

2 Genetic structure and origin of semi-domesticated reindeer

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Introduction

Domestication of reindeer, *Rangifer tarandus*, and the emergence of large-scale reindeer herding were fundamental social transformations for the Indigenous people of the circumpolar north (Krupnik 1993; Kofinas et al. 2000; Jernsletten & Klovov 2002; Bjørklund 2013; Hansen & Olsen 2013). This pastoral transition established new relationships between humans and animals and led to new settlement and land use patterns across large portions of northern Eurasia. Today, reindeer husbandry as a livelihood is increasingly threatened by changes in the climate (Vors & Boyce 2009; Pape & Löffler 2012) and in land use (Horstkotte 2013; Skarin & Åhman 2014; Sandström 2015). Future adaptation, selection and improvement of reindeer herding are dependent on the genetic variability of the animal populations (Groeneveld et al. 2010; FAO 2015).

The pastoral transition

Today's large-scale and extensive reindeer husbandry in the Nordic countries is essentially linked to animal numbers, with the pastoral economy associated with the sale of meat from slaughtered calves (Næss 2010). However, long before large-scale reindeer herding developed, the first reindeer herders primarily lived in a hunter-gatherer economy and domesticated reindeer were mainly used for transportation (Bjørklund 2013) and as decoy animals to attract wild reindeer (Tornæus & Wiklund 1900). The early use of reindeer for transport purposes is illustrated by the 3500-year-old remains of Sámi-type sledges from the burial site in the Murmansk Fjord in northwest Russia (Murashkin et al. 2016). This early phase of reindeer domestication resulted in only small changes in local modes of subsistence, which remained focused on hunting, fishing and gathering. During the 16th and 17th centuries there was development towards increasing small-scale intensive herding, usually following a nomadic lifestyle, based on the provision of transport and food products including milk (Nieminen 1992). However, driven by diverse economic, social and ecosystem forces during the 18th and 19th centuries, there was a change towards increasingly large-scale,

extensive herding with herders subsisting primarily on domesticated animals (Bjørklund 2013).

In Fennoscandia, reindeer pastoralism has been associated with the Indigenous Sámi population, and the questions related to when, why and how it came about have been the focus of recurrent scientific debates. Vorren (1973) argued that Sámi communities shifted from hunting to reindeer pastoralism during the period 1550–1750 due to increased taxation, expanding trade relations and the introduction of firearms. Others have emphasized social tensions already inherent in Sámi hunting societies, which favoured a pastoral system with individual ownership over a hunting economy based on sharing (Hansen & Olsen 2014). Some archaeologists, on the other hand, have argued that the emergence of pastoralism can be dated back to the Viking age or the 9th to 13th century (Storli 1993), or even as early as the beginning of the Christian era (Aronsson 2009). Whatever the cause of the pastoral transition, the debate continues about whether the rapid growth of semi-domesticated reindeer herds actually involved the importation of a new domesticated type of reindeer not native to Fennoscandia (Røed et al. 2018), or if it primarily involved the adoption of husbandry techniques enabling different societies to domesticate wild stocks locally (Vorren 1973).

Genetic change associated with pastoral transition

Recently, examining DNA variation in archaeological specimens of various farm animals and comparing this with present-day material has helped to reveal the origin and spread of the domestication process. In reindeer from Finnmark county in northern Norway, such studies have shown genetic changes associated with the transition from a predominantly hunting economy to reindeer pastoralism (Bjørnstad et al. 2012; Røed et al. 2018). These studies analysed the control region of the mitochondrial DNA (mtDNA). The mtDNA is non-recombining and maternally inherited and therefore suitable as a genetic marker to study preserved demographic processes; it is, therefore, able to provide clues about the early history of reindeer husbandry. Different clusters of closely related mtDNA variants (haplotypes) represent genetic lineages preserved in the maternal lines through generations. Comparing the mtDNA in reindeer from 5000-year-old archaeological sites with those from the Medieval and more recent sites up to present-day semi-domesticated reindeer reveals that reindeer in Finnmark have gone through massive genetic replacement since Medieval times. This genetic transition is characterized by a significant loss of native haplotypes, together with the introduction of new ones (Figure 2.1). Out of a total of 62 mtDNA haplotypes identified in both the modern and archaeological samples, only 14 appear among samples known to represent semi-domesticated reindeer. This implies that the transition from the historical wild reindeer to today's semi-domesticated reindeer involved a significant bottleneck with massive loss of genetic variation. The pairwise genetic differences between sample sites also show a clear pattern of

