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RESEARCH ARTICLE

Ancient DNA reveals prehistoric habitat fragmentation and recent domestic introgression into native wild reindeer

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Abstract Introgression and admixture from domestic or foreign conspecifics into wild populations are of great concern in wildlife conservation. The issue is of particular interest in ungulates where translocations and re-introductions have been common practice. In Europe, the only large remaining wild populations of reindeer (*Rangifer tarandus* L.) are found in the mountainous habitats of southern Norway. These populations have during the last centuries been exposed to extensive habitat modifications and periods of contact with domestic reindeer. Through analyses of ancient and extant mitochondrial DNA (mtDNA) we document extensive intra- and inter-population genetic changes during the last millennium. Our data indicate population reduction within a short time interval during the 11th–12th century during a period when mass trapping of reindeer was common. Significant differentiation between the ancient herds suggests an ancient genetic structuring of the reindeer herds in southern Norway, although not as strong as between modern herds. Two different mtDNA lineages characterized the ancient herds. A Bayesian approach to reconstruct the recent evolutionary history suggests that the reindeer herds in southern Norway originate from two populations separated in different refugia during the last glacial period. The presence of two additional extant lineages, characteristic of domestic herds, suggests substantial introgression into the native wild reindeer. The putatively different refugial origins of the lineages represented by the extant herds in Rondane/Dovre, Hardangervidda and those with a mainly domestic origin may well reflect different adaptations to environmental conditions, including degree of human interference. Further research on this issue would provide important insights for conservation priorities and a sustainable and flexible

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management strategy for the remaining wild reindeer herds in the Scandinavian mountains.

Keywords Ancient DNA · Approximate Bayesian computation · Conservation · mtDNA · *Rangifer tarandus*

Introduction

Globally, human induced habitat modification and introgression from domestic or other non-indigenous gene pools represent major threats to biological diversity. Habitat fragmentation and disruption of gene flow are well-known causes of genetic deterioration and inbreeding (Frankham 2005; Allendorf and Luikart 2007; Edmans 2007), while introgression may oppose local adaptations, lead to outbreeding depression and eventually result in extinction via genetic swamping (Allendorf et al. 2001; Fitzpatrick et al. 2010; Laikre et al. 2010). It is of particular importance to identify and distinguish between these processes when prioritizing conservation units, understanding the potential for future responses, and implementing sustainable conservation practices.

Habitat modification and introgression may both have played key roles in the evolutionary and demographic history of reindeer. Most reindeer herds are naturally nomadic with large seasonal migrations between inland winter pastures and coastal summer pastures, and the species is particularly vulnerable to the accelerating infrastructural developments throughout the Holarctic (Vors and Boyce 2009; Festa-Bianchet et al. 2011). Worldwide, there is population decline in nearly 60 % of the major populations (Vors and Boyce, 2009), which is mainly due to habitat alteration and climate change (Vistnes and Nelleman 2008; Hansen et al. 2011; Polfus et al. 2011). In addition, intensive reindeer husbandry has influenced the number and continuous presence of wild herds through extensive displacement of wild animals by domestic herds (Syroechkovskii 1995; Baskin 2005). Today, about two-thirds of the approximate 3,000,000 reindeer in the Old World are domesticated animals. In most areas these are managed as free ranging herds involving a substantial risk of introgression of domestic genes into the native wild populations.

The population decline of wild reindeer has been particularly dramatic in Europe where its main distribution currently is restricted to the mountain areas in southern Norway (Fig. 1). This region holds about 30,000 wild reindeer of the subspecies *R. t. tarandus*, which are managed as 23 units. Historically, many of these herds have

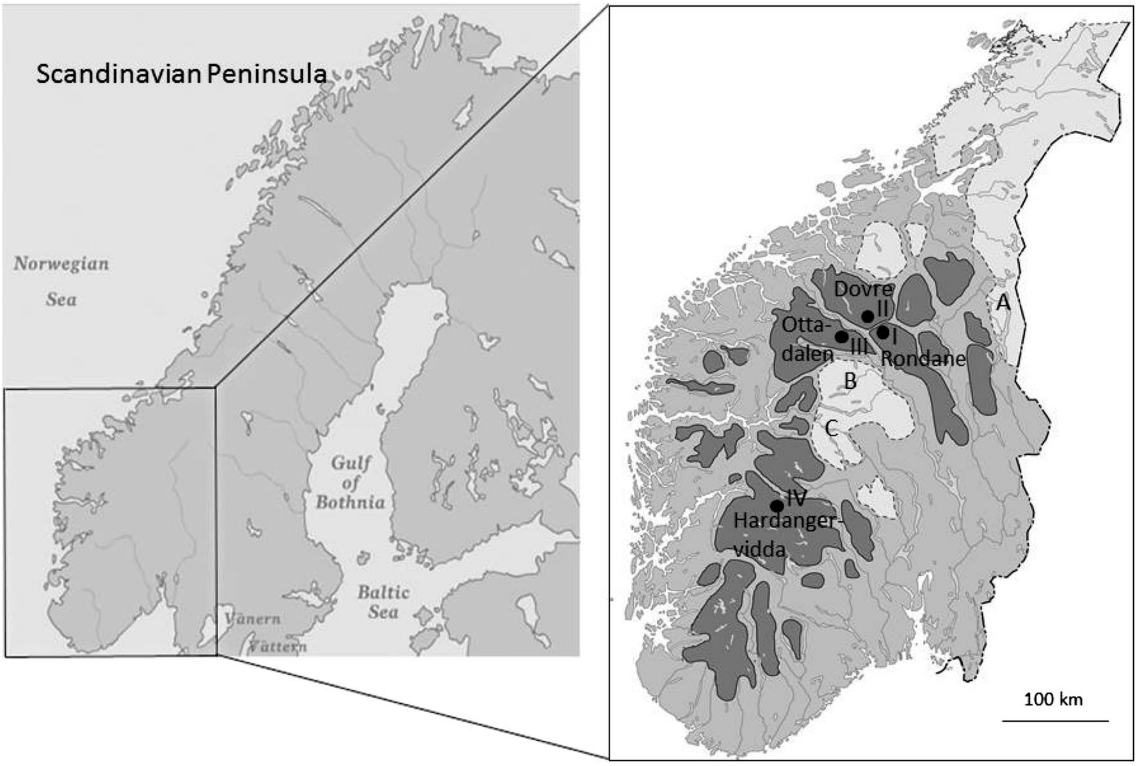

Fig. 1 Location of sampling sites of archaeological reindeer material from mountain areas in southern Norway (I = Rondane (Tøftom), II = Dovre (Vesle Hjerkinn), III = Ottadalen (Slådalen) and IV = Hardangervidda (Sumtangen)) together with areas holding extant wild (*dark shaded*) and domestic (*light shaded*; A = Røros, B = Vågå, C = Filefjell) reindeer

