as a predictor for differentiation and evolution of caribou from eastern Canada

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Abstract: Polycrylamide gel electrophoresis was used to analyse transferrin variation in caribou populations from Manitoba, Ontario, Québec/Labrador, and from Baffin Island, Northwest Territories in eastern Canada. The transferrin allele frequencies in these populations were compared with those previously reported for Canadian barren-ground caribou, *Rangifer tarandus groenlandicus*, Alaska caribou, *R.t. granti*, Peary caribou, *R.t. pearyi*, Svalbard reindeer, *R.t. platyrhynchus*, and Eurasian tundra reindeer, *R.t. tarandus*. A total of twenty different alleles was detected in the analysed material, considerable genetic heterogeneity being detected among regions. Three alleles that were relatively common in caribou from Ontario, Manitoba and Québec/Labrador, were not present in *R.t. granti*, *R.t. pearyi*, *R.t. tarandus* or *R.t. platyrhynchus*, and present only at very low frequencies in *R.t. groenlandicus*. These findings, together with genetic identity analyses, suggest that the caribou in Manitoba, Ontario, and Québec/Labrador are mainly of the *R.t. caribou* type, and that little interbreeding has occurred with other subspecies. The large genetic distance in the transferrin locus between *R.t. caribou* and other subspecies of reindeer/caribou suggests that, during the Wisconsin glaciation the ancestral populations of *R.t. caribou* survived in a refugium different from that of the ancestral populations of the other subspecies. Significant genetic differences between Baffin Island caribou and all other populations were mainly due to the presence of one allele that was in high frequency in Baffin Island caribou, but that was absent, or present in very low frequencies, in all other reindeer/caribou populations. The genetic differences between Baffin Island caribou and the other subspecies were greater than the differences between several of the currently recognized subspecies.

Rangifer, 11 (2): 65–74

Key words: caribou, transferrins, polymorphism, evolution, genetics, types of reindeer, genetic variability.

Introduction

Reindeer and caribou (*Rangifer tarandus*) are distributed throughout the northern part of the Holarctic region. Within this vast area several subspecies have been described. According to the taxonomic study of Banfield (1961), subspecies of reindeer and

caribou should be divided into two groups: tundra caribou/reindeer (*Cyclocornis*) and forest or woodland caribou/reindeer (*Compressicornis*). Within the first group, Banfield (1961) recognized two subspecies, the continental tundra forms and the Arctic island forms, thus giving three series of approxima-

tely the same level of differentiation. Woodland caribou/reindeer include the Eurasian forest reindeer, *R.t. fennicus*, and the American woodland caribou, *R.t. caribou*. Continental tundra forms include the Eurasian tundra reindeer, *R.t. tarandus*, the Alaska caribou, *R.t. granti*, and the Canadian barren-ground caribou, *R.t. groenlandicus*, while the Arctic island forms include the Svalbard reindeer, *R.t. platyrhynchus*, and the Peary caribou, *R.t. pearyi* (see Fig. 1 for the distribution of the different subspecies).

From morphological and historical data, Banfield (1961) suggested that the three series of reindeer and caribou originated in three or more isolated refugia during the last Wisconsin glaciation. The continental tundra forms originated in the Beringia refugium in Alaska-Yukon and possibly in northern Europe; the Arctic Island forms, in tundra refugia north of the continental ice-sheets in the Queen Elizabeth Islands of Arctic Canada or in Peary Land in northern Greenland, and the forest or woodland forms, in temperate refugia south of the continental ice-sheets.

One approach to the study of phylogenetic relationships is to investigate the frequency distribution of alleles at polymorphic loci. In reindeer and caribou, the serum transferrin locus has been particularly valuable in studies of genetic relationships because it possesses a high degree of genetic variation (Brænd, 1964; Zhurkevich and Fomicheva, 1976; Shubin, 1977; Storset *et al.* 1978; Soldal and Staaland, 1980; Shubin and Matyukov, 1982; Shubin and Ionova, 1984; Røed, 1985a; 1985b; 1986; Røed *et al.* 1985; 1986; 1987; Røed and Whitten, 1986; Røed and Thomas, 1990). In analysing transferrin variation in different subspecies of the tundra reindeer/caribou group, Røed and Whitten (1986) reported a major dichotomy in the allele distribution between the two continental tundra forms, Alaska caribou and Eurasian reindeer, on the one hand, and the two Arctic Island forms, Peary caribou and Svalbard reindeer, on the other, adding support to the hypothesis that these forms have evolved in different isolated refugia. Recent studies on transferrin allele frequency in the Canadian barren-ground caribou from mainland Northwest Territories (N.W.T.) revealed a relatively large amount of genetic variation and genetic differentiation from both the Alaska caribou and the Peary caribou (Røed and Thomas, 1990).

