Genetic diversity and pedigree analysis of the Finnsheep breed

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ABSTRACT: Genetic diversity in the Finnsheep breed was analyzed by quantifying the demographic trends, the depth of known pedigree, effective population size, and the amount of inbreeding, as well as identifying candidate rams within the current population for future breeding and conservation purposes. Pedigree records of 148,833 animals with a pedigree completeness coefficient ≥0.60 and born from 1989 to 2006 were used to estimate the parameters. Mean inbreeding coefficient increased by 0.10% \((P < 0.001)\) and 0.15% \((P < 0.001)\) per annum in all animals and breeding (i.e., reproducing) animals, respectively. Average relationship coefficients among rams, among ewes, and between rams and ewes in breeding animals increased over time and reached 1.67, 1.45, and 1.46% in the 2005 cohort, respectively. The average for breeding rams was above the other 2 averages in almost all birth years. The observed generally low average relationship coefficients between rams and ewes indicate that no extra restrictions on the use of the breeding animals are needed in the near future. Average generation interval was 2.85 yr in the studied period, and the effective population size was estimated to be 119 and 122 using different methods. Relationship coefficients of rams with other breeding rams and rams with breeding ewes are suggested to aid in situ and ex situ conservation decisions on maintaining genetic diversity of Finnsheep.

Key words: effective population size, Finnsheep, genetic diversity, inbreeding, pedigree analysis

INTRODUCTION

The Finnish native sheep, Finnsheep, is an extremely prolific breed, exhibiting several components of fertility such as early sexual maturity, high ovulation rate, out-of-season lambing, and large litter size (Maijala and Österberg, 1977; Maijala, 1984, 1988, 1997). In addition, a considerable proportion of the animals produce good quality wool in a variety of natural colors with desirable characteristics (Maijala, 1988, 1996). Thus, the Finnsheep has been exported to more than 40 countries for experiments on prolificacy and for creating new breeds (Fahmy, 1996).

Originally, Finnsheep were used mainly for serving domestic needs for wool and fur, but since the 1950s the main use has gradually shifted to meat production, whence prolificacy is highly appreciated. Since the 1980s, multi-purpose use has been considered important for the Finnsheep in Finland (Puntila and Maijala, 1987). Population size of the Finnsheep has varied principally according to human needs and product prices. Their numbers declined dramatically during the period of 1950 to 1970. Currently, there are fewer than 15,000 ewes and 1,000 breeding rams in Finland.

Keeping a limited number of breeding animals will inevitably lead to increased inbreeding in a closed population, and thus to reduction in additive genetic variance and possibly to inbreeding depression (Carolinno and Gama, 2008). Earlier studies evaluated genetic variation within Finnsheep using molecular genetic markers (Tapio et al., 2003, 2005), but no genetic diversity analyses based on pedigree data have been presented.

The objectives of this study were to explore the demographic trends and the status of genetic diversity in the Finnsheep population in terms of the amount of inbreeding, effective population size, and coefficients of relationship, estimate average generation intervals, and secure baseline information to advance conservation strategies aimed at maintaining genetic diversity of this sheep breed in the future.
MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because only pedigree records of animals were used.

Data

In the present analyses we considered the Finnsheep population in Finland. The database kept by ProAgria Association of Rural Advisory Centres in Finland has pedigree records for 319,119 Finnsheep individuals. The records contain information on individual identification code, sex, dam and sire identification codes, flock of origin, and birth date.

Pedigree Analysis

A breeding population changes through selection decisions. This may affect numbers of animals in time, and therefore changes in the number of animals by birth year were studied. Further pedigree analysis included calculation of pedigree completeness, inbreeding coefficients, estimation of effective population size, and average relationship coefficients between groups of animals.

