

## Transferrin variation and genetic structure of reindeer populations in Scandinavia Transferrin-variasjon og genetisk struktur hos rein i Skandinavia

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**Abstract:** Polyacrylamide gel electrophoresis was used to analyse transferrin variation in herds of semi-domestic reindeer from Scandinavia. The results are compared with previously reported values for other populations of both semi-domestic and wild reindeer using the same techniques as in the present study. In all populations the number of alleles was high, ranging from seven to eleven, and the heterozygosity was correspondingly high, with a mean of 0.749. This high genetic variation in all populations suggests that inbreeding is not widespread among Scandinavian reindeer. The pattern of allele frequency distribution indicates a high degree of genetic heterogeneity in the transferrin locus, both between the different semi-domestic herds and between the different wild populations. The mean value of genetic distance was 0.069 between semi-domestic herds and 0.091 between wild populations. Between semi-domestic and wild populations the genetic distance was particularly high, with a mean of 0.188. This high value was mainly due to a different pattern in the distribution of the two most common transferrin alleles:  $Tf^{c1}$  was most common among semi-domestic herds, while  $Tf^{f1}$  was most common among wild populations. These differences in transferrin allele distribution are discussed in relation to possible different origins of semi-domestic and wild reindeer in Scandinavia, or alternatively, to different selection forces acting on transferrin genotypes in semi-domestic and wild populations.

**Key words:** Reindeer, transferrin, polymorphism

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**Sammendrag:** Transferrin-variasjon i tamreinflokker ble analysert ved hjelp av polyacrylamid gel elektroforese. Resultatene er sammenlignet med verdier som tidligere er beskrevet for både tamrein og villrein hvor det ble benyttet samme metode som i denne undersøkelsen. I alle populasjonene ble det registrert et høyt antall alleler (7-11) og heterozygositeten var tilsvarende høy med en middelerdi på 0.749. Denne høye graden av genetisk variasjon i alle undersøkte populasjoner indikerer at det ikke foregår mye innavl blant rein i Skandinavia. Utbredelsen av de enkelte allelene viste høy grad av genetisk oppdeling i transferrin-locuset mellom flokker av både tamrein og villrein. Middelerdien for genetisk avstand var 0.069 mellom tamreinflokker og 0.091 mellom villreinflokker. Særlig stor genetisk avstand (middelerdi 0.188) ble funnet mellom tamrein og villrein. Denne store forskjellen skyldes i stor grad forskjellig mønster i utbredelsen av de to vanligste allelene:  $Tf^{c1}$  var mest vanlig blant tamrein og  $Tf^{f1}$  var mest vanlig blant villrein. Denne forskjellen er diskutert i relasjon til forskjellig opprinnelse av tamrein og villrein og alternativt, i relasjon til forskjellig seleksjonskrefter som virker på transferrin genotyper i tamrein og villrein.

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## Introduction

Reindeer in Scandinavia are separated into numerous different populations and exist both as semi-domestic and wild animals. The amount of differentiation and the evolution of the different populations are, however, highly unknown and open to speculation. Studies of the genetic structure of reindeer populations may provide some insight into the evolutionary events and processes that have shaped the present structure.

Most work on the genetic structure of reindeer populations has been based on morphological characteristics. Such studies suffer from the difficulty of distinguishing between genetic and environmental components of variation. The introduction of electrophoretic techniques allowed studies of single factors with known inheritance. Gahne and Rendel (1961) used this technique and were the first to study genetic variation in the locus coding for serum transferrin in reindeer. The variation in this locus has later been used in several more studies of population genetics in reindeer and caribou (Brænd 1964; Shubin 1969; 1977; Shubin and Ionova 1984; Shubin and Matyukov 1982; Turubanov and Shubin 1971; Zhurkevich and Fomicheva 1976; Storset et al. 1978; Soldal and Staaland 1980; Røed 1985a, 1985b, 1986; Røed and Whitten 1986; Røed et al. 1985, 1986). The main pattern of variability reported in these studies indicates considerable genetic heterogeneity in the transferrin locus among populations of reindeer. A particularly high amount of differentiation was detected between populations of semi-domestic and wild reindeer in southern Norway (Brænd 1964; Røed 1985a). The purpose of the present study was to test whether this large differentiation remains evident when several more populations from other parts of Scandinavia are included in the analyses. The transferrin allele frequencies of nine herds of semi-domestic reindeer from Norway, Sweden and Finland are presented in this study and compared with allele frequencies of both semi-domestic and wild reindeer in Norway reported in previous studies using the same techniques and allelic designation (Røed 1985a, 1986, Røed et al. 1985).