In the present study, we present transferrin allele frequencies of populations of *R.t. caribou* from regions of Ontario and Manitoba, as well as from north-

ern Québec/Labrador. Banfield (1961) classified caribou in these regions as woodland caribou, but suggested that the caribou in Québec/Labrador appeared to represent a race with characteristics of both the woodland and the barren-ground caribou. Transferrin allele frequencies in caribou from Baffin Island, N.W.T., are also presented. These caribou are usually recognized as Canadian barren-ground caribou (Banfield, 1961), although, from a geographical point of view, they are relatively isolated from the main range of this subspecies. The main objectives of the present study were to use transferrin allele frequencies 1) to test the extent to which the caribou in northern Québec/Labrador are distinct from the woodland and barren-ground caribou, 2) to assess whether the degree of genetic differentiation between woodland caribou and tundra reindeer/caribou supports the hypothesis of a different origin of these forms, and 3) to assess the degree of genetic differentiation between Baffin Island caribou and barren-ground caribou from mainland N.W.T.

Material and methods

The main distribution of the different subspecies of reindeer and caribou in North America is shown in Fig. 2, which also shows the locations of the sampling areas in the present study. Blood samples were obtained from a total of 469 caribou in Canada. From southern Baffin Island 117 caribou were sampled north and east of Frobisher Bay during the period 1983–1986. These caribou represent resident and migratory members of the South Baffin caribou population (Ferguson, 1989). Reliable and complete surveys of this population are lacking. Within the local Frobisher Bay area, caribou number at least 9000 animals based on incomplete 1982–84 surveys (Ferguson, unpublished data). From northern Labrador and northeastern Québec, 131 caribou were sampled from the George River herd during 1980–1988. This herd was estimated to be at least 730 000 in autumn 1988 (Hearn *et al.* 1990) and is considered to represent the world's largest caribou herd (Williams and Heard, 1986). A further 22 caribou were sampled in 1988 from the Leaf River herd, which is distributed in northwestern Québec. This herd exceeded 100 000 animals in 1986 (Crête *et al.* 1990). From the Gaspé Peninsula in eastern Québec south of the St. Lawrence River, 13 caribou were sampled in 1987. This herd, which numbers about 200 animals (Crête, unpublished data), is classified as endangered because it is the last wild caribou population still surviving east of the St. Lawrence Ri-

ver, excluding Newfoundland, and is considered to have been isolated from other populations of caribou for a long time. From Brunette Island off Newfoundland, 12 caribou were sampled in 1980 from a total population of about 100 individuals. This population originated from seven individuals which

were introduced to Brunette Island from Newfoundland in 1964. From Ontario, 161 woodland caribou were sampled from the Slate Islands in Lake Superior. The caribou on these islands number about 250, and movements of animals between the islands and the mainland occur occasionally (Berge-