been in contact with and extensively displaced by domestic reindeer, and the ancestry of the present sub-populations varies from assumed relatively pure native to populations where considerable introgression with domestic herds has occurred (Røed et al. 2011; Reimers et al. 2012). Conservation priorities thus vary between the different management units and particularly high priority is given to the two regions Hardangervidda and Rondane/Dovre (Andersen and Hustad 2004). The Hardangervidda herd in southern Norway currently represents the largest free-ranging reindeer population left in Europe, but it is assumed to have been considerably admixed with domestic herds during the last two centuries (Røed et al. 2011) when reindeer husbandry was practised in this region (Henriksen and Indrelid 1979). By comparison, the Rondane/Dovre herds of central Norway are considered to have a more pure wild origin, as these are the herds most genetically different from domestic herds and at the same time also show distinct genetic differences to Hardangervidda (Røed et al. 2008; Reimers et al. 2012).

To investigate the demographic history and gene flow that have formed the genetic structure of wild Scandinavian reindeer, we examine the mitochondrial DNA (mtDNA) in ancient and extant samples and use a Bayesian approach to infer the evolutionary processes of divergence and admixture. Further, we assess whether native genetic signatures have persisted from the medieval period up to the present, or if introgression from domestic stocks characterizes the extant wild herds. Finally, we examine the degree of gene flow and genetic structuring among the medieval herds and compare these levels with extant patterns.

Materials and methods

The study areas/populations

The reindeer material used in the present study was from the mountain areas of Rondane, Dovre, Ottadalen and Hardangervidda in southern Norway (Fig. 1). Rondane and Dovre are adjacent alpine areas with large mountain plateaus (Fig. 1). They are partly separated by steep mountains and valleys, and together cover an area of about 7,500 km^2. Numerous reindeer pitfall hunting systems used for thousands of years suggest the presence of important reindeer migration routes both within and between these areas (Skogland and Mølmen 1980; Jordhøy et al. 2005). During the last decades, intensified human use and development of mountain areas have contributed to increased habitat fragmentation (Skogland and Mølmen 1980), and the extant wild reindeer in these areas are now managed as five separate sub-populations (Snøhetta, Knutshø, Sølnkletten, Rondane North and Rondane South). Today these sub-populations count about 8,000–10,000 animals in total, but the population size has fluctuated considerably during the last century. As late as 1920–1925 there were probably only a few hundred animals present in this area (Skogland and Mølmen 1980).

Ottadalen is a mountain area covering approximately 5,000 km^2, adjacent to Rondane/Dovre (Fig. 1) but well separated by vigorous rivers and deep forested valleys. Extensive archaeological remains from reindeer hunting are found also in this area, suggesting previously large wild populations (Jordhøy et al. 2008). During the first part of the 20th century this wild population was highly decimated and 64 domestic reindeer were released into the area in 1959. Thus, the extant wild reindeer herd in Ottadalen is believed to mainly originate from animals bought from a domestic reindeer company that closed in 1964 (Reimers 1972). During the last decades this population has fluctuated around 3,000 animals. Surviving descedants from remnant wild animals present during the founding of this population and subsequent immigration from neighbouring wild populations seem possible, although behavioral studies together with analyses of microsatellite markers support a mainly domestic ancestry of this population (Reimers et al. 2012).

Hardangervidda is an 8,000 km^2 mountain plateau located more than 100 km south of Rondane/Dovre/Ottadalen (Fig. 1). The plateau is part of the Langfjella region consisting of the three mountain areas Setesdal/Ryfylke, Hardangervidda and Nordfjella and covering approximately 17,000 km^2. All three mountain areas have extant and viable wild reindeer populations, presently managed as separate sub-populations, although some gene flow appear to occur (cf. Røed et al. 2008). Altogether, the present sub-populations within the region currently count about 15,000 animals. Archaeological findings show that hunting of wild reindeer has been extensive in this area for thousands of years (Indrelid and Hufthammer 2011). Domestic reindeer were introduced to these mountains in the late 18th century (Henriksen and Indrelid, 1979) and during the subsequent decades wild and domestic reindeer co-existed until 1979 when the last domestic reindeer herd was killed off.

Archaeological sites and material

From Rondane, Dovre and Ottadalen altogether 104 ancient reindeer samples were analysed, Most of the ancient samples from Rondane and Dovre were obtained from two adjacent archaeological excavation sites; 23 from Tøftom in Grimsdalen in the northern part of the Rondane area and 33 from Vesle Hjerkinn in central Dovre (Fig. 1). Both sites are characterized as hunting sites with refuse heaps containing large amounts of reindeer bones (Mikkelsen 1994). Previous radiocarbon (^{14}C) dating suggests that these sites were mainly used from the late Viking Age

(AD 1000) up to the High Middle Age (AD 1300) (Weber 2007), although some dating suggests use of the Tøftom site already during the Merovingian period (AD 570–800) (Mikkelsen 1994). In addition, 12 reindeer samples that have emerged from melting alpine ice patches within the Dovre mountain region were included. Archaeological samples from Ottadalen were obtained from Slådalen (Fig. 1), where a large reindeer funnel-trapping system recently was discovered, and where remains of a fence pole were radiocarbon dated to AD 1215–1290 (Jordhøy et al. 2005). A test excavation revealed midden deposits covered by a thin sod under which reindeer bones were found. A total of 36 samples were analysed from this site. The ancient mtDNA sequences of the Hardangervidda reindeer were obtained from Røed et al. (2011). This material derive from an ancient hunting station at Sumtangen (Fig. 1) with large refuse heaps containing reindeer bones, suggesting ancient mass-trapping of reindeer (Hufthammer et al. 2011). Previous radiocarbon dating of fifteen reindeer samples from this site revealed that all were from a relatively short time span (AD 1240–1290) within the medieval period (Indrelid and Hufthammer 2011).

For a verification of the time horizon, we ^{14}C dated 19 samples; three samples from each of Tøftom, Vesle Hjerkin and Slådalen and 10 ice patch samples (Table S1, Supporting Information available online), all of which had authentic DNA results. All ^{14}C dates were calibrated using CALIB 6.1.1 (Stuiver and Reimer 1993) based on the data set IntCal09 (Reimer et al. 2009). The dating supported a somewhat earlier use of the Tøftom hunting site in Rondane (AD 620–885) as compared to the Vesle Hjerkinn site in Dovre (AD 1045–1195) and Slådalen in Ottadalen (AD 1015–1285), while the ice patch material spanned a time period of more than 4,000 years (Table S1, Supporting Information available online).