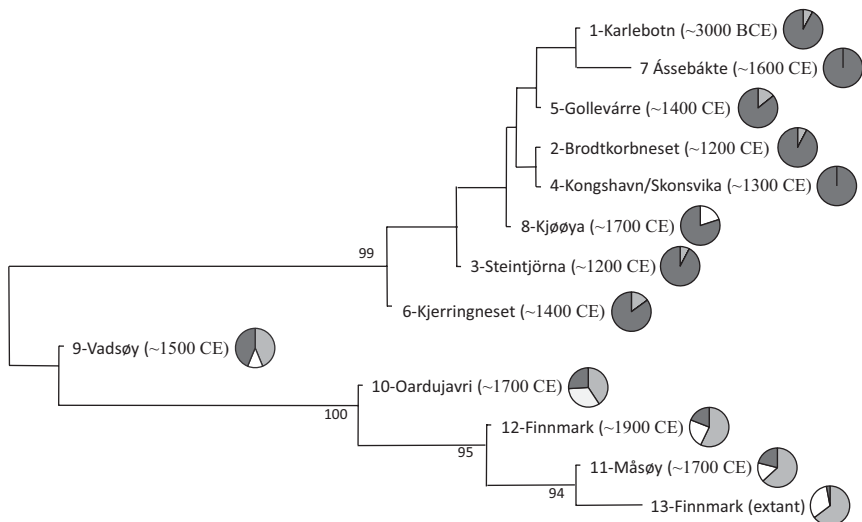


Figure 2.1 Population dendrogram based on mtDNA genetic distances and haplotype cluster distribution (pie charts) in prehistoric and historic reindeer from Finnmark county, northern Norway. In the dendrogram the support values from bootstrap replicates are given as percentages at the nodes. Number and age of sampling sites are given beside the pie charts, where dark grey represents mtDNA haplotype cluster I, light grey represents cluster Ib and white represents cluster II.

Source: (Modified from Røed et al. 2018).

low, or no, genetic differentiation between the ancient sites (1–8), while low or no genetic differentiation is found at sites 9–13, representing relatively more recent periods. However, between these two sets there is a substantial genetic difference, as illustrated by the high bootstrap values in the cluster analysis (Figure 2.1), suggesting a sudden genetic change over a relatively short period. This coincides with the transition of the Sámi economy from mainly hunting and gathering to a reliance on extensive reindeer pastoralism, indicating that the distinct genetic shift was closely associated with the beginning of pastoralism (Bjørnstad et al. 2012; Røed et al. 2018).

The fact that the archaeological samples show evidence of a reindeer population with high genetic variation and a homogeneous genetic structure up to the Late Medieval Period suggests relatively large wild reindeer herds in the region at that time. The detection of a major subsequent genetic bottleneck makes it likely that the wild reindeer populations were reduced and fragmented prior to, or during, the first phases of the pastoral transition. The putative population reduction and fragmentation of the wild reindeer herds may have allowed the domesticated type to expand rapidly. Notably, several other reindeer herding peoples across Russia experienced rapid growth in the

herd size of domesticated reindeer in the 18th and 19th centuries (Krupnik 1993). This may indicate a more general drive for pastoralism, such as the onset of the Little Ice Age with the coldest interval occurring between the 17th and mid-19th centuries (Kaufman et al. 2009). Reindeer are well-adapted to cool summers and cold winters, and increasing domesticated herd sizes may have led to increased human mobility that greatly facilitated the hunting of wild reindeer. The decline of wild reindeer populations may not have preceded but followed the increase in number of semi-domesticated reindeer, although local political and economic factors may have been influential in encouraging herders to keep large herds (Krupnik 1993; Stépanoff 2017). The pastoralism was followed by a shift towards subsisting primarily on domesticated animals. Further reduction and eventual depletion of the wild reindeer may have taken place due to the challenges associated with the co-existence of both large wild and semi-domesticated herds.

The maternal genetic shift in Finnmark reindeer was not only characterized by loss of genetic variation but also by the replacement of haplotype clusters assumed to represent different maternal lineages. The lineage characterized by the cluster **I** haplotypes dominated the ancient material but became rare and is almost absent in extant semi-domesticated reindeer, while the opposite trend was seen for the lineages characterized by haplotype cluster **II**. The most common cluster **II** haplotypes among extant domesticated reindeer were completely absent in the more ancient specimens (Figure 2.1). The pastoral transition appears, therefore, to have been founded on a limited number of individuals with a maternal ancestry of partly non-native origin. The rapid growth in herd sizes from the 17th to 19th centuries may have facilitated the development of a unique reindeer type based on a small number of imported pioneers. Where these animals came from is an intriguing but genetically still unresolved issue.