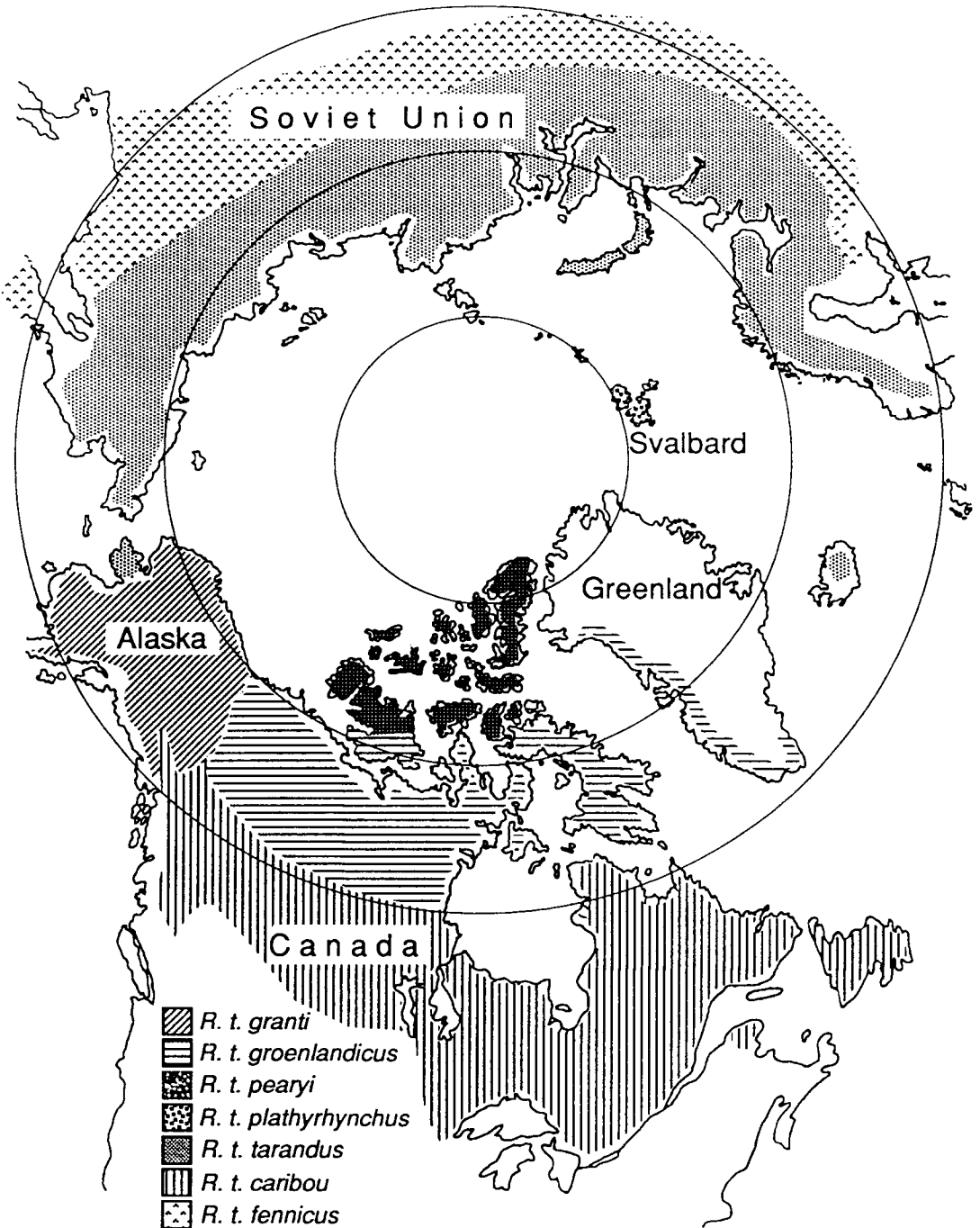


Fig. 1. Main distribution of the different subspecies of reindeer and caribou.

rud, 1980). From eastern Manitoba, 13 woodland caribou were sampled in 1980–1981 near Sasaginnigak Lake (Fig. 2). The woodland caribou in both Ontario and Manitoba are scattered throughout the provinces and number only 10–20 000 animals (Berge-rud, 1980).

Plasma/serum samples were subjected to vertical slab polyacrylamide gel electrophoresis as described by Røed (1985a). The transferrins were made visible by overnight staining with Coomassie Brilliant Blue (Diezel *et al.* 1972). Relative mobilities of transferrin bands were confirmed by re-running samples of approximately equal mobility side by side on the same gel. Reference plasma was from continental Norwegian reindeer, *R.t. tarandus*, (Røed *et al.* 1985a), Svalbard reindeer, *R.t. platyrhynchus* (Røed, 1985b), Peary caribou, *R.t. pearyi*, (Røed *et al.* 1986), Alaska caribou, *R.t. granti*, (Røed and Whitten, 1986), and Canadian barren-ground caribou, *R.t. groenlandicus*, (Røed and Thomas, 1990).

The genetic identity among populations and subspecies was calculated according to Nei (1972).

Results

A total of 20 separate alleles was resolved in the present material. Compared with the reference material, one new allele was detected. This allele coded for a protein with higher mobility than the most anodal reference allele (Tf^{A-2}) and was designated Tf^{A-3} . It was detected in all populations from Ontario, Manitoba and Québec/Labrador, except the Leaf River herd. The two alleles, Tf^{G2} and Tf^{G3} , in the reference material were not satisfactorily separated in the present material, and were therefore combined and expressed as Tf^{G2} . Chisquare tests of goodness of fit to Hardy Weinberg expectations (Sokal and Rohlf, 1969) revealed no significant deviations from expected values in any of the analysed populations.

Table 1 presents the allele frequencies in the caribou populations sampled in this study, together with previously reported values for Canadian barren-ground caribou from the Beverly herd in central N.W.T. (Røed and Thomas, 1990). The pattern of allele frequencies at the transferrin locus revealed considerable genetic heterogeneity among