The archaeological samples from Tøftom (Rondane), Vesle Hjerkinn (Dovre) and Slådalen (Ottadalen) were provided by the osteological collections of the University Museum of Bergen. Additional archaeological material emerging from melting alpine ice patches from Dovre was provided by the NTNU University Museum.

Reindeer teeth, bones and antlers were carefully selected, and if possible, the sampling strategy aimed at selecting samples representing different individuals using skeletal elements which could be identified and classified according to morphology, size, age group and excavation layer.

Extant reindeer

Tissue samples of the extant wild reindeer herd in Ottadalen were obtained by hunters during the regular hunt. DNA sequences of extant reindeer from the five wild herds of Rondane/Dovre (Snøhetta, Knutshø, Sølnkletten, Rondane North and Rondane South) and from the three herds of Langfjella (Nordfjella, Hardangervidda and Setesdal/Ryfylke), together with three domestic herds (Filefjell, Vågå and Røros) from nearby mountain areas in central/southern Norway (see Fig. 1), were obtained from Røed et al. (2008).

Laboratory methods

For the archaeological material, DNA was extracted from bone, tooth or antler powder using DNeasy Blood and Tissue kit (Qiagen) following Bjørnstad and Røed (2010). To ensure authenticity and minimize the risk of contamination, standard precautions for working with ancient samples were undertaken (see Hofreiter et al. 2001; Wandeler et al. 2007). All equipment and working surfaces were cleaned using sodium hypochlorite, ethanol or UV-light. Drilling of tooth/bone powder, DNA isolation and PCR setup was carried out in spatially separate lab facilities at the Norwegian School of Veterinary Science in Oslo, where modern reindeer DNA has never been present. Lab coats and breathing masks were used, and gloves and drill bits were changed for each sample. Samples were mechanically cleaned and the outer surface was removed before drilling out the powder. To test for contamination, blank extraction and PCR controls were used in each PCR reaction and only DNA sequences which could be replicated from at least two independent amplifications of each primer pair were accepted. Some samples were extracted twice and to ensure reproducibility and authenticity, 20 samples were also analysed in a separate lab (Norwegian Institute for Nature Research, Trondheim).

From the ancient material a 266 base pair (bp) fragment of the mtDNA control region was amplified using either the primer pair 259F/524R (5′-TGCCCCATGCTTATAAGCAAG-3′/5′-GTGAGATGGCCCTGAAGAAA-3′), or by amplifying two overlapping amplicons of respectively 140 bp with primers 259F and 398R (5′-CCTTTCTTGTCAACATGCGTA-3′) and 178 bp with primers 347 F (5′-TGCCCCATGCTTATAAGCAAG-3′) and 524R. PCR amplification and sequencing were performed as in Bjørnstad and Røed (2010). For the extant reindeer, DNA isolation, amplification and sequencing of a 470 bp fragment of the mtDNA control region was performed as given in Røed et al. (2008).

All sequences reported in this study have been deposited in GenBank (accession numbers KJ557013-KJ557106, Table S2, Supporting Information available online).

Data analyses

After removing primer sequences, sequence lengths were trimmed and adjusted to 190 bp according to previously published sequences of extant and ancient reindeer in Røed et al. (2008, 2011). Arlequin v. 3.5 (Excoffier et al. 2005) was used to estimate nucleotide and haplotype diversity and to obtain pairwise F_{ST} estimates, taking haplotype frequencies as well as nucleotide variation among haplotypes into account. Statistical significance was assessed using 1,000 permutations. Genetic distances between samples were further calculated using Kimura's two-parameter model (Kimura 1980) and a population dendrogram was constructed from the neighbour joining algorithm as implemented in the software SENDBS (http://www.kms.ac.jp/~genomelb/genomelab.eng.html#software). Node support values were estimated from 1,000 bootstrap replicates. The dendrogram generated is not to be treated in a strict phylogenetic context, but is a useful way to summarize the relationships presented in distance matrices. The phylogenetic relationship among haplotypes was analysed using a median-joining network (Bandelt et al. 1999) in Network v. 4.6.1.1 (www. fluxus-engineering.com).

A Bayesian Skyline Plot (BSP) as implemented in BEAST v1.7.4 (Drummond and Rambaut 2007) was used to infer demographic history, using the extant Rondane/Dovre samples together with pooled ancient Rondane/Dovre/Ottadalen population which genetically was relatively homogenous, although sampled across a relatively long time interval. The age of most archeological samples was not directly radiocarbon dated but obtained from the same sites as radiocarbon dated material and thus had a certain age range. Based on the radiocarbon analyses, an averaged age of 800 calendar years before present (yrBP) was used for the samples from the hunting stations in both the Ottadalen and Dovre while 1250 yrBP was used for the Rondane hunting station samples. For each icepatch-emerged sample, the calibrated age from radiocarbon dating was used except for the one which was too young to be radiocarbon dated, but clearly not recent, and which was given an age of 50 yrBP to keep it separated from the fresh samles. The HKY + G + I model of nucleotide substitution and strict molecular clock was assumed. Markov Chain Monte Carlo (MCMC) simulations were run with 5×10^7 iterations, 10 % burn-in and trees sampled every 5,000 MCMC cycles. To estimate model parameters we ran two independent runs and log-files were combined and inspected using TRACER v.1.5 (http://www.beast.bio.ed.ac.uk/Tracer). Effective sample sizes were used to evaluate MCMC convergence within chains. To evaluate support for the BSP model we also analysed the data using a constant coalescent tree-size prior instead of the BSP, comparing the different runs using Bayes factor tests according to Suchard et al. (2001).

Approximate Bayesian computation (ABC) (Beaumont et al. 2002) using a coalescence framework within the DIYABC software v. 1.0.4.39 (Cornuet et al. 2010) was used to further infer alternative historic scenarios of divergence and admixture that may explain the observed sequence data. We used both extant and ancient sequences, but because of similar dating and lack of genetic differentiation we pooled the archaeological sequences obtained from the hunting stations in Rondane, Dovre and Ottadalen. Five reindeer among the extant Rondane/Dovre herds had haplotypes previously not present in any ancient Norwegian material but private to domestic reindeer (see Røed et al. 2011; Bjørnstad et al. 2012), suggesting these to originate from immigration or introgression from herds with domestic ancestry. The ABC analyses were done both with and without these five reindeer included. Sampling time of both the ancient Rondane/Dovre and Hardangervidda populations was equally set to 250 generations before present based on an assumed average generation time of reindeer of 4 years (Couturier et al. 1990; Adams and Dale 1998).