Possible eastern influence on the early history of reindeer husbandry

The dominance of the genetic lineage characterized by mtDNA cluster **II** haplotypes among extant Nordic domesticated reindeer may imply a common ancestry. It has been suggested that cluster **II** evolved during the last glaciation period in a few refugia in southern Europe, isolated from the general Euro-Beringia lineage that survived the glaciation as part of the large Beringia refugium encompassing a major part of north-eastern Russia and parts of north-western America (Flagstad & Røed 2003). The cluster **II** lineage then migrated northwards as the ice retreated. Among Nordic semi-domesticated reindeer, cluster **II** haplotypes consisted of one haplotype at high frequency, with all other haplotypes radiating from this by one or two mutations, a pattern suggesting a sudden population expansion 2500–6000 years ago (Røed et al. 2021). This is well before the rapid growth associated with the pastoral transition and points towards the possibility of the modern semi-domesticated reindeer originating from one or a few rapidly growing wild populations.

The absence of the characteristic cluster **II** haplotypes in ancient reindeer from both Medieval and earlier sites in southern and northern Norway (Røed et al. 2011; 2014; 2018) suggests colonization of these haplotypes from the east. This is also in accordance with the decreasing gradient for this lineage from east to west among the modern semi-domesticated reindeer population in the Nordic countries (Røed et al. 2021). Probable refuge areas for these ancestral wild populations could have been in the current taiga areas in Fennoscandia or western Russia. Today, this is the habitat of the wild Finnish forest reindeer living in Finland and north-western Russia (Banfield 1961). Based on morphological data, the origin of the Scandinavian semi-domesticated reindeer from this population was first suggested by Lönneberg (1909). The present-day Finnish forest reindeer population is descended from a previously large population with a geographical distribution that probably covered the northern part of Finland and Sweden as well as western Russia. The population became nearly extinct in Finland and Sweden in the early 20th century but then recovered as some herds migrated from Russia to the Kainuu district in Finland during the 1950s (Nieminen 2013). The mtDNA haplotype cluster dominating in the Nordic semi-domesticated population (cluster **II**) has been reported to be present in this population, although at low frequency (Røed et al. 2008). More common distribution of this haplotype that has changed during the population decline in the early 20th century might be the case.

The present-day domesticated reindeer within the Nordic countries

Today, there are approximately 200,000 semi-domesticated reindeer in each of Norway, Sweden and Finland, and the husbandry area covers approximately 30%–50% of the area of each country. The number of animals kept on winter pastures is regulated by administrative units (Reinbeitedistrikter in Norway, Samebyar in Sweden and Paliskunta in Finland) and varies substantially from about 500 reindeer in Ikonen paliskunta in Finland to just above 20,000 reindeer in Karasjok reinbeitedistrikt in Norway. Reindeer husbandry represents a socio-ecological system with considerable cultural and ecological variation (Holand et al. 2021). This herding is traditionally associated with the Indigenous Sámi and has evolved as an adaptation to natural conditions, being moulded by history, competing land use and legal rights (Käyhkö & Horstkotte 2017). In contrast to Norway and Sweden where Sámi are the only people permitted to practice reindeer husbandry, all local citizens are entitled to own reindeer in Finland, with Sámi husbandry mainly confined to northern Lapland. In the mountain areas of south-central Norway, which is outside the Sámi herding areas, there are local farmers practising reindeer husbandry.

Genetic structure of Nordic semi-domesticated reindeer

To better understand both ancient and more recent processes that affect the genetic structure and variation in the Nordic semi-domesticated reindeer,

Røed et al. (2021) analysed variation in both the control region of mtDNA and in 18 DNA microsatellites in reindeer from 31 reindeer herding districts in Norway, Sweden and Finland (Figure 2.2). Microsatellites are highly variable nuclear markers, inherited by both males and females, and are thus particularly appropriate to reveal demographic processes related to both sexes. The characterizing of the genetic structure in the Nordic herds revealed genetic variation both within and between reindeer husbandry areas. In extant reindeer in Finland, compared to Sweden and Norway, there is distinct differentiation with respect to the nuclear markers, but less so in the maternal marker (mtDNA). The general pattern of relatively high levels of microsatellite variation within all husbandry areas indicates relatively large effective population sizes (i.e. with limited effects of ongoing inbreeding and genetic drift). Compared to the microsatellites, levels of mtDNA variation were greater between reindeer herding areas, with several herds showing highly reduced levels of genetic variation indicating previous bottlenecks (small effective population sizes) in the number of reproducing females. The discrepancy between the microsatellite and mtDNA variation can be explained by mtDNA being more prone to genetic loss and fixation, since its effective population size is only a quarter that of microsatellites (Moore 1995). Alternatively, the discrepancy may reflect the greater mobility of males compared to females both at present and historically, as well as introgression within the Nordic reindeer husbandry areas.