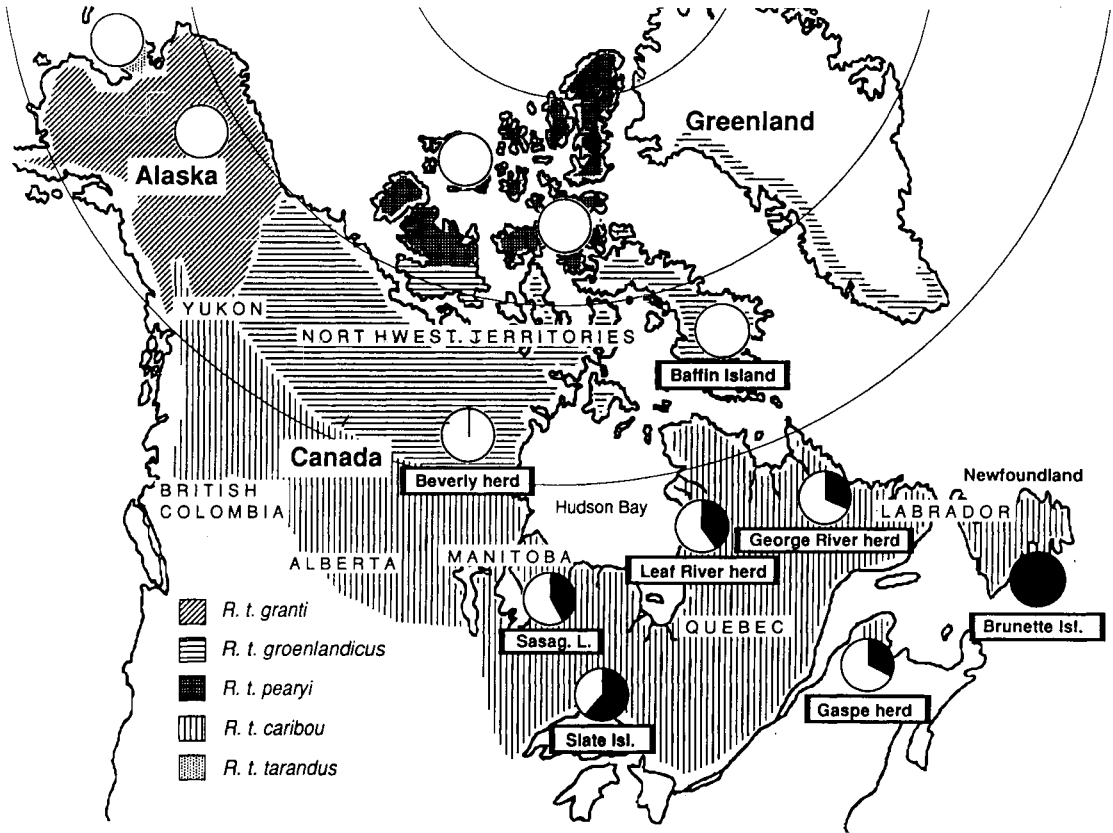


Fig. 2. Main distribution of different subspecies of caribou in North America together with locations of sampling areas given as framed names, and the frequency distribution of pooled Tf^{A-3} , Tf^{A-2} , and Tf^{A-1} alleles given as sections of pies.

caribou populations. Estimates of population heterozygosity were variable, and could be due in part to small sample sizes in some populations. Among Baffin Island caribou the Tf^{L2} allele was the most common allele (p=0.521), while this allele was absent, or present in very low frequencies, in other caribou populations (Table 1), including the Canadian barren-ground caribou from the Beverly herd. A large genetic difference between Baffin Island caribou and the Beverly herd was also indicated by eight alleles found in the Beverly herd which were absent from the Baffin Island samples.

The allele frequencies of caribou from Québec/Labrador, Ontario and Manitoba are strikingly different from those from Baffin Island and the Beverly herd. This is illustrated by the frequency of Tf^{A1} allele which was the most common allele in both Leaf River (p=0.364), Brunette Island (p=0.958), and Slate Islands (p=0.363) populations. The Tf^{A1} allele was the second most common allele

in Georg River caribou (p=0.221), but was absent in Baffin Island and was present in very low frequency in the Beverly herd (p=0.005). Similar difference in allele frequency was found in Tf^I, which was relatively common in both the Baffin Island (p=0.094) and the Beverly (p=0.121) populations, but was absent, or present at very low frequencies, in populations from all other areas.

The allele frequency distribution also revealed considerable genetic heterogeneity among the different populations of *R.t. caribou*. The Tf^{A3} allele was relatively frequent in caribou populations from Gaspé Peninsula (p=0.154), Slate Islands (p=0.174) and Manitoba (p=0.231), but was absent in the Leaf River herd, and was rare in the George River herd (p=0.053). Even between the two geographically close George River and Leaf River herds, the contingency chi-square test for homogeneity among populations revealed statistical differences in the frequency of the Tf^{A1} allele ($X^2=5.14$, $p < 0.05$).

Table 1. Transferrin allele frequencies of caribou in different regions of Canada. N=number of individuals analysed.

Allele	Québec/Labrador				Ontario	Manitoba	N.W.T.	
	George River N=131	Leaf River N=22	Brunette Island N=12	Gaspé herd N=13	Slate Island N=161	Sasag. Lake N=13	Baffin Island N=117	Beverly herd ¹⁾ N=95
A-3	0.053		0.042	0.154	0.174	0.231		
A-2	0.057	0.045		0.192	0.069			0.005
A-1	0.221	0.364	0.958		0.363	0.198		0.005
A	0.038	0.068		0.077	0.003	0.193		0.032
C1	0.019	0.023					0.021	0.063
C2	0.118	0.023		0.577	0.214	0.231	0.026	0.068
E1	0.015	0.023					0.026	0.111
E2							0.004	
G1							0.068	0.047
G2	0.305	0.318			0.127	0.038	0.030	0.116
H1							0.034	0.011
H2	0.103	0.068			0.043	0.038	0.128	0.153
I		0.023					0.094	0.121
J	0.008						0.021	0.037
K1	0.015						0.017	0.032
K2								0.016
L1	0.004				0.003			0.053
L2	0.015					0.077	0.521	0.011
M								0.042
N	0.011	0.045						0.005
O1								0.026
O2	0.015				0.003		0.004	0.032
O3							0.004	0.016