Because we identified different levels of genetic variation in ancient Rondane/Dovre and Hardangervidda, which could be explained either by introgression or by demographic processes, two alternative historic scenarios of divergence and admixture were specified and explored both without (Fig. 2) and with demographic events (altogether eight scenarios, Fig. S1, Information available online). For both scenarios, the extant Hardangervidda herd was modelled as deriving from an introgression of the domestic lineage into the ancient Hardangervidda herd. In the first scenario, ancient Rondane/Dovre and Hardangervidda were assumed to originate from isolation and genetic drift, while the second scenario assumed that ancient Rondane/Dovre originated from admixture with an unsampled population, with a much older origin (i.e. that ancient Rondane/Dovre and Hardangervidda would have been much more genetically similar if it had not been for this admixture event). Prior parameter ranges were as given in Table 1, all with a uniform distribution. The prior range for the assumed admixture event at time t_3 was set to after the last glaciation (12,000 yrBP, i.e. 3,000 generations ago), as well as after t_4. In both scenarios, a most recent common ancestor (MRCA) is assumed for all sampled populations at time t_5 (Fig. 2). The scenarios were also explored with possible population reduction in Rondane/Dovre (prior range 0–500 generations ago and after t_3) or in ancient Hardangervidda (prior range 251–3,000 generations ago) or in both (Fig S1, Supporting Information available online).

Each scenario was simulated based on neutral coalescence for 1×10^6 iterations and summary statistics were computed for each simulation. The scenarios were compared directly through their frequencies among the 0.1 % of simulated data sets that were most similar to the

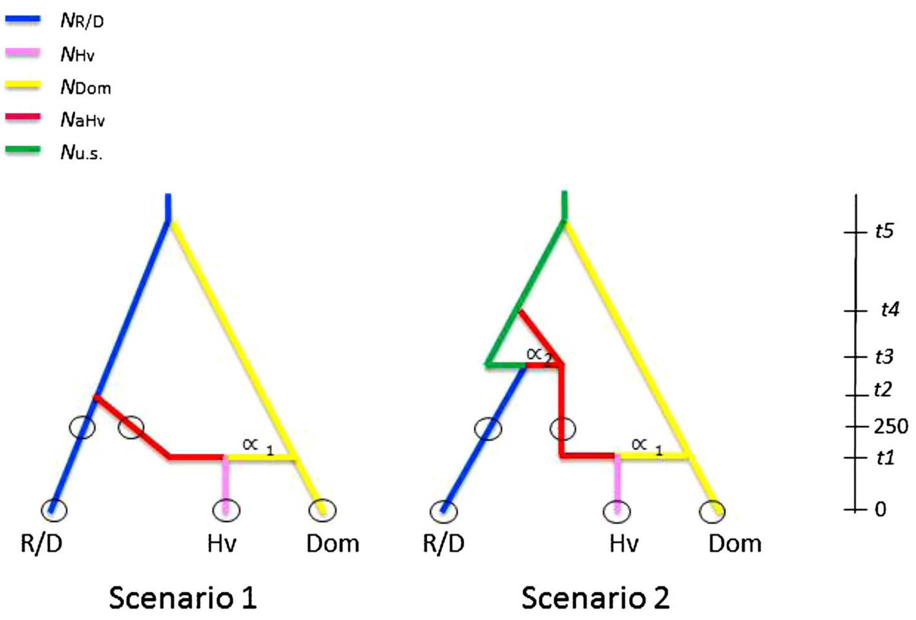

Fig. 2 The two main scenarios explored with the Approximate Bayesian (DIYABC) modelling to explain the genetic structure of Norwegian reindeer populations in Rondane/Dovre (R/D in *blue*), Hardangervidda (Hv in *pink*) and the domestic herds (Dom in *yellow*). We assumed a combined origin of Hv from domestic reindeer of fraction $\alpha 1$ and ancient Hardangervidda reindeer (aHv in *red*) of fraction 1- $\alpha 1$ at time t_1. Scenario 1 represents a simple split model in which aHv separated from ancient R/D at t_2 and these ancestors diverged from the ancient domestic lineage at time t_5. In scenario 2 R/D derives from admixture of aHv with proportion α_2 and some unsampled population (u.s. in *green*) with proportion 1- α_2 at time t_3. Further back the split between aHv and the unsampled population occurred at time t_4 following the earliest split between the unsampled and domestic lineages at time t_5. Sampling times are marked with circles. On the vertical axis, together with the times of major events (t_1–t_5), 250 generations BP is indicated, reflecting the age of the majority of the ancient material. (Color figure online)

Table 1 Parameter ranges, mean and median posterior estimates with 95 % highest posterior density interval (HPD) and mean relative posterior estimate bias (MRB) calculated from the most probable demographic scenario (scenario 2 in Fig. 2) in the Approximate Bayesian (DIYABC) modelling

Parameter	Prior parameter range	Mean	Median	$q_{0.05}$	$q_{0.95}$	MRB
$Nef_{\mathrm{R/D}}$	20–20,000	5,070	3,640	810	16,700	0.82
Nef_{Hv}	20–20,000	15,200	16,100	5,270	19,900	1.01
Nef_{Dom}	20–100,000	49,200	46,300	16,100	94,400	0.83
$Nef_{\mathrm{u.s.}}$	20–100,000	38,900	39,200	15,600	58,700	2.96
Nef_{aHv}	20–60,000	44,600	41,200	6,270	94,600	0.91
t_1	1–249	53	37	2	193	1.14
t_3	251–3,000	349	298	254	775	0.23
t_4	251–10,000	5,100	4,900	1,030	9,680	0.28
t_5	251–50,000	17,500	15,200	4,370	43,500	0.24
α_1	0.001–0.999	0.79	0.80	0.59	0.93	0.89
α_2	0.001–0.999	0.44	0.42	0.03	0.90	1.97
μ	10^{-9}–10^{-6}	7.24×10^{-7}	7.54×10^{-7}	3.10×10^{-7}	9.90×10^{-7}	1.26
t_2^{a}	251–3,000					

Parameter estimates are in units of female effective population size (*Nef*), time in generations (*t*) and mutation rate (μ) in substitution rate per site per year

R/D Rondane/Dovre, *Hv* extant Hardangervidda, *Dom* domestic reindeer, *u.s.* unsampled population, *aHv* ancient Hardangervidda