## Material and methods

Blood samples were obtained from 842 reindeer belonging to the following 9 semi-

domestic reindeer herds or areas in Scandinavia (Fig. 1): Finland: Kaamanen (1), in the northern part of the country. Norway: Vuorjenjarg (2), Arnøy (3) and Laggonjargga (4) from Finnmark county, Kanstadsfjord (5) from Troms county and Essan (9) from Sør-Trøndelag county. Sweden: Rån/Umbryn (6) in Västerbotten county, Arvidsjaur (7) in Norrbotten county and Handölsdalen (8) in Jämtland county. Location of those populations from Norway included for comparisons in the present study are also given in Fig. 1: Aborassa (10), Joakkenjargga (11), Riast/Hylling (12), Trollheimen (13), Jotunheimen (14), Fillefjell (15), Hol (16), Hardangervidda (17), Hallingskarvet (18), Snøhetta (19), Knudshø (20) and Forelhogna (21). All herds belong to the subspecies Eurasian tundra reindeer, *R. t. tarandus*. The herd sampled in Arvidsjaur area (7) was of the forest reindeer type while the others were of the mountain reindeer type. Populations 17-21 are wild reindeer, among which the Forelhogna (21) population is believed to have its origin mainly from semi-domestic reindeer from Sweden (Skogland 1984). The semi-domestic Riast/Hylling herd (12) is identical to the Røros herd in a previous report (Røed 1985a).

Blood samples were taken into heparinized test tubes and centrifuged, after which the plasma fraction was removed and stored at  $-20^{\circ}\text{C}$  until the electrophoretic analysis was performed. Plasma samples were subjected to vertical slab polyacrylamide gel electrophoresis as previously described by Røed (1985a). The transferrins were stained with Coomassie Brilliant Blue R250 (Diezel et al. 1972).

## Results

Nine separate alleles, each consisting of a double band, could be resolved in the present material after re-running similar alleles side by side to confirm their electrophoretic identity. Each allele was scored as a double band as given in Fig. 2. The allele frequencies in the transferrin locus for each population are given in Table 1, together with frequencies of those populations included for comparisons. Table 2 shows the amount of genetic variation in the transferrin locus for each of these populations. The heterozygosity in Table 2 is calculated as expected frequencies of heterozygotes from observed allele frequencies (Lewontin and Hubby 1966). In all populations the number of