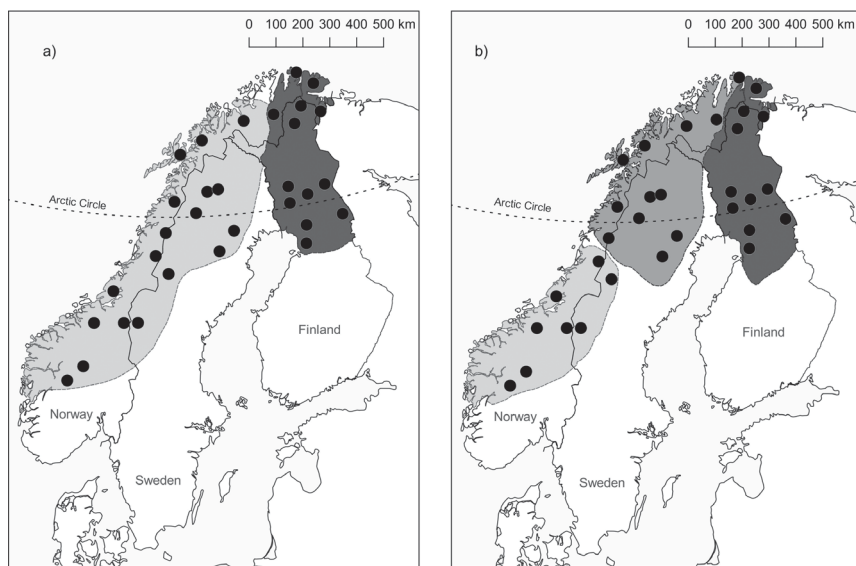


Figure 2.2 Spatial interference of the microsatellite ancestry distribution of semi-domesticated reindeer in the Nordic countries for (a) the main structure of two gene pools and (b) the three-part structure. Black dots indicate locations of husbandry areas sampled.

Source: (Modified from Røed et al. 2021).

Despite the relatively high amount of genetic variation in microsatellites, there were also substantial genetic differences between the Nordic populations. Analysing microsatellite genetic structure, based on the assignment of individual reindeer to genetic clusters, revealed two distinct gene pools, one dominating in Finland and one in Norway and Sweden combined, with the exception of the most northern herds in Norway which shared a gene pool with the Finnish reindeer (Figure 2.2a). In addition to this main structure, there was a substructure in which the joint Swedish and Norwegian gene pool could be divided into southern and northern parts, again except for the small area in northern Norway which was similar to the Finnish reindeer (Figure 2.2b).

In Finland, early nomadic reindeer husbandry is believed to have spread from the mountain areas of northern Sweden and Norway to the Käsivarsi area in north-western Finland early in the 17th century, from where large-scale reindeer herding gradually spread to other areas (Kortessalmi 2008). During the 17th and 18th centuries there was also frequent trade and transport of animals between the Finnish herders and the Indigenous reindeer herding people in the neighbouring eastern region (Kuusela et al. 2016). At that time, the taiga type of reindeer husbandry was common in both present Arkhangelsk Oblast and the Republic of Karelia on the eastern side of the current border between Finland and Russia (Koz'min 2003), implying a possible transfer of both knowledge and animals from these areas into the Finnish reindeer herding culture. The importation of particularly strong male reindeer with an eastern ancestry from Finland mostly to northern Norway for transport purposes could explain the present shared genomic pattern between these areas (Figure 2.2). Elsewhere more persistent maintenance of female-based herds primarily used for subsistence, including milking, may have been an important factor for the Swedish and Norwegian gene pool.

The distinct genetic separation of reindeer herds in Finland versus herds in Sweden and Norway combined has probably also been influenced by isolation after the closure of the border between Russia–Finland and both Norway in 1852 and Sweden in 1889. At the beginning of the 19th century, the yearly movements of reindeer were huge, with tens of thousands of reindeer crossing what have become the present borders between the four countries. After the border closures, these crossings became impossible, and this greatly affected the Nordic reindeer herders' pastoral livelihood. The restrictions on the seasonal migration pattern probably caused diversification of the reindeer genetic resources in Finland and the combined Sweden and Norway area. Notably, dissolution of the Swedish–Norwegian Union in 1905 appears not to have had similar genetic consequences, despite the resulting loss of access of particularly Swedish herders to important grazing and fishing grounds along the Norwegian coast (Riseth et al. 2016).