[a] Scenario 1

Table 2 Levels of genetic variability in 190 bp fragment of the mtDNA control region in ancient and extant wild reindeer herds and extant domestic herds in southern Norway

Mountain area	N	nh	h (SD)	Mean pairwise difference	π (SD)
Rondane/Dovre					
Ice patches	10	7	0.911 (0.077)	4.156 (2.238)	0.022 (0.010)
Tøftom	14	7	0.824 (0.078)	4.066 (2.145)	0.021 (0.013)
Vesle Hjerkinn	24	10	0.837 (0.051)	3.826 (1.987)	0.021 (0.012)
Ancient pooled	48	14	0.832 (0.036)	3.922 (1.998)	0.021 (0.012)
Extant[a]	70	10	0.422 (0.073)	2.008 (1.143)	0.011 (0.007)
Ottadalen					
Slådalen (ancient)	29	6	0.756 (0.053)	4.074 (2.092)	0.021 (0.012)
Extant	17	2	0.441 (0.098)	4.853 (2.478)	0.026 (0.015)
Hardangervidda					
Sumtangen (ancient)[b]	51	8	0.708 (0.059)	1.784 (1.049)	0.009 (0.006)
Extant[a]	68	21	0.800 (0.040)	6.348 (3.047)	0.033 (0.018)
Domestic (extant)[a]	42	6	0.530 (0.082)	4.677 (2.337)	0.025 (0.014)

N number of individuals, *nh* number of haplotypes, *h* haplotype diversity (±SD), π = nucleotide diversity (±SD)

[a] From Røed et al. (2008)

[b] From Røed et al. (2011)

observed data in summary statistics. They were also compared by logistic regression based on predicting the probability of a scenario from the deviation in the summary statistics among the closest simulated and observed data sets using the 1 % of simulated data closest to the observed data set (Cornuet et al. 2010). Confidence in scenario choice was evaluated by a posteriori simulations separately for the best model using the same prior distributions. To obtain parameter estimates, the most likely scenario was re-simulated for 1×10^7 iterations, and using the 0.1 % simulations most similar to the observed data set in summary statistics. In order to evaluate the performance of the estimation procedure, we also estimated the mean relative bias (MRB) by comparing 500 generated pseudo-observed data sets with known parameter values drawn from the posterior distribution of the most likely scenario (Cornuet et al. 2010).

Results

Among the 104 ancient samples analysed, reproducible mtDNA sequences were obtained from 77 (Table 2). Nucleotide substitutions defined 16 mtDNA haplotypes, of which seven were singletons and six were detected more than twice. Including the 51 ancient Hardangervidda samples (Røed et al. 2011), the total number of haplotypes increased to 20 defined by 13 variable sites. From the 17 extant Ottadalen reindeer the 470 bp sequence defined three mtDNA haplotypes, all of which previously have been detected among the extant Fennoscandian reindeer (Røed et al. 2008). These three haplotypes were reduced to two after adjusting the sequences to 190 bp.

The amount of variation and the haplotype distribution in the material from the ice patches and from the hunting station in Tøftom and Vesle Hjerkinn were similar (Table 2). There was no genetic differentiation between the three sample sets ($F_{ST} \sim 0$, $P > 0.3$), thus the three sets were pooled (i.e. Rondane/Dovre) in further between-population analyses.

The nucleotide diversity was similar for the ancient Rondane/Dovre and ancient Ottadalen reindeer while the haplotype diversity was slightly lower in Ottadalen than in Rondane/Dovre (Table 2). The ancient Hardangervidda reindeer had a lower level of variation as compared to the two other ancient samples (Table 2). The ancient Rondane/Dovre reindeer showed higher variation than the extant herds from the same region, with 14 haplotypes observed among 38 ancient specimens compared to 10 haplotypes in 70 extant specimens. The nucleotide and haplotype diversity estimates were approximately halved in the extant Rondane/Dovre herds compared to the ancient herds, while the opposite trend was indicated in the Hardangervidda reindeer with lower haplotype and nucleotide diversity in the ancient as compared to the extant reindeer (Table 2).

Strong genetic differentiation was found both temporally, among extant and among ancient wild reindeer herds, except between ancient Rondane/Dovre and ancient Ottadalen ($F_{ST} = 0.047$, $P = 0.054$) (Table 3). In the haplotype network (Fig. 3) most of the haplotypes were included in the five previously denoted clusters; **I**, **Ib**, **II**, **III** and **IV** (Røed et al. 2008; Bjørnstad and Røed 2010). Six of the haplotypes have not been previously published. These were located within haplotype cluster **I** or **III** together with all the other haplotypes of the ancient material (Fig. 3). Notably, most haplotypes in extant Rondane/Dovre also belonged to haplotype clusters **I** or **III**. By comparison, the two extant Ottadalen haplotypes, most domestic and many of the extant Hardangervidda haplotypes were located in haplotype clusters **Ib** and **II**,

Table 3 Pairwise genetic differences (F_{ST}) between ancient and extant reindeer herds in Norway

Mountain area	Rondane/Dovre		Ottadalen		Hardangervidda	
	Ancient	Extant	Ancient	Extant	Ancient	Extant
Rondane/Dovre						
Ancient						
Extant	0.231***					
Ottadalen						
Ancient	0.047^{ns}	0.414***				
Extant	0.447***	0.584***	0.460***			
Hardangervidda						
Ancient	0.286***	0.568***	0.297***	0.671***		
Extant	0.315***	0.393***	0.330***	0.131*	0.397***	
Domestic						
Extant	0.519***	0.602***	0.532***	0.285***	0.619***	0.057**

Significant levels given as ***$P < 0.0001$, **$0.001 < P < 0.01$, *$0.01 < P < 0.05$ and *ns* non-significant

