

Transferrin variation and evolution of Alaskan reindeer and caribou, *Rangifer tarandus* L.

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Abstract: Polyacrylamide gel electrophoresis was used to analyse transferrin variation in wild caribou (*Rangifer tarandus granti*) and domestic reindeer (*R.t. tarandus*) from Alaska. Eighteen alleles were detected in caribou and ten alleles were detected in reindeer. The most common allele was Tf^{F1} with a frequency of 0.304 and 0.408 in caribou and reindeer, respectively. The allele frequency distributions were significantly different in reindeer and caribou. This finding, together with the absence in reindeer of nine alleles present in caribou, suggests that little genetic exchange has taken place between caribou and reindeer in Alaska. The allele frequency distribution in Alaska caribou and reindeer are compared with those for other populations of caribou and reindeer. This comparison indicates that Alaskan caribou as well as Eurasian reindeer have evolved from a common ancestral population different from the ancestral population of Peary caribou (*R.t. pearyi*) and Svalbard reindeer (*R.t. platyrhynchus*).

Key words: *Rangifer*, caribou, reindeer, transferrin, polymorphism, Alaska.

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Introduction

In Alaska domestic reindeer, *Rangifer tarandus* L., originate from animals introduced from Eurasia and not from the native caribou. Reindeer have been introduced both from the Soviet Union (Banfield, 1961) and from Norway (Skjenneberg and Slagsvold, 1968). The present domestic reindeer are, however, assumed to originate mainly from the first introduction in 1892, when 1280 reindeer were imported from Eastern Siberia and brought to the Seward Peninsula in Alaska (Stern *et al.*, 1980). These animals subsequently increased in number to approximately 600.000, and had become widespread in large parts of Alaska by the early 1930s (Klein, 1980; Stern *et al.*, 1980, Thomas and Arobio, 1983). A rapid decline in numbers followed this peak population and a loss resulting

from intermingling with wild caribou, *R. t. granti*, presumably contributed to the population decline (Klein, 1980; Thomas and Arobio, 1983). This loss led to extensive speculations about the genetic influence of domestic reindeer on wild caribou in Alaska (cf. Greig, 1979; Klein, 1980).

One approach to the study of genetic exchange between populations is to investigate the distribution of alleles at polymorphic loci. The transferrin locus in reindeer and caribou is of particular value since it possesses a high degree of variation. Several studies have used the transferrin allele frequency distribution to test for genetic exchange between populations of reindeer and caribou (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, in press; Røed *et al.*, 1986). We report here the result of an electrophoretic examination of the transferrin locus in caribou and domestic reindeer in Alaska in order to determine the amount of genetic exchange that has taken place between these populations. The allele frequency distribution is further compared with those in other populations of reindeer and caribou and the results are discussed in relation to the origin of different subspecies of the genus.

Material and methods

Blood samples were obtained from 103 reindeer and 112 caribou. The reindeer samples were from the Seward Peninsula and the caribou samples were from the Central Arctic herd and the Delta herd (see Davis *et al.*, (1983) and Whitten and Cameron (1983) for descriptions of

these populations.) The blood samples were centrifuged and the serum removed and stored at -20°C until analysis. Vertical slab polyacrylamide gel electrophoresis was used to analyse transferrin variation using the Jolley and Allen (1965) buffer system. The acrylamide concentrations in the stacking and separating gels were 2.5% and 7%, respectively. Twenty specimens were run on each gel, beginning at 5 v/cm for the first half hour, and continuing at 30 v/cm for approximately 3.5 hours. To localize the transferrin on the gel most other proteins were precipitated from the serum by pretreatment with rivanol before electrophoresis (Chen and Sutton, 1967). Transferrins were made visible by overnight staining with Coomassie Brilliant Blue R250 (Diezel *et al.*, 1972). Relative mobilities of transferrin bands were confirmed by re-running samples of approximately the same mobility side

Table 1. Transferrin allele frequencies of wild caribou and domestic reindeer in Alaska together with allele frequencies of other reindeer/caribou populations.