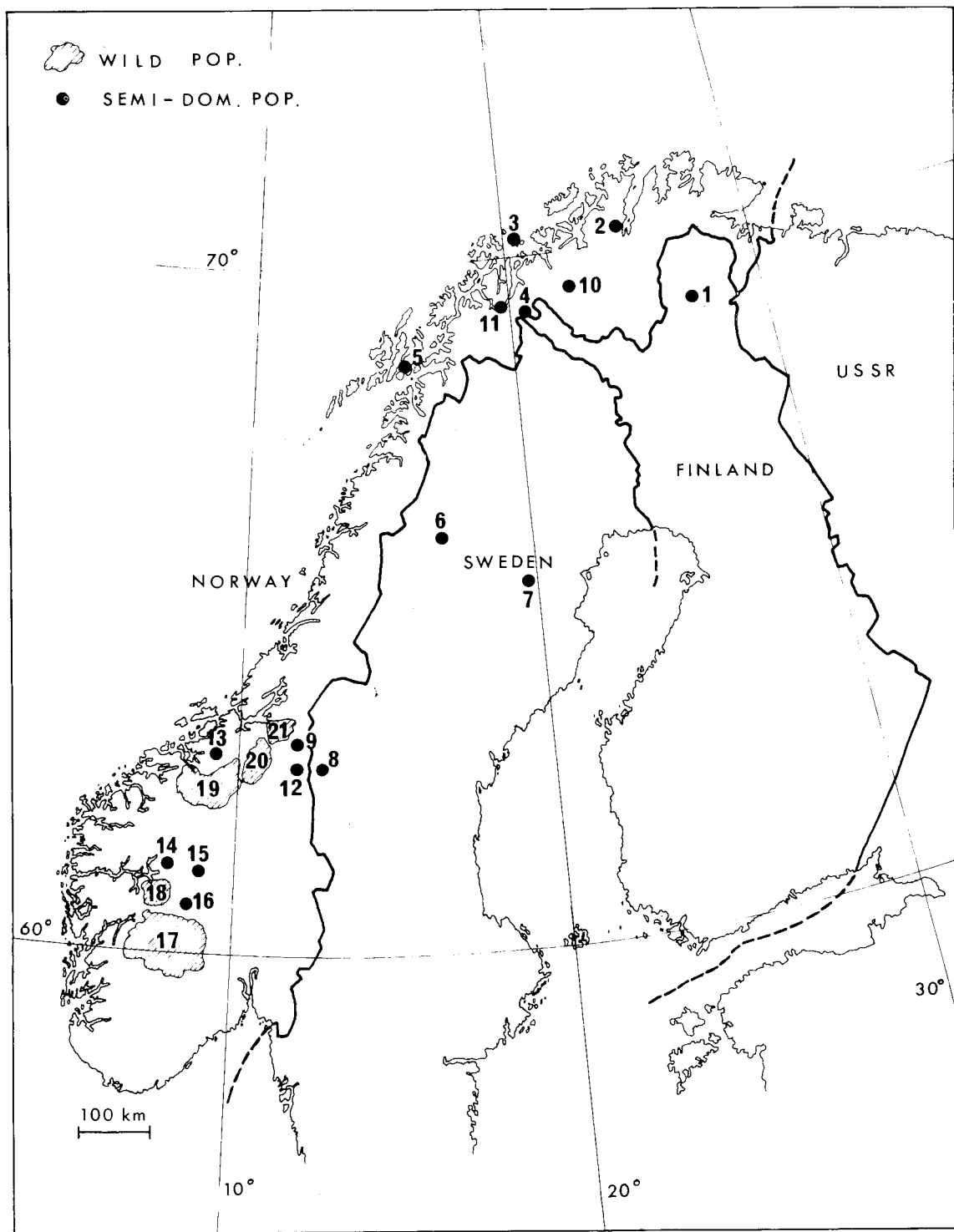


Fig. 1. Map showing locations of the sampled populations of semi-domestic (1-16) and wild (17-21) reindeer.  
 Fig. 1. Kart som viser lokalisering av populasjoner av tamrein (1-16) og villrein (17-21) som er analysert.

Table 1. Transferrin allele frequencies in different populations of reindeer in Scandinavia. N = number of individuals analysed.  
 Tabell 1. Frekvenser av transferrin alleler i forskjellige rein-populasjoner i Skandinavia. N = antall individer analysert.

Population	N	Tf <sup>A</sup>	Tf <sup>C1</sup>	Tf <sup>C2</sup>	Tf <sup>D</sup>	Tf <sup>E1</sup>	Tf <sup>E2</sup>	Tf <sup>G1</sup>	Tf <sup>H1</sup>	Tf <sup>H2</sup>	Tf <sup>I</sup>	Tf <sup>K</sup>	Tf <sup>M</sup>	Reference
1 Kaamanen	133	.000	.444	.008	.000	.320	.000	.056	.000	.056	.075	.026	.015	Present study
2 Vuorjenjarg	90	.006	.433	.000	.000	.311	.000	.017	.000	.089	.022	.100	.022	Present study
3 Arnøy	135	.004	.293	.004	.000	.274	.000	.011	.000	.185	.044	.181	.004	Present study
4 Laggonjargga	44	.023	.409	.000	.000	.239	.000	.023	.000	.170	.045	.091	.000	Present study
5 Kanstadvjord	75	.007	.607	.020	.000	.160	.000	.000	.000	.073	.020	.013	.047	Present study
6 Ran/Umbyn	89	.039	.303	.034	.000	.332	.000	.006	.000	.090	.112	.067	.017	Present study
6 Arvidsjaur	84	.012	.405	.012	.000	.381	.000	.012	.000	.077	.060	.042	.000	Present study
8 Handölsdalen	119	.017	.361	.038	.000	.269	.000	.025	.000	.080	.143	.029	.038	Present study
9 Essan	73	.007	.295	.062	.000	.226	.000	.068	.000	.096	.130	.062	.055	Present study
10 Aborassa	100	.055	.375	.000	.000	.225	.000	.005	.000	.155	.025	.135	.025	Røed 1985b
11 Joakkonjargga	99	.010	.455	.000	.000	.268	.000	.015	.000	.131	.020	.091	.010	Røed 1985b
12 Riast/Hylling	179	.025	.332	.014	.003	.268	.000	.059	.000	.056	.176	.034	.034	Røed 1985a
13 Trollheimen	98	.000	.270	.066	.000	.321	.000	.061	.000	.051	.153	.041	.036	Røed 1985a
14 Jotunheimen	115	.022	.383	.022	.000	.230	.004	.035	.004	.083	.126	.022	.070	Røed 1985a
15 Fillefell	71	.028	.338	.049	.000	.204	.007	.056	.007	.021	.204	.042	.042	Røed 1985a
16 Hol	181	.006	.331	.030	.000	.320	.000	.055	.033	.044	.119	.047	.014	Røed 1985a
17 Hardangervidda	121	.012	.202	.095	.000	.277	.000	.008	.099	.116	.107	.066	.017	Røed 1985a
18 Hallingskarvet	60	.000	.183	.025	.000	.358	.000	.067	.125	.083	.133	.017	.008	Røed 1985a
19 Snøhetta	103	.034	.117	.000	.000	.476	.034	.029	.019	.267	.024	.000	.000	Røed 1985a
20 Knudshø	44	.045	.239	.000	.000	.477	.023	.000	.011	.114	.091	.000	.000	Røed 1986
21 Forelhogna	28	.071	.232	.018	.000	.357	.036	.018	.000	.089	.125	.054	.000	Røed 1986