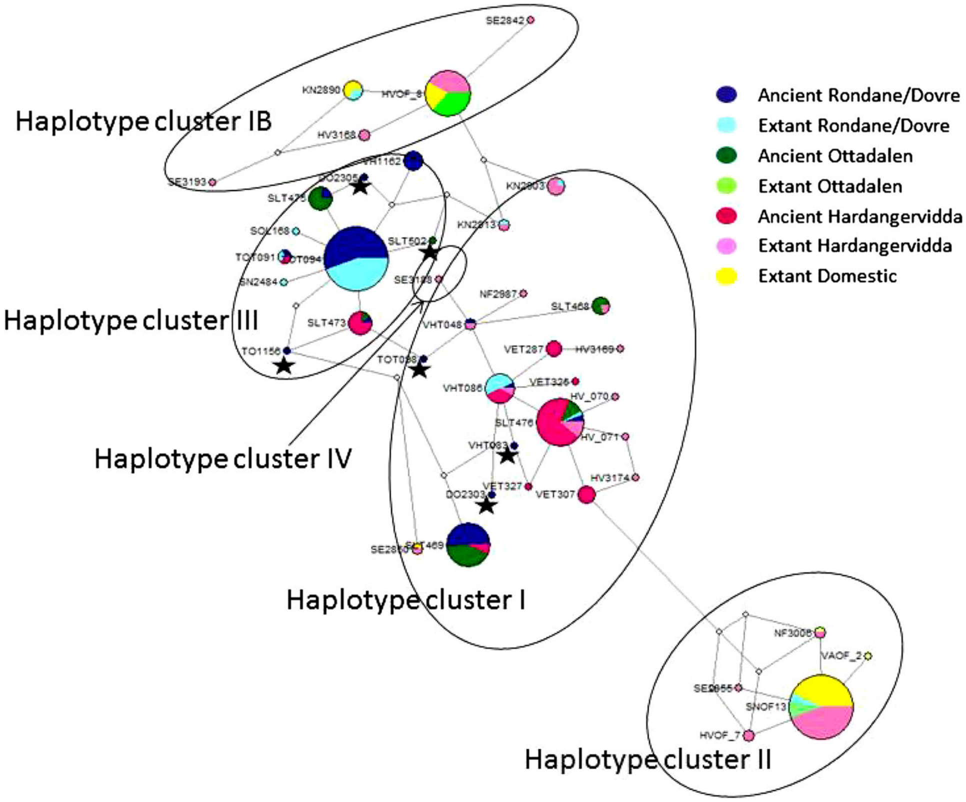

Fig. 3 Median-joining network of the mtDNA haplotypes obtained from ancient and extant reindeer herds in south-central Norway. The size of the circles reflects the relative frequencies of the haplotypes. Haplotypes belonging to clusters are encircled based on the clustering groups employed in extant reindeer using a 470 bp fragment (Røed et al. 2008) and in museum samples using a 190 bp fragment (Bjørnstad and Røed 2010). Notably, the haplotypes Kn2803 and Kn2813, present only in extant wild reindeer, could according to the network be located to haplotype cluster **Ib** or **III** but were previously located to cluster **I** (Røed et al. 2008). New haplotypes are marked with a *star*

demonstrating a major genetic change in the Hardangervidda and Ottadalen herds since the medieval period (cf. Fig. 4).

Temporal change and loss of genetic variation in the Rondane/Dovre herds was reconstructed in the Bayesian skyline plot (Fig. 5). The Bayes Factor test indicated that the skyline population size model was a better fit to the data than the constant population size model (Bayes factor $>10^4$). The analyses suggested a decreased female effective population size within few centuries around 1,000 yrBP (Fig. 5). The estimated substitution rate was 8.26×10^{-7} substitutions per site per year [95 % highest posterior density interval (HPD) 1.5×10^{-7}–1.6×10^{-6}]. Excluding the ancient Ottadalen haplotypes gave the same temporal pattern of population decline (data not shown).

The modelling within the DIYABC framework gave similar posterior probabilities and parameter estimates whether the five extant reindeer in Rondane/Dovre with assumed domestic ancestry were included or not. Only results where they were excluded are presented. The ABC

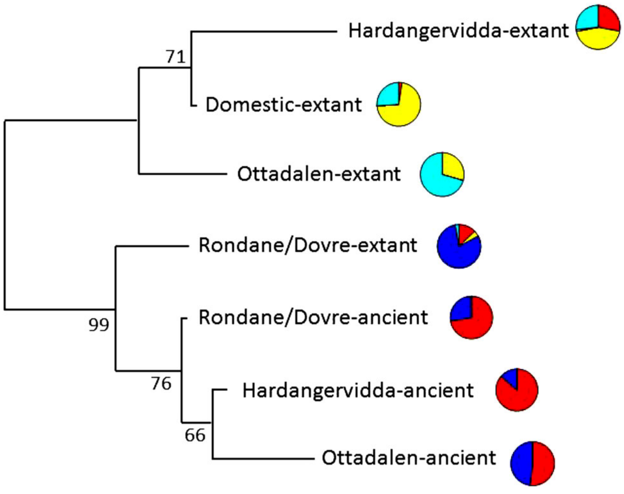

Fig. 4 Population dendrogram based on mtDNA genetic distances between reindeer herds (ancient and extant) in southern Norway with support values from 1,000 bootstrap replicates at the nodes. The proportional presence of the haplotype clusters in each of the populations are shown in pie diagrams (*red* cluster **I**, *turquoise* cluster **Ib**, *yellow* cluster **II**, *blue* cluster **III** and *grey* cluster **IV**). (Color figure online)

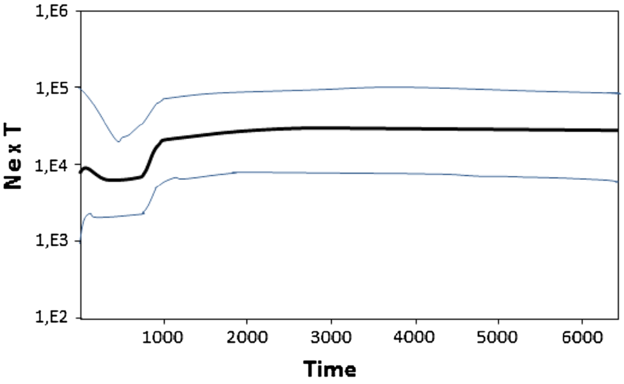

Fig. 5 Bayesian skyline plot of temporal changes in population size of reindeer in the Rondane/Dovre/Ottadalen mountain area in central Norway derived from 77 ancient (Rondane/Dovre/Ottadalen) and 70 extant (Rondane/Dovre) sequences (190 bp) of mtDNA control region. Time refers to calendar years before present and the y-axis gives the product of effective population size (*Ne*) and generation time (*t*). *Black line* represents median estimate and *blue lines* the 95 % highest posterior density intervals. (Color figure online)

modelling revealed that the most likely among the eight explored scenarios involved a common origin of ancient Rondane/Dovre and ancient Hardangervidda, but subsequent immigration and admixture into the ancient Rondane/Dovre herds from an unsampled population of an older origin (scenario 2, Fig. 2). The posterior probability (PP) for this scenario using a direct estimate and logistic regression was 0.70 (95 % HPD 0.58–0.82) and 0.96 (95 % HPD 0.92–1.00), respectively. Support for the pure split model (scenario 1, Fig. 2) was much lower with both a direct estimate (0.15, 95 % HPD 0.05–0.24) and logistic regression (0.04, 95 % HPD 0.00–0.07). Even less support was found for the models including demographic events ($PP < 0.1$, Table S3, Supporting Information available online).