Social-ecological drivers of genetic structure

Rather than following the national borders, the genetic resources of reindeer in Norway and Sweden separated into southern and northern clusters, reflecting social-ecological processes across the countries. Possible relationships between the

three-part genetic structure of the semi-domesticated reindeer in the Nordic countries and different social-cultural factors have been examined by Røed et al. (2021). Besides the national and ethnic contrasts, there is social-cultural variation within Sámi society as represented by the many Sámi languages (Sammallahti 1998). The cultural boundaries do not follow the national borders as most of the Sámi languages are spoken in more than one country. The language variants belong to the Fenno-Ugrian languages and can be divided into three main types: Eastern Sámi spoken mainly on the Kola Peninsula and in some parts of north-eastern Finland; Central Sámi spoken mainly in northern Finland, Sweden and Norway; and Southern Sámi spoken in southern areas of Norway and Sweden (Hermanstrand et al. 1919). Northern Sámi belongs to the Central Sámi language and is the most common Sámi language spoken in northern Finland, Sweden and Norway.

The three-part genetic structure of the Nordic semi-domesticated reindeer is strongly associated with nation states (Norway, Sweden and Finland), ethnicity (Sámi versus non-Sámi) and languages that characterize the different herding areas (Norwegian, Finnish, South Sámi and Central Sámi), with language group being clearly the best factor to explain the genetic clustering shown in Figure 2.2b. Particularly in Norway, the distribution of the genetic clusters follows the traditional language borders, with South Sámi dominating the southern sub-cluster and Central Sámi the more northern genetic sub-cluster. This illustrates that the different reindeer husbandry systems within the Nordic countries are closely associated with the socio-cultural gradients within Sámi society. Like other traditional subsistence uses of natural resources, reindeer husbandry is based on cultural transmission of traditional ecological knowledge to exploit and adapt to environmental changes. Both the long-term pattern of reindeer migration and awareness of preserving the cultural identities including the exchange of animals as part of dowries and friendship have probably contributed to the genetic structure seen today.

The characterization of the genetic structure among the Nordic domesticated reindeer herds revealed no obvious differences in herding practices between the two genetic sub-clusters in Sweden and Norway. Within the same genetic cluster, the different herding types from the coastal climate in northern Norway across the alpine area in inland Sweden to more coastal and forested areas in north-eastern Sweden reflect ecological plasticity rather than genetic adaptations. Although one would expect some adaptive processes responding to the ecological diversity, the genetic structure detected by neutral genetic markers appears primarily to reflect history and spread of the pastoralist culture, while social-cultural variation across the Nordic reindeer husbandry areas is a secondary influence.

The distinct genetic structure of Eurasian semi-domesticated reindeer

At least two hypotheses regarding when and where reindeer herding originated in Eurasia have been debated (Gordon 2003). One theory, the diffusion theory or monocentric hypothesis, suggests that semi-domesticated reindeer first appeared a few thousand years ago east of the Urals in the southern part of the

Siberian taiga, when they spread to other regions. A second theory, the evolutionary theory or polycentric hypothesis, suggests that domestication of reindeer occurred independently multiple times in different parts of Eurasia. Studies based on both mtDNA and microsatellites show distinct genetic differentiation between Nordic and Russian semi-domesticated reindeer (Røed et al. 2008; Kvie et al. 2016) – a pattern also reported when using whole-genome DNA sequencing (Weldenegodguad et al. 2020). The differentiation probably reflects historic and evolutionary events and further implies that semi-domesticated reindeer in the two regions have different domestication origins.

A separate analysis of both microsatellites and the mitochondrial control region of semi-domesticated reindeer from 25 sites across Eurasia yielded a similar distinct genetic differentiation between Nordic and Russian reindeer (Kvie et al. unpublished), adding more support to the polycentric hypothesis (Figure 2.3a).