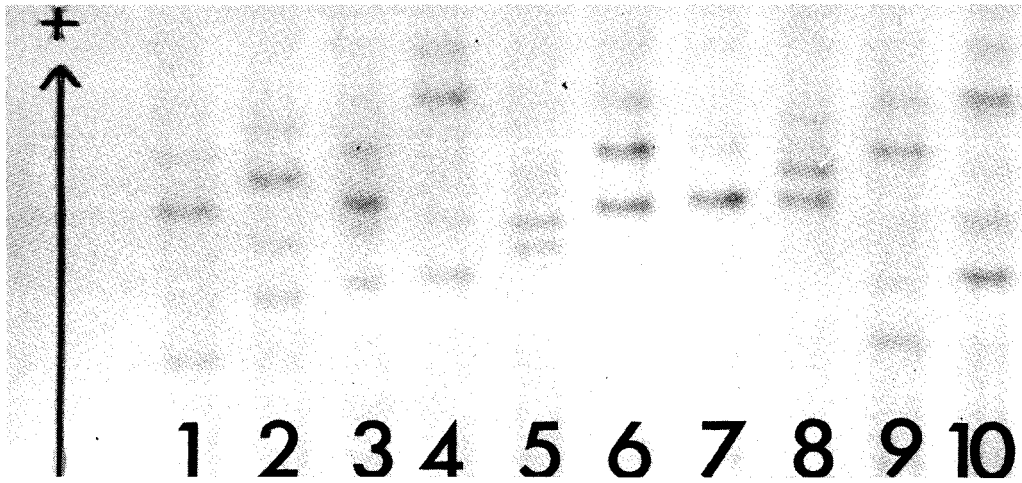


Fig. 2. Transferrin phenotypes in reindeer examined in vertical slab polyacrylamide gel electrophoresis.  
 1:  $Tf^M Tf^{E1}$ ; 2:  $Tf^K Tf^{C2}$ ; 3:  $Tf^f Tf^{E1}$ ; 4:  $Tf^{H2} Tf^A$ ; 5:  $Tf^{H1} Tf^{C1}$ ; 6:  $Tf^{E2} Tf^{C1}$ ; 7:  $Tf^{E1} Tf^{E1}$ ;  
 8:  $Tf^{E1} Tf^{C2}$ ; 9:  $Tf^M Tf^{C1}$ ; 10:  $Tf^K Tf^A$ .

Fig. 2. Transferrin fenotyper hos rein undersøkt ved hjelp av vertikal polyakrylamid gel elektroforese.

alleles was high, ranging from seven to eleven, and the heterozygosity was correspondingly high, with a mean for all populations of 0.749. The mean heterozygosity was 0.746 among the semi-domestic herds and 0.764 among the wild populations. Test of goodness-of-fit to the Hardy-Weinberg equilibrium did not reveal any significant deviations among any herds in the present study. This together with the high variation detected in all populations suggests that inbreeding is not widespread among reindeer populations in Scandinavia.

The two alleles  $Tf^{C1}$  and  $Tf^{E1}$  were the most common alleles in all populations of Scandinavian reindeer. The pattern of allele frequency distribution at the transferrin locus indicates, however, considerable genetic heterogeneity among populations. The contingency chi-square test for homogeneity among populations was highly significant, both for the nine populations analysed in this study ( $X^2=307$ ,  $p<0.01$ ) and among all sixteen semi-domestic herds ( $X^2=702$ ,  $p<0.01$ ) and among all populations of both semi-domestic and wild reindeer ( $X^2=1295$ ,  $p<0.01$ ). Significant differences were also detected between closer populations, as in the frequency of  $Tf^{C1}$  between Arnøy (3) and Vuorjenjarg (2) ( $X^2=9.42$ ,  $p<0.01$ ) within Finnmark county in Norway, and in the frequency of  $Tf^{C1}$  between Ran/Umbyn (6) and

Table 2. Amount of genetic variability in the transferrin locus in Scandinavian reindeer populations.