DIYABC parameter estimation for scenario 2 involved medium to low MRB with the time estimates at the low scale (Table 1). Based on an assumed average generation time of four years, the estimated time since a MRCA (t_5) and since the origin of the unsampled population (t_4) correspond to some 70,000 and 20,000 years ago which are both well into the last ice age period (Weichselian) when Scandinavia was covered with ice. By comparison, the introgression from the unsampled population into the Dovre/Rondane area (at time t_3) was estimated to have occurred more recently, possibly during the first millennium AD (Table 1). The estimate of some 40–50 generations since the admixture of the domestic lineage and the ancient Hardangervidda herds corresponds well with the first known introduction of domestic reindeer to Hardangervidda in 1785, giving further confidence to the parameter estimates of this model. The analysis assumes no migration between historic events, implying that the divergence time estimates are to be treated as minimum estimates. A skew in the posterior distribution of the time estimates was particularly apparent for t_4 (Fig. S2, Supporting Information available online) where a shoulder-shaped tail may reflect an older split between ancient Rondane/Dovre/Hardangervidda and the unsampled population, followed by subsequent gene flow.

Discussion

Our genetic analyses show the presence of two mtDNA lineages among the samples of ancient reindeer, while two additional lineages are found among the extant Norwegian wild reindeer (cf. Fig. 4). Previous investigations suggest that the two former lineages are typical for native wild reindeer in Scandinavia while the two latter lineages, which characterise domestic reindeer, are indicative of a non-indigenous origin (Flagstad and Røed 2003; Røed et al. 2008, 2011). The two lineages found among the ancient samples still characterize the extant populations in the Rondane/Dovre mountain area, while the two additional lineages are common in extant Hardangervidda and dominate the extant Ottadalen and domestic reindeer. All herds have to various extents gone through profound genetic changes in their maternally inherited mitochondrial genome since the medieval period. Extant Rondane/Dovre reindeer have been exposed to demographic fluctuation resulting in loss and alteration of genetic variation, while the reindeer of Hardangervidda and Ottadalen appear to have been exposed to large-scale genetic alterations due to intercrosses or swamping from a domestic gene pool.

The sequence fragment used in the present study is located within the most variable part of the control region, involving possible overestimates of diversity and substitution rates, particularly when comparing with other studies. However, loss of genetic diversity in extant populations compared to ancient gene pools has also been reported in other large ungulates (Anderung et al. 2006; Campos et al. 2010; Rosvold et al. 2012). Our Bayesian skyline reconstruction of changes in genetic diversity through time in the Rondane/Dovre reindeer suggests a relatively stable female effective population size until the late Viking age/early medieval period when the effective population size decreased over a short time period during the 11th–12th centuries. This clearly predates the beginning of the 20th century when this population was reported to be at a very low number after the introduction of firearms (Skogland and Mølmen 1980). During the late Viking/early Middle Ages there were no known environmental or climatic changes that would explain a population reduction of reindeer in southern Norway (Matthews and Dresser 2008). Rather, the decline coincides well with a period of extensive mass-trapping of reindeer in the mountains of southern Norway, as documented by large scale trapping systems and the many large refuse heaps dominated by reindeer bones (Jordhøy 2008; Indrelid and Hufthammer 2011). One example is the trapping system at Sumtangen (Hardangervidda) where one part of the trapping location had an estimated outtake of 7,800 individuals during a period of probably less than 50 years during the 13th century (Hufthammer et al. 2011).

Population reduction has probably also affected gene flow and population fragmentation. Indeed, the much stronger spatial genetic differentiation between extant Rondane/Dovre and Ottadalen as compared to between the ancient herds in Rondane/Dovre and Ottadalen suggests considerably more ancient than extant gene flow between these mountain areas. Location and organization of some of the ancient trapping systems suggest ancient spring migration of reindeer from Rondane/Dovre to Ottadalen (Jordhøy et al. 2005). In central and southern Norway seasonal migration of reindeer largely follows an east–west gradient, with wintering in the eastern continental climate and summering in the moist western climate (Skogland and Mølmen 1980) and ancient reindeer pitfall systems have thus traditionally been located crosswise such migration routes (Jordhøy et al. 2005). However, infrastructure development during the last century in the valleys separating these mountain regions have been extensive and includes heavily used railways and main roads, human settlements, cabin villages and hydropower development, all constituting migration obstacles for reindeer (Vistnes et al. 2004, Panzacchi et al. 2013).

Although the genetic constitution of the reindeer in Rondane/Dovre has changed since the medieval period, its extant herds are most similar to its ancient herds in their mitochondrial genomes (see Fig. 4), suggesting a mainly native origin for these herds. However, the extant herds in Rondane/Dovre also hold a small fraction (0.07) of haplotypes belonging to cluster **Ib** and **II**, not detected in the ancient material. These haplotypes are characteristic of the domestic reindeer in Scandinavia (Røed et al. 2008, 2011; Bjørnstad et al. 2012), and their presence in the extant wild gene pool indicates domestic introgression. This fraction of domestic introgression into the Rondane/Dovre herds may well be downward biased as only mtDNA analyses were applied and male-biased dispersal have been reported for reindeer (Roffler et al. 2012). However, individual ancestry analyses based on nuclear microsatellites show that among extant wild and domestic herds in southern Norway, the Rondane/Dovre reindeer assigns as a separate cluster holding only a very small fraction of individuals (<0.03) with ancestry of significance (>20 %) to the domestic cluster (Reimers et al. 2012). This suggests that the domestic introgression into the wild Rondane/Dovre has had a limited impact on both the mitochondrial and the nuclear genome.

The neighboring mountains to the north, Trollheimen and Forollhogna, presently harbor domestic herds and wild reindeer with a recent and mainly domestic origin (Røed et al. 1987; Reimers et al. 2012) and recent gene flow from these areas seems likely. Prehistoric migration of wild reindeer between these areas and Rondane/Dovre is indicated by the many strategically located reindeer pitfall systems across potential migration routes (Jordhøy et al. 2005), supporting an ancient far-ranging use of the mountain habitats by the reindeer. The large ancient population sizes of Rondane/Dovre indicated by the BEAST and ABC analyses could thus also reflect a broader population in ancient times, including Trollheimen and Forollhogna.