¹⁾ From Røed and Thomas (1990)

The genetic identity between populations was highly variable (Table 2). The two most genetically similar herds were from George River and the Leaf River ($I=0.926$), and the two most genetically different were the caribou from Baffin Island and Brunette Island ($I=0.000$). The Baffin Island population was genetically most similar to the Beverly herd ($I=0.316$). The genetic identity between the herds from northern Québec/Labrador and the caribou from Ontario and Manitoba, was on average greater ($I=0.647$) than the average identity between herds from northern Québec/Labrador and the Beverly herd ($I=0.414$) which in turn was greater than the average identity between the Beverly herd and the populations in Ontario and Manitoba ($I=0.272$).

The transferrin allele frequencies in the Baffin Island population, and in the *R.t. caribou* from all populations from Québec/Labrador, Manitoba and Ontario, are given in Table 3, together with previously reported values for other subspecies of *R. tarandus*. As illustrated in Table 3, the Tf^{1,2} allele was present in high frequency in Baffin Island population, but was not present in *R.t. granti*, *R.t. pearyi*, *R.t. tarandus*, or *R.t. platyrhynchus*. Moreover, the allele frequencies in *R.t. caribou* were highly different from the other recognized subspecies of reindeer/caribou. The three most anodal alleles, Tf^{A-1}, Tf^{A-2}, and Tf^{A-3}, were all relatively common in *R.t. caribou*, being present at a combined frequency of 0.489 in this subspecies, while these alleles were absent in all the other subspecies, except in *R.t. groenlandicus*, where Tf^{A-1} and Tf^{A-2} were present at very low frequencies ($p=0.005$ for each).

The genetic identities were very low when both *R.t. caribou* and Baffin Island caribou were compared with the other subspecies (Table 4). The highest

genetic identity value between *R.t. caribou* and the other subspecies was about $I=0.5$, and between Baffin Isl. caribou and the different subspecies, about $I=0.3$, while all the other subspecies had their highest genetic identity value in the range of $I=0.7-0.9$.

Discussion

This study is based on analysis of a single locus. To characterize the levels of genetic difference between subspecies or populations, the estimate should, however, be based on comparison of allele frequencies from a large number of loci (Nei, 1973). Care should therefore be taken before too farreaching conclusions of biogeographic nature are drawn from the present data. However, a similar pattern as detected in transferrin variation was also detected in other loci when 35 electrophoretically scorable loci were compared in Eurasian and Svalbard reindeer (Røed, 1985b). This, together with presence of so many alleles in the transferrin locus in reindeer and caribou, indicates that analysis of this locus provides information relevant to the evolutionary relationships of caribou and reindeer.

The allele frequency distribution found in this study suggests great genetic heterogeneity in the transferrin locus among different herds of caribou from eastern Canada. Particularly great differences were detected when *R.t. caribou* from Manitoba, Ontario, and Québec/Labrador, and the caribou from Baffin Island were compared with other subspecies of reindeer and caribou. The main contributor to the divergence between *R.t. caribou* and the other subspecies was in the frequency distribution of the three most anodal alleles. These alleles were among the most frequent alleles in samples collected in Manitoba, Ontario, and northern Québec/La-

Table 2. Genetic identities (Nei, 1972) between different Canadian populations of caribou.

Population	<i>R. t. caribou</i>						<i>R.t. groenlandicus</i>	
	George River	Leaf River	Brunette Island	Gaspe	Slate Island	Sasag. Lake	Baffin Island	Beverly
George River	*****							
Leaf River	0.926	*****						
Brunette Island	0.533	0.728	*****					
Gaspe	0.341	0.086	0.011	*****				
Slate Islands	0.806	0.766	0.771	0.539	*****			
Sasag. Lake	0.583	0.475	0.465	0.667	0.797	*****		
Baffin Island	0.149	0.080	0.000	0.042	0.056	0.216	*****	
Beverly	0.543	0.413	0.018	0.233	0.276	0.268	0.316	*****

Table 3. Transferrin allele frequencies in Baffin caribou and in different subspecies of reindeer/caribou.

