



Sheep and cattle population dynamics based on ancient and modern DNA reflects key events in the human history of the North-East Baltic Sea Region



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ABSTRACT

Genetic data from ancient and modern domestic animals holds tremendous potential to reveal long term trends in population histories. Reconstruction of effective population sizes based on temporally well covered data may reveal the effects of particular events in the early history of animal populations as well as reflect the changes in the lifestyle and society of past human populations. We used an Extended Bayesian Skyline Plot approach to estimate the effective population sizes (N_e) and their temporal changes in sheep and cattle from Late Bronze Age to present in North-East Baltic Sea Region (NEBSR). The results support previous results from ancient DNA analyses (mtDNA, Y-chromosome, *MC1R*) in the NEBSR for cattle and reveal previously unidentified temporal fluctuation for sheep (mtDNA, Y-chromosome). The sheep and cattle N_e increased during the Iron Age, reaching their maximum at the Late Iron Age/Medieval period followed by deep decline in sizes until the present. Decline in N_e simultaneously with increase in total population sizes indicate selection and increasing inbreeding from the beginning of Post Medieval period to the middle of the 20th century. The timing of the increase in sheep and cattle N_e is roughly the same as the timing of transition from hunting-gathering to farming in Iron Age (400–1000 CE).

1. Introduction

Cattle and sheep were domesticated from wild ox and Asiatic mouflon in the Near East around 10,500 and 11,000 BP, respectively (Bollongino et al., 2012; Zeder, 2008). Domesticated cattle and sheep reached Northernmost Europe by 3000 BP (Bläuer and Kantanen, 2013). After the first arrivals, the amount of domestic animals likely stayed low for thousands of years (Bläuer and Kantanen, 2013). From Middle and Late Iron Age (MIA, 400–800 CE and LIA, 800–1200 CE) a larger amount of domestic animal bones has been found from archaeological sites (Bläuer, 2015; Rannamäe et al., 2016b). Official statistics and historical inventories from Finland indicate increase in the total amount of cattle and sheep in Finland from Post-Medieval (PME) until industrialization and urbanisation at the latter half of the 20th century (Fig. 1). Changes in the effective population sizes (N_e), needed for the understanding of history and diversity of cattle and sheep in Northern Europe are, however, poorly recorded.

Earlier genetic studies on North-East Baltic Sea Region (NEBSR) cattle and sheep have suggested partly contradictory conclusions between the two species. Temporal fluctuation detected in cattle (Niemi et al., 2015; Niemi et al., 2016) was not detected in sheep (Niemi et al.,

2013; Rannamäe et al., 2016a, 2016b), although similar geographical pattern of appearance or loss of specific mtDNA haplotypes during the expansion from Near East across Europe to NEBSR have been suggested for both species (Niemi et al., 2015; Rannamäe et al., 2016a).

Here we combine genetic, historical, and statistical approaches in order to explore more closely the timing and causes of temporal fluctuation in domestic animal populations within the NEBSR. For this purpose, we reanalyse existing ancient and modern genetic datasets from NEBSR sheep and cattle along with new *MC1R* sequences from 34 present-day Finncattle. By adopting Extended Bayesian Skyline Plot (EBSP) approach, we reconstruct the effective population sizes (N_e) of cattle and sheep through time. We compare and combine the estimated N_e to the total number of animals (N) reconstructed based on official statistics of modern times and research on historical Medieval and Post-Medieval writings and stock inventories. We explore the heterochrony bias in the NEBSR sheep and cattle cohorts pooling samples from narrow to wide time spans, and compare temporally grouped approaches to temporally continuous analyses of the EBSP. Results obtained with the EBSP, population diversity estimates and bias within data are compared and discussed in perspective of known historical events in the NEBSR.

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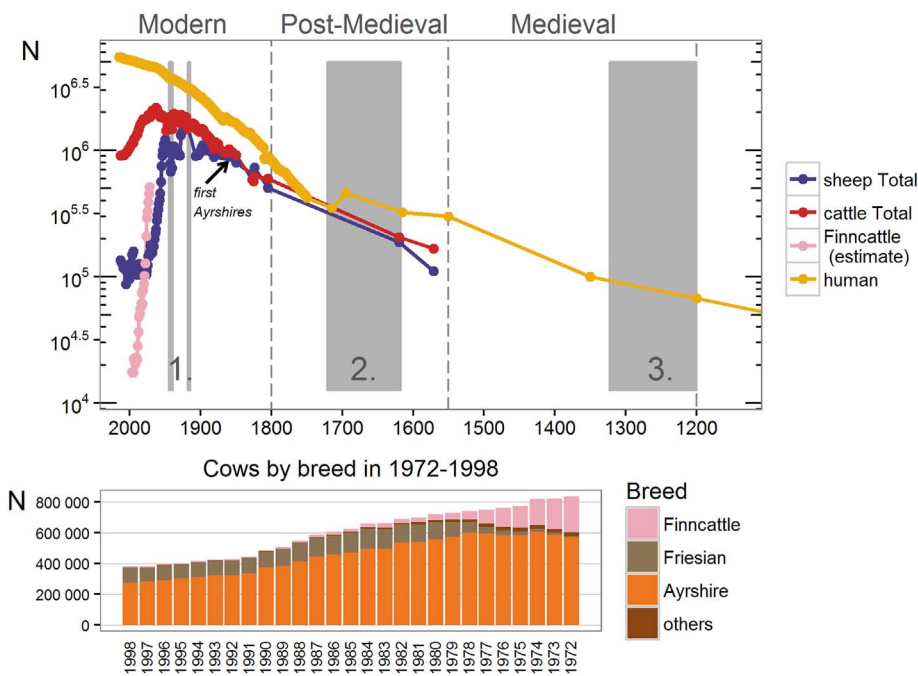