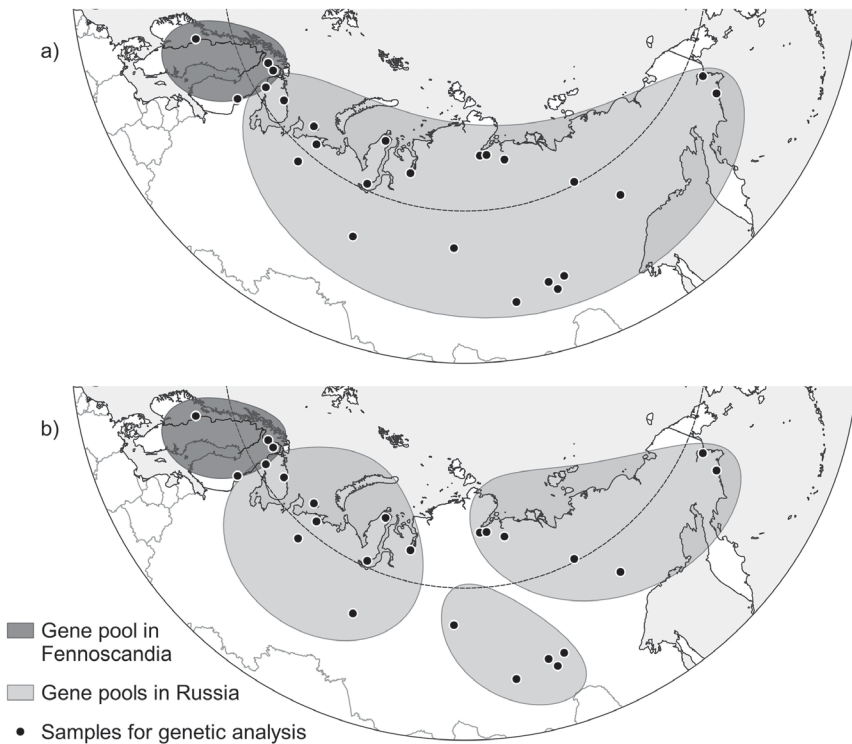


Figure 2.3 Genetic separation of Eurasian semi-domesticated reindeer into two and four groups based on individual assignment analyses in the software STRUCTURE. (a) The main structure with a separation between the Nordic and the Russian semi-domesticated reindeer. (b) Further sub-structuring divides the Russian semi-domesticated reindeer into north-western, north-eastern and southern genetic groups.

From the analysis, further sub-structuring was apparent, supporting the presence of as many as four genetic clusters within Eurasian semi-domesticated reindeer (Figure 2.3b). Among them, the semi-domesticated reindeer in the Nordic countries still comprise a distinct cluster, while those in Russia could be separated into north-western, north-eastern and southern clusters. This separation was evident only from the microsatellite data and could not be confirmed from mtDNA analyses – implying that these clusters probably reflect more recent demographic processes, rather than different domestication origins within Russia. Reindeer husbandries in Russia are usually separated into tundra and taiga forms. Beyond this general distinction, they are subdivided into four official breeds: Nenets, Even, Evenkiyskaya and Chukot (hargin), which are named after the ethnic groups assumed to have established these breeds showing particular traits and adaptations to their own environment (Zabrodin & Borozdin 1989). Analyses of single nucleotide polymorphisms (SNPs) in Russian reindeer by use of a Bovine 700K SNP Chip have revealed the genetic uniqueness of each of these breeds; it has been suggested that this reflects ecological processes, internal gene flow, breeding practices and geographical features (Kharzinova et al. 2020). Gene flow and breeding practices are also emphasized by Kvie et al. (unpublished) to explain the three-part genetic structure revealed by microsatellites, which appear to overlap with established Russian husbandry zones, namely the north-western, north-eastern and southern (Siberian taiga) zones (Klokov 2012).

However, Russian reindeer herding is without doubt very diverse and includes several different economic strategies associated with the natural and social environment (Klokov 2012). Hence, future studies on population genomics may be able to provide clearer answers about the extent to which human impact and adaptation to different environments drove the differentiation within Russia. Nevertheless, analyses based on neutral markers, e.g., microsatellites and mtDNA, have revealed that the semi-domesticated reindeer in the Nordic countries form a distinct group, probably originating from a different source population than the Russian domesticated reindeer. This further implies that Nordic domesticated reindeer should probably be considered a separate genetic type within Eurasia, with the conservation and management responsibilities that follow such a status.

References

- Aronsson, K-Å. (2009). Relations between man and reindeer – traces of reindeer herding. In *Recent perspectives on Sámi archaeology in Fennoscandia and North-West Russia*. *ISKOS*. 17, 17–24.
- Banfield, A. W. F. (1961). *A revision of the reindeer and caribou, genus Rangifer*. National Museum of Canada. Bull. No. 177. Biol. Ser.66.
- Bjørklund, I. (2013). Domestication, reindeer husbandry and the development of pastoralism. *Acta Borealia*. 30(2), 174–189.
- Bjornstad, G., Flagstad, Ø., Hufthammer, A. K. & Røed, K. H. (2012). Ancient DNA reveals a major genetic change during the transition from hunting economy to