Allele	Alaskan wild caribou	Alaskan domestic reindeer	Norwegian domestic reindeer	Norwegian wild reindeer	Peary caribou	Svalbard reindeer
A	0.027	0.005	0.016	0.032	0.041	
B	0.013				0.006	
C1	0.085	0.078	0.331	0.195	0.058	
C2	0.036	0.010	0.036	0.028	0.099	
C3					0.006	
D			0.001			
E1	0.304	0.408	0.269	0.389	0.023	
E2	0.036		0.002	0.019		
G1	0.054	0.053	0.053	0.024		
G2	0.049				0.297	0.745
G3						0.255
G4	0.004					
H1	0.013		0.009	0.051	0.023	
H1b	0.009	0.053				
H2	0.147	0.073	0.051	0.134	0.180	
I	0.134	0.306	0.156	0.096	0.163	
J	0.013				0.006	
K	0.013		0.037	0.027		
K2		0.010				
L	0.018				0.041	
M	0.040	0.005	0.039	0.005	0.017	
N					0.006	
O					0.023	
O2	0.004					
P					0.017	

Table 2. Paired combinations of genetic identity between populations of reindeer/caribou.

Population	A	B	C	D	E
(A) Alaskan caribou	*****				
(B) Alaskan reindeer	0.912	*****			
(C) Norwegian domestic reindeer	0.803	0.778	*****		
(D) Norwegian wild reindeer	0.942	0.864	0.890	*****	
(E) Peary caribou	0.516	0.365	0.345	0.340	*****
(F) Svalbard reindeer	0.120	0.000	0.000	0.000	0.691

by side on the same gel. Reference plasma was from continental Norwegian wild and domestic reindeer, *R.t. tarandus* (Røed, 1985a), from Svalbard reindeer, *R.t. platyrhynchus* (Røed, 1985b), and from Peary caribou, *R. t. pearyi* (Røed, et al, 1986.)

Results

The amount of genetic variation at the transferrin locus was high in both Alaskan caribou and reindeer, with a total of 19 separate alleles resolved. Eighteen of these were present in caribou and 10 in reindeer. Compared with the reference plasma, four new alleles were detected. These have been designated according to their mobility relative to the reference alleles: one with a banding pattern slightly cathodal to Tf^{G3} was labeled Tf^{G4} , one with bands between Tf^{H11} and Tf^{H12} was labeled Tf^{H1b} , one scored between Tf^K and Tf^L was labeled Tf^{K2} and one between Tf^O and Tf^P was labeled Tf^{O2} .

Table 1 presents the allele frequencies in the Alaskan caribou and reindeer together with previously reported values for Norwegian domestic reindeer, *R. t. tarandus*, (mean frequencies of five herds, Røed, 1985a), Norwegian wild reindeer, *R. t. tarandus*, (mean frequencies of five populations, Røed, in press), Peary caribou, *R. t. pearyi*, (Røed et al., 1986) and Svalbard reindeer, *R. t. platyrhynchus*, (Røed, 1985b), where the same techniques and allelic designations were used.

Tests of goodness-of-fit to the Hardy-Weinberg equilibrium did not reveal any significant deviations either in the caribou or in the reindeer from Alaska.

The most common allele in both caribou and reindeer from Alaska was definitely Tf^{G1} , with a frequency of 0.304 and 0.408 in caribou and reindeer respectively. The same allele is also very common among Norwegian reindeer, but not in Peary caribou and Svalbard reindeer, where Tf^{G2} is the most common allele.

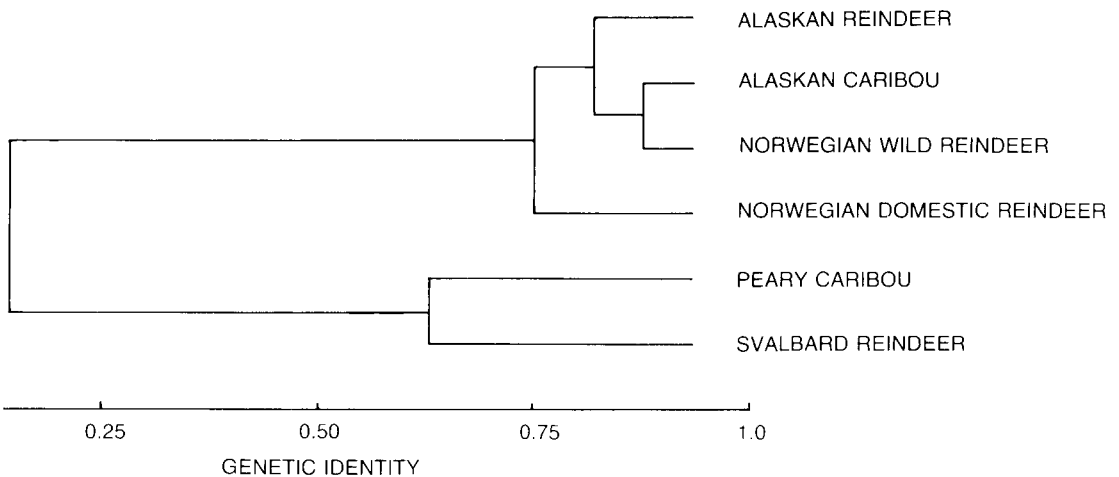


Fig. 1. Genetic identity dendrogram (Nei's coefficient) for transferrin variation of populations of reindeer and caribou.