Allele	Baffin Island	<i>R.t. caribou</i>	<i>R.t.¹⁾ groenlandicus</i>	<i>R.t.²⁾ granti</i>	<i>R.t.³⁾ pearyi</i>	<i>R.t.⁴⁾ tarandus</i>	<i>R.t.⁵⁾ platyrhynchus.</i>
A-3		0.115					
A-2		0.063	0.005				
A-1		0.311	0.005				
A		0.030	0.032	0.027	0.041	0.016	
B				0.013	0.006		
C1	0.021	0.009	0.063	0.085	0.058	0.270	
C2	0.026	0.173	0.068	0.036	0.099	0.038	
C3					0.006		
D						6)	
E1	0.026	0.007	0.111	0.304	0.023	0.307	
E2	0.004			0.036		0.006	
G1	0.068		0.047	0.054		0.046	
G2	0.030	0.193	0.116	0.049	0.297		1.000
G4					0.004		
H1	0.034		0.011	0.013	0.023	0.036	
H1b				0.009			
H2	0.128	0.064	0.153	0.147	0.180	0.090	
I	0.094	0.001	0.121	0.134	0.163	0.130	
J	0.021	0.003	0.037	0.013	0.006		
K1	0.017	0.006	0.032	0.013		0.034	
K2			0.016				
L1		0.003	0.053	0.018	0.041		
L2	0.521	0.009	0.011				
M			0.042	0.040	0.017	0.028	
N		0.007	0.005		0.006		
O1			0.026		0.023		
O2	0.004	0.007	0.032	0.004			
O3	0.004		0.016				
P					0.017		

¹⁾ From Røed and Thomas (1990)

⁴⁾ From Røed (1985a)

²⁾ From Røed and Whitten (1986)

⁵⁾ From Røed (1985b)

³⁾ From Røed et al. (1986)

⁶⁾ Frequency < 0.001

Table 4. Genetic identities (Nei, 1972) between different subspecies of reindeer and caribou and caribou from Baffin Island.

	Baffin Island	<i>R.t. caribou</i>	<i>R.t. groenlandicus</i>	<i>R.t. granti</i>	<i>R.t. pearyi</i>	<i>R.t. tarandus</i>
Baffin island	*****					
<i>R.t. caribou</i>	0.098	*****				
<i>R.t. groenlandicus</i>	0.316	0.391	*****			
<i>R.t. granti</i>	0.225	0.174	0.823	*****		
<i>R.t. pearyi</i>	0.233	0.502	0.842	0.516	*****	
<i>R.t. tarandus</i>	0.175	0.092	0.680	0.886	0.363	*****
<i>R.t. platyrhynchus</i>	0.054	0.447	0.397	0.127	0.728	0.000

brador, while in the other subspecies these alleles were absent, except in *R.t. groenlandicus* (i.e. the Beverly herd) where two of these alleles were present at very low frequencies ($p=0.005$ for each). The almost exclusive presence of certain alleles at high frequencies in *R.t. caribou* and their absence in the other subspecies, indicates that the alleles in question are characteristic for *R.t. caribou*. The allele frequency distribution of serum transferrin should therefore be a suitable genetic marker in studies of evolution and classification of possible intergrades between *R.t. caribou* and other subspecies.

The pooled frequency distribution of the three alleles characteristic for *R.t. caribou* in different caribou populations in North America is given in Fig. 2. As can be seen, the high pooled frequencies of these alleles in caribou from Manitoba, Ontario, the Gaspé Peninsula, and Brunette Island indicate that all these caribou are mainly of the *R.t. caribou* subspecies. Tf^{A-1} and Tf^{A-2}, the only alleles detected in 12 caribou from Brunette Island, indirectly suggest that caribou on Newfoundland, from where the Brunette Island caribou originated, are also mainly of the same subspecies. The genetic identity analysis also shows that northern Québec/Labrador caribou have higher genetic identity with the woodland caribou (*R.t. caribou*) from Ontario and Manitoba than with the barren-ground caribou (*R.t. groenlandicus*) from mainland N.W.T.

Although the present data suggest common origin of present Québec/Labrador caribou and the woodland caribou from Manitoba and Ontario, the data also indicate that some gene exchange may have occurred between caribou from mainland N.W.T. and those from northern Québec/Labrador. The Beverly herd exhibited greater genetic similarity to northern Québec/Labrador caribou than to the woodland caribou from Manitoba and Ontario, and, as many as six alleles were present in both the Beverly herd and in the George River/Leaf River herds without being present in any of the woodland caribou from Ontario and Manitoba. A possible route of genetic exchange may have been across northern Hudson Bay via Southhampton, Coates, and Mansel islands (Banfield, 1961).