- reindeer husbandry in northern Scandinavia. *Journal of Archaeological Science*. 39(1), 102–108.
- FAO (2015). *Coping with climate change – the roles of genetic resources for food and agriculture*, Rome, Italy.
- Flagstad, Ø. & Røed, K. H. (2003). Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. *Evolution* 57, 658–670.
- Gordon, B. (2003). Rangifer and man: an ancient relationship. *Rangifer*. 14, 15–28.
- Groeneveld, L. F., Lenstra, J. A., Eding, H., Toro, M. A., Scharf, B., Piling, D., Negrini, R., Finlay, E. K., Jianlin, H., Groeneveld, E., Weigend, S. & The GLOBALDIV Consortium (2010). Genetic diversity in farm animals – A review. *Animal Genetics*. 41, 6–31.
- Hansen, L. I. & Olsen, B. (2013). *Hunters in Transition: An Outline of Early Sámi History*. Leiden: Brill.
- Hermanstrand, H., Kolberg, A., Nilssen, T. R. & Sem, L. (2019). *The Indigenous Identity of the South Saami: Historical and Political Perspectives on a Minority Within a Minority*. New York: Springer Nature.
- Holand, Ø., Moen, J., Kumpula, J., Löf, A., Rasmus, S. & Røed, K. (2021). Project ReiGN: Reindeer Husbandry in a Globalizing North – Resilience, Adaptations and Pathways for Actions. In: Nord, D. C. (ed.) *Nordic Perspectives on the Responsible Development of the Arctic: Pathways to Actions*. Springer Polar Sciences. New York: Springer Nature. 227–248.
- Horstkothe, T. (2013). *Contested Landscapes: Social-Ecological Interactions Between Forestry and Reindeer Husbandry*. Ph.D. diss., Umeå University.
- Jernsletten, J. L. & Klokov, K. B. (2002). *Sustainable Reindeer Husbandry*. University of Tromsø, Tromsø, Norway.
- Kaufman, D. S., Ager, T. A., Anderson, N. J., Anderson, P. M., Andrews, J. T., Bartlein, P. J., Brubaker, L. N., Coats, L. L., Cwynar, L. C., Duvall, M. L., Dyke, A. S., Edwards, M. E., Eisner, W. R., Gajewski, K., Geirsdottir, A., Hu, F. S., Jennings, A. E., Kaplan, M. R., Kerwin, M. W., Lozhkin, A. V., MacDonald, G. M., Miller, G. H., Mock, C. J., Oswald, W. W., Otto-Bliesner, B. L., Porinchu, D. F., Ruhland, K., Smol, J. P., Steig, E. J. & Wolfe, B. B. (2009). Holocene thermal maximum in the western Arctic (0–180 W). *Quaternary Science Reviews*. 23(5–6), 529–560.
- Käyhkö, J. & Horstkothe, T. (2017). *Reindeer Husbandry Under Global Change in the Tundra Region of Northern Fennoscandia*. Report number 1. Turku: University of Turku.
- Kharzinova, V., Dotsev, A., Solovieva, A., Sergeeva, O., Bryzgalov, G., Reyer, H., Wimmers, K., Brem, G. & Zinovieva, N. (2020). Insight into the current genetic diversity and population structure of domestic reindeer (*Rangifer tarandus*) in Russia. *Animals*. 10, 1309.
- Klokov, K. B. (2012). Changes in reindeer population numbers in Russia: an effect of the political context or of climate. *Rangifer*. 32(1), 19–33.
- Kofinas, G., Osherenko, G., Klein, D. & Forbes, B. (2000). Research planning in the face of change: the human role in reindeer/caribou systems. *Polar Research*. 19(1), 3–21.
- Kortessalmi, J. J. (2008). *Poronhoidon syntyy ja kehitys Suomessa*. Helsinki: Suomalaisen Kirjallisuuden Seura.
- Koz'min, V. A. (2003). *Olenevodcheskaia Kul'tura Narodov Zapadnoi Sibiri*. Saint-Petersburg: Izdatel'stvo Peterburgskogo Universiteta.
- Krupnik I. (1993). *Arctic Adaptations. Whalers and Reindeer Herders of Northern Eurasia*. London: University Press of New England.