Fig. 1. Development of total population sizes of sheep, cattle and humans in Finland from Medieval to modern periods. Estimate for the total number of Finncattle (given in pink for the years 1972–1998, upper panel) is based on the proportion of Finncattle cows from all cows (lower panel) from the corresponding period (lower panel). The introduction of global dairy breed Ayrshire in 1847 is indicated (black arrow, upper panel) for timing the start of replacement of native cattle breeds with commercial dairy breeds. Figures are based on Official statistics of Finland, Tike, Statistics Finland and historical inventories (Appendix A.1). Grey horizontal rectangles in the upper panel show the timing of tree historical events: 1.) wars (1914–1918, 1939–1945 CE) in modern times, 2.) The Swedish Empire [(1617–1721 CE), including the Thirty Years War (1618–1648 CE), severe starvation (1695–1697 CE) and the Great Northern War (1700–1721 CE)] in Post-Medieval, and 3.) several crusades, spread of Christianity and church establishing (1200–1323 CE) in early Medieval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Material and methods

2.1. Mitochondrial DNA data

In total, 95 and 45 ancient Finnish and Estonian sheep and cattle mtDNA sequences dating from Late Bronze Age (700 BCE) to the Post-medieval (1800 CE) time (Niemi et al., 2013, 2015; Rannamäe et al., 2016a, 2016b) were retrieved from GenBank (accession codes provided in Appendix A.1). Samples for which the dating (radiocarbon or dating by the context) was vague, ranging over 300 years, were excluded. The temporal coverage of the data was complemented by inclusion of a modern cohort of native breeds. The breeds used to form the modern cohort were Finnsheep ($n = 15$), Viena ($n = 9$), Åland ($n = 9$), Kainuu Grey sheep ($n = 8$) (Niemi et al., 2013) and Estonian Kihnu ($n = 44$) (Rannamäe et al., 2016b) for sheep, and Eastern ($n = 18$), Western ($n = 7$) and Northern ($n = 8$) Finncattle, Estonian red ($n = 4$) and Estonian native ($n = 5$) for cattle (Kantanen et al., 2009). The more recently imported commercial breeds, like Finnish Ayrshire, were excluded from the data. The breeds used to form the modern cohort are the known local breeds to the NEBSR, and therefore form suitable continuum for the ancient data.

In order to evaluate possible geographical differences in temporal development of N_e , additional grouping by the country (Finland or Estonia) was conducted for sheep. The Finnish data consists of 26 and 41 samples from ancient sheep and four modern local breeds from the corresponding geographical region from Finland and Russian Karelia (Finnsheep, Viena, Finnish grey landrace and Åland sheep). The Estonian data consists of 69 Estonian ancient and 44 samples from Estonian native Kihnu sheep. For cattle the possible geographical differences were not considered due to insufficient amount of data for the division by the country.

2.2. Genomic DNA data

For cattle two nuclear loci were used in the analyses along with mtDNA data. For ancient samples we used 23 sequences from the *Melanocortin 1 Receptor (MC1R)*, targeting two SNPs defining the tree main alleles underlying red, wild and black coat colour (Niemi et al., 2016), and 7 sequences from the Y-chromosomal *UTY19* marker defining the Y1 and Y2 haplotypes (Niemi et al., 2015). The colour of

cattle at NEBSR was not selected in historical periods. Systematic selection for colour started first in the 20th century when phenotypes of red, red-and-white and white with black or red marks were set for Western, Eastern and Northern Finncattle, respectively (Niemi et al., 2016). All *MC1R* alleles (E^D , E^+ and e) are still common and not (yet) fixed in Finncattle (this study, see Section 2.3). Thus selection for colour (*MC1R* locus) should not have affected the reconstruction in cattle. The modern *UTY19* data consist of 21 individuals from three NEBSR breeds: Western, Eastern and Northern Finncattle (Götherström et al., 2005; Edwards et al., 2011). To analyse *MC1R* from the same three contemporary Finncattle breeds, hair samples from 34 individuals (18, 12, and 4 from Western, Eastern and Northern Finncattle, respectively) were collected from Ahlman (Tampere, Finland) institutes' conservation stocks. DNA was extracted from the hair samples and sequenced as described in Appendix A.1. For sheep, Y-chromosome SNP marker genotypes for *oY1* from 5'-promoter region of the *SRY* gene were deduced from published sequence for six ancient (Niemi et al., 2013; Rannamäe et al., 2016a) and 24 contemporary NEBSR sheep (Finnsheep, Viena and Åland sheep breeds; (Meadows et al., 2006)), and analysed along with the mtDNA.

2.3. Alignments and summary statistics

Mitochondrial DNA d-loop sequences were aligned separately for both species with ClustalW (Thompson et al., 1994) in Mega6 (Tamura et al., 2013) excluding alignment gaps. The lengths for the common alignment were 523 and 245 base pairs (bp) for sheep and cattle, respectively. Diversity estimates (S , h , Hd and π) for each cohort of sheep and cattle were calculated using DnaSP v5.10.01 (Librado and Rozas, 2009). Next we selected the most appropriate evolutionary model for DNA substitution and rate variation among sites to be used in the EBSP analyses and to generate initial trees for the reconstruction. We used Bayesian Information Criterion (BIC) to select among 88 candidate models in jModelTest v2.1 (Posada, 2008). The best fit models for sheep and cattle were Hasegawa-Kishino-Yano model with invariant sites (HKY + I) and the same model with gamma shape (HKY + G), respectively.

The newly sequenced *MC1R* sequences of contemporary Finncattle were aligned with ClustalW (Thompson et al., 1994) in Mega6 (Tamura et al., 2013). Allele frequencies (0.66, 0.10, and 0.24, for e (68 bp), E^D

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