The degree of genetic identity in the transferrin locus between *R.t. caribou* and the different subspecies of tundra caribou in North America was generally low compared to that between the different subspecies within the tundra caribou group. Such a pattern provides evidence of a generally pronounced genetic isolation of *R.t. caribou* from the other subspecies, both in recent time and during the past. Several re-

cords of ancient reindeer/caribou occurrences suggest that, at the height of the Wisconsin glaciation, reindeer/caribou were distributed both in a tundra belt across the southern edge of the ice-sheet, and in the unglaciated Beringia refugium in Alaska/Yukon (Banfield, 1961). The magnitude of genetic difference between *R.t. caribou* and the other subspecies could therefore reflect an origin of present *R.t. caribou* from ancestral populations that survived the Wisconsin glaciation in refugia south of the continental ice sheet, whereas the other subspecies originated from ancestral populations that survived north of the ice sheet. Thus, as the ice-barriers retreated during the late Wisconsin period and early Holocene epoch, those caribou from Beringia that colonized the Eurasian tundra region became present Eurasian tundra reindeer, those that colonized the Canadian mainland became present barren-ground caribou, and those that remained in Beringia became present Alaska caribou. The caribou surviving south of the ice-sheet probably colonized the Maritimes Provinces and the Québec/Labrador Peninsula after the ice retreated, and served as ancestors of present both tundra-adapted George River and Leaf River herds, and forest-adapted woodland caribou in Ontario and Manitoba.

The transferrin allele frequencies in the Baffin Island caribou revealed surprisingly large genetic difference from all other populations. This was mainly due to the allele Tf^{L-2}, which was the most dominant allele in Baffin Island ($p=0.521$), while in all other populations this allele was absent or present at only very low frequencies ($p < 0.1$). Such a pattern indicates very little genetic exchange between Baffin Island caribou and other populations. The levels of genetic differences from the other subspecies were even greater than between subspecies of tundra caribou and *R.t. caribou*, in which the genetic differentiation is assumed to reflect different ancestral origin during the Wisconsin glaciation. Portions of northern and eastern Baffin Island remained ice-free at the maximum extent of the Laurentide Ice Sheet, which covered almost all of Canada 18 000 BP, and since about 13 000 BP the northern and eastern coastlines of Baffin Island have roughly resembled those of today (Dyke and Prest, 1987a). These areas remained essentially separated from continental North America by the remains of the Laurentide Ice Sheet until 8 000–7 000 BP (Dyke and Prest 1987b). Some immigration of caribou onto Baffin Island after 8 000 BP might have happened, and the allele frequencies give evidence that such immigration could not have involved *R.t. caribou* from Québec/Labra-

dor regions, but was more probably a migration of barren-ground caribou from Melville or Boothia Peninsula. However, the level of genetic identity between Baffin Island caribou and *R.t. groenlandicus* ($I=0.316$) is less than that between other pairs of subspecies which were probably never in direct contact since the last glaciation (e.g. *R.t. caribou* vs. *R.t. pearyi*, $I=0.502$; *R.t. tarandus* vs. *R.t. pearyi*, $I=0.363$).

Richardson (1829) first named the barren-ground caribou of the mainland N.W.T. as *Cervus tarandus* var. *arctica* (or *arcticus*, Banfield 1961). Richardson's work covered the western N.W.T. now occupied by the Bluenose and Bathurst caribou herds, the range of the latter being adjacent to that of the Beverly herd referred to in Table 1. Richardson (1829) did not actually describe Baffin Island caribou as implied by Banfield (1961). Banfield (1961) renamed the caribou on mainland N.W.T., *R.t. groenlandicus*, based on the assumption that they were related to Greenlandic caribou via emigrants from Baffin Island. Based on the present genetic differentiation between the Beverly herd and Baffin Island caribou, one could question whether or not mainland N.W.T. caribou should be named *R.t. groenlandicus*. Analyses of transferrin allele frequencies from caribou populations from western Greenland would therefore be of great interest, and could contribute significantly to a better understanding of the origin and taxonomic identity of caribou on both Baffin Island and western Greenland.

Acknowledgements

We sincerely thank those who helped collecting blood samples in the field: D. Le Hénaff, M. Hoppe, T. Ikummaq, J. Kilabuk, P. Kilabuk, J. Koomarkjuk, M. Labine, P. Larocque, D. Naulaq, R. Nault, E. Nauyuk, I. Nauyuq, J. Noble, E. Papatsie, R. Patenaude, J. Sheutiapik, and J. Shoo. We also thank E. Broughton who helped facilitate the shipment of blood samples to Norway.