The evolutionary history of reindeer has probably been highly influenced by glacial and interglacial effects, and a large continuous Eurasian glacial population appears to be the most influential origin of the current gene pool of the species (Flagstad and Røed 2003; Yannic et al. 2014). Haplotype cluster **II,** dominating the domestic reindeer in Scandinavia, has previously been hypothesized to have evolved in southern Europe isolated from this large Eurasian population (Flagstad and Røed 2003). This scenario is supported by the ABC modelling, giving an estimated mean separation time of this lineage more than 15,000 generations ago. Apparently, haplotype cluster **II** and **Ib** were absent from the ancient herds in both south-central

Norway and northern Norway (cf. Bjørnstad et al. 2011), leaving an unresolved question of where these lineages were distributed before mixing with husbandry practices.

The Last Glacial Maximum (LGM; 19–27,000 yrBP, Clark et al. 2009) coincides well with the ABC estimate mean of 5,000 generations since a common origin of the unsampled population and ancient herds in southern Norway (t_4). During both this period and later periods, genetic differentiation could have developed within the large Eurasian population due to founder events and isolation after successive leading edge expansions. The different lineages dominating the ancient herds in Hardangervidda and Rondane/Dovre could thus possibly reflect origins from such different sub-populations with subsequently different colonization routes or colonization waves of reindeer after the retreat of the ice. Alternatively, these lineages separated after the colonization of Norway through population expansion and subsequent fragmentation. As the climate got warmer, the habitat changed and large parts of Hardangervidda became forested during the Holocene warm period (9,000–5,000 YrBP, Moe 1973; Nesje et al. 2006). However, even though the range of the ABC estimate is wide (t_4, Table 1), its posterior distribution (Fig. S2, Supporting Information available online) rather suggests an ancient split 5–6,000 generations ago. Thus, the genetic signatures in ancient Rondane/Dovre and Hardangervidda most likely reflect two different migration routes into Southern Scandinavia and how these waves of migration affected the two populations differently.

The temporal shift of haplotypes on Hardangervidda from an ancient dominance of haplotype cluster **I** and **III** to modern high frequencies of cluster **II** and **Ib** was probably caused by large-scale introgression of domestic reindeer during the last century when reindeer husbandry was practiced in this mountain region (Røed et al. 2011). In Ottadalen, there was a more dramatic change to only haplotypes of cluster **Ib** and **II** in contemporary samples, which is in accordance with the domestic stock used to re-establish this population about 50 years ago. Extensive introgression or encroachment of domestic or feral animals into wild taxa has also been reported in a wide range of species including American mink (*Mustela vison*; Bowman et al. 2007; Kidd et al. 2009), European cats (*Felis silvestris;* Oliveira et al. 2008) and European wild boar (*Sus scrofa*; Goedbloed et al. 2013), while a more restricted hybridization has been reported in introduced versus native taxa as in red fox (*Vulpes vulpes*; Sacks et al. 2011), arctic fox (*V. lagopus;* Norén et al. 2009) and the wolf-dog (*Canis lupus*) complex (Randi 2008; Anderson et al. 2009). Recently, Mager et al. (2013) documented some admixture of introduced domestic reindeer and native wild caribou herds in Alaska and suggested that herd size may have influenced the susceptibility to reindeer introgression. Similarly, our results indicate that the wild Norwegian reindeer herds experienced population reductions and fragmentation prior to the introduction of domesticated herds which may have facilitated the introgression of foreign genes into the herds.

The ecological and evolutionary effects of swamping native genomes have received increased attention within animal conservation. Introgression of domestic alleles might disrupt local adaptations, lead to population decline, loss of genetic diversity and population extinction (e.g. Allendorf et al. 2001; Randi 2008; Laikre et al. 2010). However, exogenous alleles may also compensate for loss of genetic variation or act as a source of novelty that might increase the potential for adaptation to changing environments (Anderson et al. 2009; Fitzpatric et al. 2010; Feulner et al. 2013; Lamaze et al. 2013). To what extent the domestication process of reindeer has altered genetic adaptability is uncertain, as the domestication process is considered to be in an early phase (Reimers and Colman 2006). Herding practices are usually characterized by keeping animals in large free-ranging herds in their natural habitat where natural selection may act. In most species domestication has involved selection for tameness and reduced escape behaviors (Price 1984). Behavioral studies of Norwegian wild reindeer herds have shown a reduced vigilance, alert and flight response associated with the degree of domestic ancestry in each herd (Reimers et al. 2012), indicating introgression of genes associated with tameness from the domestic stock. A continued prevalence of any such introgressed genes would not be surprising given the efficient predator control that has characterized the management policy of the Norwegian wild reindeer habitat during the last century.

Conservation and management implications

Conservation of native gene pools compared to foreign ones generally has higher priority within wildlife management (e.g. Laikre et al. 2010). The extant reindeer herds distributed in the mountains of Rondane/Dovre mainly represent the native gene pool and seem to be the only contemporary population that harbor haplotypes of cluster **III**, suggesting that a particularly high priority should be given to the protection of these herds. However, the small but significant introgression from the domestic gene pool may, if continued, threaten the genetic distinctness of this population. The previous genetic homogeneity points towards a common management of the herds in the region rather than the present practice with separate management for the sub-population within the region. Also the Hardangervidda mountain plateau warrants high priority as it harbors the largest extant wild reindeer population left in

Europe and because it still contains a considerable proportion of the ancient native gene pool which is different from that in Rondane/Dovre.

A more challenging issue is whether introgression from the foreign domestic gene pool and/or using domestic animals for re-establishing wild populations represents sustainable strategies to compensate for the ongoing alpine habitat deterioration and loss of the native gene pools. Such re-establishment appears to have been successful, at least on a short term scale, for both the presently studied Ottadalen population and for other wild reindeer populations in southern Norway (e.g. Forollhogna and Reinsjø-Norefjell, cf. Reimers et al. 2012). This may reflect a wide adaptability of the semi-domestic form of the species, possibly particularly within a highly fragmented landscape with substantial human influence.

The putatively different refugial origins of the lineages represented by the extant herds in Rondane/Dovre, Hardangervidda and those with a mainly domestic origin may well reflect different adaptation to environmental conditions including degree of human interference. Future research on the phylogeographic origin and colonization of these lineages into Scandinavia following the retreat of the glaciation would be informative regarding understanding the adaptations underlying their potential functional differences. This would provide important insights for sustainable and flexible management strategies of the remaining wild reindeer herds in the Scandinavian mountains.

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