Tabell 2. Grad av genetisk variasjon i transferrinlocuset i rein-populasjoner i Skandinavia.

Population	Number of alleles	Heterozygosity
1 Kaamanen	8	.691
2 Vuorjenjarg	8	.700
3 Arnøy	9	.773
4 Laggonjargga	7	.744
5 Kanstadsfjord	8	.602
6 Ran/Umbyn	9	.774
7 Arvidsjaur	8	.683
8 Handölsdalen	9	.769
9 Essan	9	.826
10 Aborassa	8	.766
11 Joakkonjargga	8	.699
12 Riast/Hylling	10	.779
13 Trollheimen	8	.790
14 Jotunheimen	11	.774
15 Fillefjell	11	.797
16 Hol	10	.766
17 Hardangervidda	10	.837
18 Hallingskarvet	9	.799
19 Snøhetta	8	.688
20 Knudshø	7	.699
21 Forelhogna	9	.799

Table 3. Paired combinations of genetic distance ( $D \times 10^1$ ) between reindeer populations in Scandinavia.  
 Tabell 3. Parvise kombinasjoner av genetisk avstand ( $D \times 10^1$ ) mellom rein-populasjoner i Skandinavia.

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1 Kaamanen	★																				
2 Vuorjengarg	18	★																			
3 Arnøy	124	64	★																		
4 Laggonjargga	46	22	47	★																	
5 Kanstadvjord	80	82	243	80	★																
6 Ran/Umbyn	43	46	73	67	202	★															
7 Arvidsjaur	14	18	93	52	134	19	★														
8 Handölsdalen	22	46	17	55	114	24	32	★													
9 Essan	50	69	98	66	159	39	65	17	★												
10 Aborassa	73	28	34	10	104	76	71	80	84	★											
11 Joakkonjargga	29	7	64	7	58	68	36	54	75	17	★										
12 Riast/Hylling	36	75	145	88	162	33	51	9	21	116	90	★									
13 Trollheimen	62	98	144	133	261	25	53	32	30	159	131	25	★								
14 Jotunheimen	24	47	136	50	76	51	49	8	24	73	47	21	63	★							
15 Fillefjell	72	122	215	132	158	82	109	29	36	160	132	17	56	34	★						
16 Hol	21	46	116	81	170	18	20	18	33	104	70	18	17	38	53	★					
17 Hardangervidda	150	149	118	153	355	61	110	99	84	163	170	114	67	139	157	76	★				
18 Hallingskarvet	169	207	211	244	482	93	129	140	139	278	252	124	71	189	195	79	50	★			
19 Snøhetta	344	326	223	323	757	197	236	326	319	341	358	344	243	395	535	271	179	144	★		
20 Knudshø	133	147	165	191	420	53	71	125	156	212	190	128	77	176	234	83	100	63	73	★	
21 Forelhogna	101	112	115	137	343	20	57	72	87	145	145	67	41	115	133	48	72	69	133	24	★

Arvidsjaur (7) in Sweden ( $X^2=3.82$ ,  $p<0.05$ ). Significant differences were not detected between Laggonjargga (4) and Vuorjenjarg (2) populations in Finnmark county or between Handølsdalen (8) in Sweden and Essan (9) in Norway.

Coefficient of genetic distance, D, was calculated according to Nei (1972). Table 3 gives the genetic distance between each pair of populations and Table 4 gives the average genetic distance between populations of semi-domestic reindeer within and between different countries in Scandinavia and also when compared with the populations of wild reindeer. The genetic distance between populations was highly variable, ranging from 0.007 between the two Finnmark herds Laggonjargga (4) and Joakkonjargga (11) to 0.757 between the wild reindeer in Snøhetta (19) and the semi-domestic animals in Laggonjargga (4). The genetic distance between countries within Scandinavia was not particularly high, and the genetic distance between semi-domestic herds within Norway was on the average greater than the genetic distance between countries (Table 4). The mean value of D was 0.069 among the sixteen semi-domestic herds and 0.091 among the five wild populations. The greatest genetic distance was, however, certainly between semi-domestic and wild populations, ranging from 0.020 to 0.757 and with a mean of 0.188. This high difference between semi-domestic and wild populations is mainly due to a different pattern in the distribution of the two most common transferrin alleles in semi-domestic and wild populations (Table 5):  $Tf^{CI}$  is more frequently distributed among semi-domestic

herds than wild populations and  $Tf^{EI}$  is more frequently distributed among wild populations than semi-domestic herds.