References

- Banfield, A. W. F. 1961. *A revision of the reindeer and caribou, genus Rangifer*. Bull. Natl. Mus. Can., Biol. Ser. No 66.
- Bergerud, A. T. 1980. Status of *Rangifer* in Canada 1. Woodland caribou (*Rangifer tarandus caribou*). - *Proceedings of the 2nd International Reindeer/Caribou Symposium Røros, Norway 1979*. Direktoratet for vilt og ferskvannsfisk, Trondheim. pp. 748 - 753.
- Brænd, M. 1964. Genetic studies on serum transferrin in reindeer. - *Hereditas (Lund, Swed.)*, 52: 181 - 188.
- Crête, M., Huot, J. and Gauthier, L. 1990. Food selection during early lactation by caribou calving on the tundra in Québec. - *Arctic* 43: 9 - 20.
- Diezel, W., Kopperschlager, G. and Hoffmann, E. 1972. An improved procedure for protein staining in polyacrylamide gels with a new type of Coomassie Brilliant Blue. - *Anal. Biochem.* 48: 617 - 620.
- Dyke, A. S. and Prest, V. K. 1987a. Late Wisconsinan and Holocene history of Laurentide ice Sheet. - *Geographie physique et Quaternaire*. 41: 237 - 263.
- Dyke, A. S. and Prest, V. K. 1987b. *Paleogeography of northern North America, 18 000 - 5 000 years ago; Map 1703A, scale 1:125 000, Sheet 1-3*. Geological Survey of Canada, Ottawa.
- Ferguson, M. 1989. Baffin Island. - In: *People / Caribou in the Northwest Territories* (E. Hall, ed.). Department of Renewable Resources, Government of N.W.T., Yellowknife. pp. 141 - 149.
- Hearn, B. J., Luttich, S. N., Crête, M. and Berger, M. B. 1990. Survival of radio-collared caribou (*Rangifer tarandus caribou*) from the George River, Nouveau-Québec - Labrador. - *Can. J. Zool.* 68: 276 - 283.
- Nei, M. 1972. Genetic distance between populations. - *Amer. Natur.* 106: 283 - 292.
- Nei, M. 1973. Analysis of gene diversity in subdivided populations. - *Proc. Natl. Acad. Sci. USA*. 70: 3321 - 3323.
- Richardson, J. 1829. *Fauna Boreali-Americana: Par 1, containing the Quadrupeds*. John Murray, London. pp. 240 - 251.
- Røed, K. H. 1985a. Genetic differences at the transferrin locus in Norwegian semi-domestic and wild reindeer (*Rangifer tarandus* L.). - *Hereditas (Lund, Swed.)*. 102: 199 - 206.
- Røed, K. H. 1985b. Comparison of the genetic variation in Svalbard and Norwegian reindeer. - *Can. J. Zool.* 63: 2038 - 2042.
- Røed, K. H. 1986. Genetic variability in Norwegian wild reindeer (*Rangifer tarandus* L.). - *Hereditas (Lund, Swed.)*. 104: 293 - 298.
- Røed, K. H., Soldal, A. V. and Thorisson, S. 1985. Transferrin variability and founder effect in Iceland reindeer, *Rangifer tarandus* L. - *Hereditas (Lund, Swed.)*. 103: 161 - 164.
- Røed, K. H., Staaland, H., Broughton, E. and Thomas, D. C. 1986. Transferrin variation in caribou (*Rangifer tarandus* L.) on the Canadian Arctic islands. - *Can. J. Zool.* 64: 94 - 98.
- Røed, K. H. and Whitten, K. R. 1986. Transferrin variation and evolution of Alaska reindeer and caribou, *Rangifer tarandus* L. - *Rangifer, Special Issue* No. 1: 247 - 251.
- Røed, K. H., Mossing, T., Nieminen, M. and Rydberg, A. 1987. Transferrin variation and genetic structure of reindeer populations in Scandinavia. - *Rangifer*. 7: 12 - 21.
- Røed, K. H. and Thomas, D. C. 1990. Transferrin variation and evolution of Canadian barren-ground caribou. - *Rangifer, Special Issue* No. 3: 385 - 389.

- Shubin, P. N.** 1977. Electrophoretic study of proteins in two races of reindeer. – *Izv. Akad. Nauk SSSR, Ser. Biol.* 6: 819 – 828. (In Russian).
- Shubin, P. N.** and **Matyukov, V. S.** 1982. Genetic differentiation of reindeer populations. – *Genetika (Moscow)*, 18: 2030 – 2035. (In Russian).
- Shubin, P. N.** and **Ionova, T. A.** 1984. Genetic interrelation between the domestic and wild reindeer (*Rangifer tarandus*). – *Zoologichsky Zhurnal*. 63: 1725 – 1731. (In Russian).
- Sokal, R. R.** and **Rholf, F. J.** 1969. *Biometry*. W. H. Freeman and Co. San Francisco, CA.
- Soldal, A. V.** and **Staalnd, H.** 1980. Genetic variation in Norwegian reindeer. – *Proceedings of the 2nd International Reindeer/Caribou Symposium, Røros, Norway 1979*. Direktoratet for vilt og ferskvannsfisk, Trondheim. pp. 396 – 402.
- Storset, A., Olaisen, B., Wika, M.** and **Bjargov, R.** 1978. Genetic markers in the Spitsbergen reindeer. – *Hereditas (Lund, Swed.)*. 88: 113 – 115.
- Williams, J. J.** and **Heard, D. C.** 1986. World status of wild *Rangifer tarandus* populations. – *Rangifer Spec. Issue*, No. 1, pp. 19 – 28.
- Zhurkevich, N. M.** and **Fomicheva, I. I.** 1976. Genetic polymorphism of transferrin of blood serum in reindeer (*Rangifer tarandus* L.) indigenous to northeastern Siberia. – *Genetika*. 12: 56 – 65. (In Russian).

Manuscript accepted 23 November, 1991