- Kuusela, J. M., Nurmi, R. & Hakamäki, V. (2016). Co-Existence and colonisation: re-assessing the settlement history of the pre-Christian Bothnian Bay coast. *Norwegian Archaeological Review*. 49(2), 177–203.
- Kvie, K. S., Heggenes, J. & Røed, K. H. (2016). Merging and comparing three mitochondrial markers for phylogenetic studies of Eurasian reindeer (*Rangifer tarandus*). *Ecology and Evolution*. 6(13), 4347–4358.
- Kvie et al. (in prep) *Genetic Variation and Structure in Wild and Domestic Reindeer Across Eurasia*.
- Lönneberg, E. (1909). Taxonomic notes about Palearctic reindeer. *Arkiv for Zoologi*. 6(4), 1–18.
- Moore, W. S. (1995). Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. *Evolution*. 49(4), 718–726.
- Murashkin, A. I., Kolpakov, E. M., Shumkin, V. Y., Khartanovich, V. I. & Moiseyev, V. G. (2016). Kola Oleneostrovskiy grave field: a unique burial site in the European Arctic. *ISKOS*. 21, 186–99.
- Næss, M. W. (2010). Contradictory evidence as a guide for future research: Investigating the relationship between pastoral labour and production. *Nomadic Peoples*. 14(1), 51–71.
- Nieminen, M. (1992). Siperian matkakuvia ja kokemuksia. II. *Porojen maitotalous entisessa Neuvostolotossa. Poromies*. 9, 10–15.
- Nieminen, M. (2013). Response distance of wild forest reindeer (*Rangifer tarandus fennicus Lönnb*) and semi-domestic reindeer (*R.t. tarandus L.*) to direct provocation by a human on foot/snowshoes. *Rangifer*. 33(1), 1–15.
- Pape, R. & Löffler, J. (2012). Climate change, land use conflicts, predation and ecological degradation as challenges for reindeer husbandry in northern Europe: what do we really know after half a century of research? *Ambio*. 41(5), 421–434.
- Riseth, J. Å., Tømmervik, H. & Bjerke, J. W. (2016). 175 years of adaptation: North Scandinavian Sámi reindeer herding between government policies and winter climate variability (1835–2010). *Journal of Forest Economics*. 24, 186–204.
- Røed, K. H., Flagstad, Ø., Nieminen, M., Holand, Ø., Dwyer, M. J., Røv, N. & Vilà, C. (2008). Genetic analyses reveal independent domestication origins of Eurasian reindeer. *Proceedings of the Royal Society B-Biological Sciences*. 275(1645), 1849–1855.
- Røed, K. H., Flagstad, Ø., Bjørnstad, G. & Hufthammer, A. K. (2011). Elucidating the ancestry of domestic reindeer from ancient DNA approaches. *Quaternary International*. 238(1–2), 83–88.
- Røed, K. H., Bjørnstad, G., Flagstad, Ø., Haanes, H., Hufthammer, A. K., Jordhøy, P. & Rosvold, J. (2014). Ancient DNA reveals prehistoric habitat fragmentation and recent domestic introgression into native wild reindeer. *Conservation Genetics*. 15(5), 1137–1149.
- Røed, K. H., Bjørklund, I. & Olsen, B. J. (2018). From wild to domestic reindeer – Genetic evidence of a non-native origin of reindeer pastoralism in Northern Fennoscandia. *Journal of Archaeological Science: Reports*. 19, 279–286.
- Røed, K. H., Kvie, K. S., Bårdsen, B.-J., Laaksonen, S., Lohi, H., Kumpula, J., Aronsson, K.-Å., Åhman, B., Våge, J. & Holand, Ø. (2021). Historical and social-cultural processes as drivers for genetic structure in Nordic domestic reindeer. *Ecology and Evolution*. 11, 8910–8922.
- Sammallahti, P. (1998). *The Saami Languages. An Introduction*. Davvi Girji, Kárášjohka, Norway.

- Sandström, P. (2015). *A toolbox for co-production of knowledge and improved land use dialogues: the perspective of reindeer husbandry*. Ph.D. diss., Swedish University of Agricultural Sciences.
- Skarin, A. & Åhman, B. (2014). Do human activity and infrastructure disturb domesticated reindeer? The need for the reindeer's perspective. *Polar Biology*. 37(7), 1041–1054.
- Stépanoff, C., Marchina, C., Fossier, C. & Bureau, N. (2017). Animal autonomy and intermittent coexistences: North Asian modes of herding. *Current Anthropology*. 58(1), 57–81.
- Storli, I. (1993). Sami Viking age pastoralism—or the fur trade paradigm' reconsidered. *Nonvegian Archaeological Review*. 26(1), 1–20.
- Tornæus, J. & Wiklund, K. B. (1900). *Johannis Törnæi Berättelse om Lapmarckerna och deres tilstånd*. Uppsala: Wretmans tryckeri.
- Vorren, Ø. (1973). Some trends of the transition from hunting to nomadic economy in Finnmark. In: Berg, G. (ed.) *Circumpolar Problems: Habitat, Economy and Social Relations in the Arctic*. Oxford: Pergamon Press. 185–194.
- Vors, L. S. & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global Change Biology*. 15(11), 2625–2633.
- Weldenegodguad, M., Pokharel, K., Ming, Y., Honkatukia, M., Peippo, J., Reilas, T., Røed, K. H. & Kantanen, J. (2020). Genome sequence and comparative analysis of reindeer (*Rangifer tarandus*) in northern Eurasia. *Scientific Reports*. 10, 8980.
- Zabrodin, V. A. & Borozdin, E. K. (1989). Deer. In: Dmitriev, N. G. & Ernst, L. K. (eds) *Animal Genetic Resources of the USSR*. Rome: FAO.