A dendrogram (Fig. 3) summarizing the genetic distance was constructed using UPGMA (unweighted pair method based on arithmetic averages) cluster method (Sneath and Sokal 1973). This analysis illustrates the genetic dichotomy between the wild populations on the one hand and the semi-domestic herds on the other. Among the semi-domestic herds it seems that Kanstadsfjord (5) is genetically separated from the others. Furthermore, there also seems to be a major genetic separation in semi-domestic reindeer between the northern (11, 4, 10, 2, 7 and 1) and the southern herds (13, 16, 4, 6, 14, 12, 9 and 15). The clustering of the wild Forelhogna population (21) together with the semi-domestic herds is also noteworthy and in agreement with a mainly semi-domestic origin of this population.

## Discussion

The transferrin allele frequency distribution of Scandinavian reindeer found in this study includes a) high amount of genetic variation in both semi-domestic and wild populations, b) considerable genetic heterogeneity in this locus within both semi-domestic and wild populations, and c) particularly high genetic difference between semi-domestic herds on one hand and wild populations on the other. The great genetic differentiation in the transferrin locus between semi-domestic and wild populations in southern

Table 4. Average genetic distance (with range) between populations of semi-domestic and wild reindeer within and between different countries in Scandinavia.

Tabell 4. Middelerdi (med variasjon) for genetisk avstand mellom populasjoner av tamrein og villrein innen og mellom land i Skandinavia.

Population	1	2	3	4
1 Finland semi-domestic	***** (***** - *****)			
2 Sweden semi-domestic	0.026 (0.014-0.043)	0.025 (0.019-0.032)		
3 Norway semi-domestic	0.053 (0.018-0.124)	0.059 (0.008-0.202)	0.082 (0.007-0.261)	
4 Norway wild	0.179 (0.101-0.344)	0.119 (0.020-0.326)	0.205 (0.041-0.757)	0.091 (0.024-0.179)

Norway previously reported by Brænd (1964) and by Røed (1985a) seems therefore also to be valid when several more populations from different parts of Scandinavia are compared.

What is the reason for the very great differences in the transferrin allele distribution of semi-domestic and wild reindeer? The high amount of variation in all populations compared throughout this study suggests that founder effect, as allele frequency changes caused by small populations, has not been the principal factor determining the genetic differentiation. Rather it appears that either a different origin of semi-domestic and wild reindeer or different selection is acting upon genotypes at the transferrin locus in these animals.

The wild reindeer in Scandinavia are believed to originate from animals colonizing the Eurasian tundra regions as the ice barriers retreated during the late Weichselian. There is very little reliable information available in how reindeer domestication evolved in Europe. The question is still open as to whether reindeer husbandry developed independently in Scandinavia by domestication of wild populations, or

Table 5. Mean ( $\pm$ SD) frequencies of the most common transferrin alleles in Scandinavian semi-domestic and wild reindeer populations.

Tabell 5. Middelværdi ( $\pm$ SD) for frekvenser av de mest vanlige transferrin allelene i populasjoner av tamrein og villrein i Skandinavia.

Allele		Semi-domestic	Wild
$Tf^{C1}$	p	0.377	0.195
	SD	0.084	0.049
$Tf^{E1}$	p	0.272	0.389
	SD	0.057	0.086
$Tf^{H2}$	p	0.091	0.134
	SD	0.047	0.076
$Tf^I$	p	0.092	0.096
	SD	0.061	0.043

was brought in by some movement of the Saami people or by contact with Samoyeds (Skjenneberg 1984). On the assumption that the rate of allelic substitution in the transferrin locus is proportional to time, the present results of