The pattern of allele frequency distribution in Alaska reindeer and caribou, with an absence in reindeer of 9 alleles present in caribou, indicates considerable genetic difference between caribou and reindeer. Contingency chi-square tests for heterogeneity were an addition highly significant at both Tf^{11} ($X^2=5.10$, $P<0.05$), Tf^{12} ($X^2=6.01$, $P<0.05$) and Tf^2 ($X^2=18.71$, $P<0.01$).

Table 2 gives the coefficient of genetic identity (Nei, 1972) calculated from the allele frequencies in Table 1. The genetic identity between Alaskan caribou and reindeer was 0.912. Alaskan caribou were most similar to the Norwegian wild reindeer and Alaskan reindeer were most similar to Alaskan caribou. Both displayed low identity when compared with Svalbard reindeer and also with Peary caribou. A dendrogram (Fig. 1) summarizing the genetic identities was constructed using UPGMA (unweighted pair group method based on arithmetic averages) cluster analysis (Sneath and Sokal, 1973). As illustrated in Fig. 1 this analysis reveals a major dichotomy between Alaskan and Norwegian caribou and reindeer on the one hand and Peary caribou and Svalbard reindeer on the other.

Discussion

In Alaska the wild caribou appear to have several more alleles coding for transferrin than do the domestic animals. This, in combination with the considerable difference in the allele frequency distribution, indicates low genetic similarity of reindeer and caribou. The previously large loss of reindeer to wild caribou herds in Alaska seems therefore not to have resulted in appreciable genetic exchanges. This study therefore does not support a view of large-scale interbreeding between reindeer and caribou in Alaska. Low breeding success of domestic reindeer joining the wild herds may be explained by several factors. The breeding season of domestic reindeer usually precedes that of caribou by several weeks (Klein, 1980) and synchronous mating and calving appear to be strongly selected for among caribou (Dauphiné and McClure, 1974). Further, male domestic reindeer are usually substantially smaller than male wild caribou and therefore presumably would be less effective in competing for access to the females (Klein, 1980). Also the weaker migratory urge of domestic animals might work against the interbreeding since the breeding of

wild caribou usually takes place during fall migration from the summer to the winter ranges. The long migrations and difficult winter foraging conditions that are often characteristic of wild herds may also reduce the survival of domestic reindeer joining the wild animals. The domestic reindeer are probably also more exposed to predation and hunting, because they are less wary than the wild animals. Relatively higher mortality of domestic reindeer compared with wild animals has been reported in the Taymyr region in the Soviet Union, where considerable numbers of domestic reindeer had been absorbed by the wild herds (Geller and Vostryakov, 1975). In this region considerable genetic differences in the transferrin locus between domestic and wild reindeer have been reported (Shubin and Ionova, 1984). Similar genetic differences have also been reported between domestic and wild reindeer in Norway (Røed, 1985a). It appears therefore that the amount of genetic exchange between domestic and wild reindeer is generally very restricted.

The origin of reindeer/caribou and how they have spread into their present habitats is largely unknown. The genus has been traced back to about 440,000 B.P. in Eurasia and its existence in North America may well be equally long (Banfield, 1961). The caribou in North America segregate several more alleles in the transferrin locus than do reindeer from Eurasia. Eight alleles present in North American caribou are not detected in Eurasian reindeer, while only two alleles present in Eurasian mainland reindeer are not detected in North American caribou. Such a pattern could be explained by a longer evolutionary time of North American caribou and an origin of present Eurasian reindeer from ancestral populations in North America. Concerning the origin of the different subspecies of reindeer and caribou, it has been hypothesized that continental tundra forms evolved in the Beringia refugium in Alaska-Yukon during the Wisconsin glaciation, the woodland caribou south of the ice sheet, and the Peary caribou in a refugium in the Canadian Arctic Archipelago or in northern Greenland (Banfield, 1961; Macpherson, 1965). A common genetic origin of Svalbard reindeer and Peary caribou has also recently been suggested (Røed, 1985b; Røed *et al.*, 1986). The findings of considerable genetic differentiation between Svalbard reindeer and Peary caribou on the one hand and the Eurasian

reindeer and Alaskan caribou on the other (Fig. 1) clearly support the view that Alaskan caribou and Eurasian reindeer have evolved from a common ancestral population different from the ancestral population of Peary caribou and Svalbard reindeer.

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