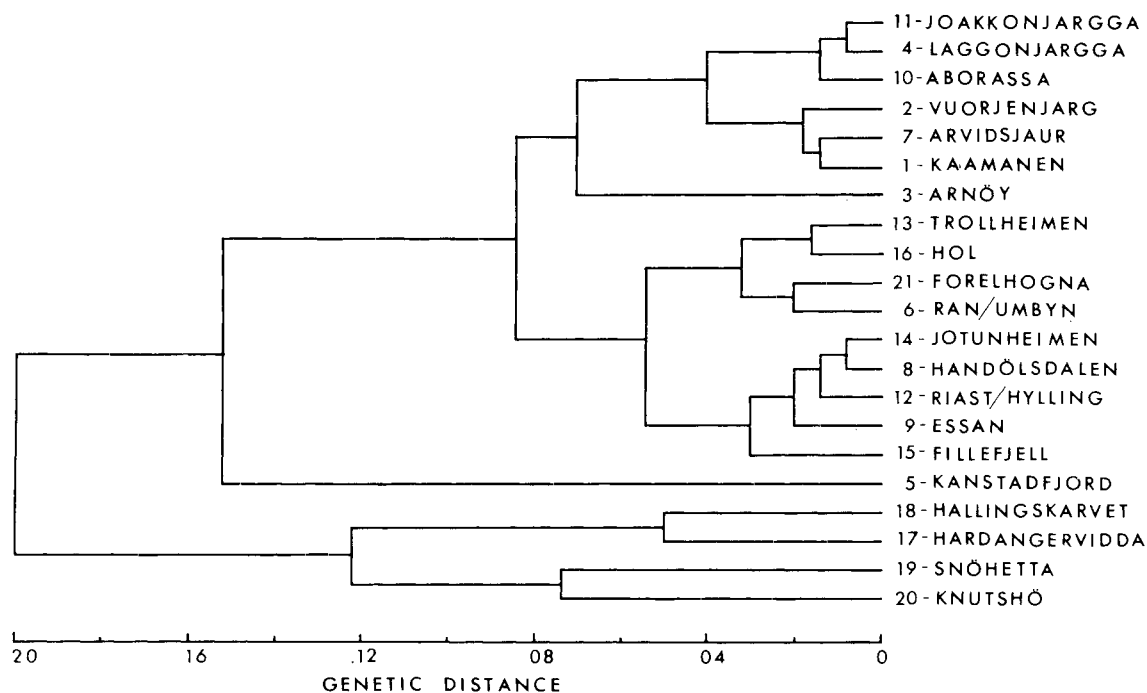


Fig. 3. Genetic distance dendrogram for transferrin variation of semi-domestic (1-16) and wild (17-21) populations of reindeer in Scandinavia.

Fig. 3. Dendrogram som viser den genetiske avstanden mellom populasjoner av tamrein (1-16) og villrein (17-21) i Skandinavia basert på transferrin-variasjon.



generally high genetic differentiation in the transferrin locus between semi-domestic and wild populations would indicate that the differentiation between these animals had to be initiated a very long time ago.

The alternative explanation of different selection in semi-domestic and wild populations should, however, be considered. Several phenomena have been demonstrated which indicate that selection is important in maintaining the transferrin polymorphism in reindeer. Zhurkevich and Fomicheva (1976) have indicated association between transferrin genotypes and variability of environmental conditions and also between certain genotypes and susceptibility to epidemic and bacterial infections. Correlations between body weight and transferrin alleles have furthermore been found by Røed (1987). In that study  $Tf^{C1}$  was positively associated with high weight among calves and not among yearlings, while  $Tf^{E1}$  was indicated to be positively associated with high weight among male yearlings and not among calves. This, together with the reported increase in  $Tf^{C1}$  and decrease in  $Tf^{E1}$  along with intensified selection for calf body weight in a semi-domestic herd (Røed 1985a), gives evidence that reindeer husbandry acts as a selective force upon genotypes at the transferrin locus. Increased calf body weight is probably among the most important aims of reindeer husbandry. The selective breeding for high calf weight could thus explain the generally higher frequency of  $Tf^{C1}$  and lower frequency of  $Tf^{E1}$  in semi-domestic than in wild reindeer populations.

The possibility that the divergence between the wild and semi-domestic populations could be explained by selective forces acting on wild reindeer also must be considered. Harvest through the regular hunt is the most important mortality factor among Norwegian wild reindeer (Reimers et al. 1980). In an open habitat the hunter should be able to classify and select single specimens of species living in flocks, such as the reindeer. However, the allele frequencies in the wild Forelhogna (21) population, which is believed to have its origin mainly from semi-domestic reindeer in Sweden (Skogland 1984), were detected to be most genetically similar to the semi-domestic Ran/Umbryn (6) herd in Sweden. As illustrated by the cluster analyses (Fig. 3), the Forelhogna population seems also to be in general more genetically similar to the semi-domestic herds than to the

wild populations. It seems therefore that the transferrin allele frequency has not significantly changed since 1955 when this population began to be harvested through the regular hunt. «Gun selection» seems therefore not to act as a strong selective force upon genotypes at the transferrin locus. The alternative explanation of reindeer husbandry as a selective force is therefore a more reasonable explanation for the high genetic divergence in the transferrin locus between semi-domestic and wild populations in Scandinavia.

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### References

- Brønd, M. 1964. Genetic studies on serum transferrin in reindeer. — *Hereditas* 52: 181 - 188.
- Diezel, W., Kopperschläger, G. and Hofmann, E. 1972. An improved procedure for protein staining in polyacrylamide gels with a new type of Coomassie Brilliant Blue. — *Analytical Biochem.* 48: 617 - 620.
- Gahne, B. and Rendel, J. 1961. Blood and serum groups in reindeer compared with those in cattle. — *Nature* 192: 529 - 530.
- Lewontin, R. C. and Hubby, J. L. 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. — *Genetics* 54: 595 - 609.
- Nei, M. 1972. Genetic distance between populations. — *Amer. Natur.* 106: 283 - 292.
- Reimers, E., Villmo, L., Gaare, E., Holthe, V. and Skogland, T. 1980. Status of Rangifer in Norway including Svalbard. — *In Proc. 2nd Int. Reindeer/Caribou Symp., Røros, Norway 1979* (Eds. E. Reimers, E. Gaare and S. Skjenneberg), Direktoratet for vilt og ferskvannsfisk, Trondheim: 774 - 785.
- Røed, K. H. 1985a. Genetic differences at the transferrin locus in Norwegian semi-domestic and wild reindeer (*Rangifer tarandus* L.). — *Hereditas* 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* 104: 293 - 298.
- Røed, K. H. 1987. Transferrin variation and body size in reindeer, *Rangifer tarandus* L. — *Hereditas* 106. (In press).

- Røed, K. H., Soldal, A. V. and Thórisson, N.** 1985. Transferrin variability and founder effect in Iceland reindeer, *Rangifer tarandus* L. — *Hereditas* 102: 161 - 164.
- Røed, K. H., Staaland, H., Broughton, E. and Thomas, D. C.** 1986. Transferrin variations in caribou on the Canadian Arctic islands. — *Can. J. Zool.* 64: 94 - 98.
- Røed, K. A. and Whitten, K.** 1986. Transferrin variation and evolution of Alaskan reindeer and caribou, *Rangifer tarandus* L. — *In Proc. 4th Int. Reindeer/Caribou Symp., Whitehorse, Canada 1985. Rangifer Special Issue No. 1*: 247 - 251.
- Shubin, P. N.** 1969. The genetics of transferrins in the reindeer and European elk. — *Genetika* 5: 37 - 41 (in Russian).
- Shubin, P. N.** 1977. Electrophoretic study of proteins in two races of reindeer. — *Izvestiya Akademii Nauk CCP, Seriya Biologicheskaya* 6: 819 - 828. (In Russian).
- Shubin, P. N. and Ionova, T. A.** 1984. Genetic interrelations between the domestic and wild reindeer (*Rangifer tarandus*). — *Zoologicheskyy Zhurnal* 63: 1725 - 1731. (In Russian).
- Shubin, P. N. and Matyukov, V. S.** 1982. Genetic differentiation of reindeer populations. — *Genetika* 18: 2030 - 2035 (In Russian).
- Skjenneberg, S** 1984. Reindeer. *In Evolution of domesticated animals. (Ed. I. L. Mason). Longman Group Limited.*
- Skogland, T.** 1984. The effects of food and maternal conditions on fetal growth and size in wild reindeer. — *Rangifer* 4: 39 - 46.
- Sneath, P. H. A. and Sokal, R. R.** 1973. Numerical Taxonomy. *Freeman, San Francisco.*
- Soldal, A. V. and Staaland, H.** 1980. Genetic variation in Norwegian reindeer. — *In Proc. 2nd. Int. Reindeer/Caribou Symp., Røros, Norway 1979 (Eds. E. Reimers, E. Gaare, and S. Skjenneberg), Direktoratet for vilt og ferskvannsfisk, Trondheim:* 396 - 402.
- Storset, A., Olaisen, B., Wika, M. and Bjarghov, R.** 1978. Genetic markers in the Spitsbergen reindeer. — *Hereditas* 88: 113 - 115 (In Russian).
- Turubanov, M. N. and Shubin, P. N.** 1971. New alleles of the transferrin locus in reindeer (*Rangifer tarandus* L.). — *Genetika* 7: 171 - 173 (In Russian).
- Zhurkevich, N. M. and Fomicheva, I. I.** 1976. Genetic polymorphism of transferrins of blood serum in reindeer (*Rangifer tarandus* L.) indigenous to northeastern Siberia. — *Genetika* 12: 56 - 65. (In Russian).