Pedigree Completeness. As the quality of available pedigree information is of great importance in assessing inbreeding and trends in inbreeding, a coefficient for pedigree completeness (PEC) was computed, and the degree of completeness of pedigree was assessed using the index proposed by MacCluer et al. (1983):

\[ PEC_{animal} = \frac{2C_{sire} C_{dam}}{C_{sire} + C_{dam}}, \]

where \( C_{sire} \) and \( C_{dam} \) are contributions from the paternal and maternal lines, respectively. The contributions are computed as

\[ C = \frac{1}{d} \sum_{i=1}^{d} g_i, \]

where \( g_i \) is the proportion of ancestors present in generation \( i \) and \( d \) is the total number of generations taken into account. In this study, 5 ancestor generations were considered (\( d = 5 \)). The average pedigree completeness index for the 5 generations was calculated according to the birth year. Only animals with \( PEC \geq 0.6 \) were included in further analyses. The analyses sometimes involved all animals with \( PEC \geq 0.6 \), and at other times they were restricted to the subset of animals that comprised just the breeding (i.e., reproducing) animals.

Generation Intervals. The generation intervals \( (l) \) were calculated along the 4 gametic pathways: ram to son \( (l_{mm}) \), ram to daughter \( (l_{mf}) \), ewe to son \( (l_{fm}) \), and ewe to daughter \( (l_{ff}; \text{Rendel and Robertson, 1950}) \). The 4 section pathways were obtained from records of birth dates of breeding animals in each year and the birth dates of their sires and dams. The average generation interval (\( \bar{l} \)) was subsequently computed from

\[ \bar{l} = \frac{l_{mm} + l_{mf} + l_{fm} + l_{ff}}{4}. \]

Inbreeding Coefficient. Inbreeding coefficients \( (F) \) for all animals and breeding animals (i.e., all with \( PEC \geq 0.6 \)) were computed using the RelaX2 program (Strandén and Vuori, 2006). The average inbreeding coefficients were then calculated to monitor the changes in the level of inbreeding by year. A linear regression line was fitted to these values to estimate annual average increase in inbreeding within the 2 animal groups.

Effective Population Size. The effective population size is the number of breeding animals that would lead to the observed increase in inbreeding if they contributed equally to the next generation (Gutiérrez et al., 2003). The effective population size \( (N_e) \) was estimated as

\[ N_e = \frac{1}{2\Delta F} \]

(Wright, 1931), where \( \Delta F \) is the rate of inbreeding per generation. The rate of inbreeding was estimated by 2 methods described in Gutiérrez et al. (2003) and Gutiérrez et al. (2008). The earlier method assumes discrete generations, and the latter allows overlapping generations.

Rate of inbreeding is estimated in Gutiérrez et al. (2003) by

\[ \Delta F = \frac{l \times b}{1 - (F_{last} - (l \times b))}, \]

where \( l \) is the average generation interval, \( b \) is the average annual increase in inbreeding coefficient, estimated by regressing \( F \) on birth year, and \( F_{last} \) is the inbreeding coefficient in the last year studied.

The other estimate for rate of inbreeding is the average individual increase in inbreeding values (Gutiérrez et al., 2008). Increase in inbreeding for individual \( i \) is defined as

\[ \Delta F_i = 1 - \sqrt{1-F_i}, \]

where \( F_i \) is inbreeding of individual \( i \), and \( t_i \) is equivalent complete generations (Maignel et al., 1996). Equivalent complete generations for animal \( i \) is

\[ t_i = \sum_{j=1}^{k_i} \left( \frac{1}{2} \right)^{n_j}, \]
where $k_i$ is the number of ancestors for animal $i$, and $n_j$ is the number of generations between animal $i$ and its ancestor $j$.

**The Coefficients of Relationship.** The average coefficient of relationship ($R$) between breeding animals predicts the future level of the inbreeding coefficient. We calculated average coefficients of relationship between groups of rams and ewes by birth year, as well as among rams and among ewes, using the RelaX2 program of Strandén and Vuori (2006). A further analysis was conducted using the scatter plot of average relationship coefficients of a ram to other rams and of the ram to ewes, with the aim of identifying rams with a low relationship coefficient to the current Finnsheep ram and ewe populations. These rams may be of value in monitoring the annual increase of the average relationship in a closed purebred Finnsheep population (in situ conservation of the living Finnsheep population), but could also be donors of genetic material for long-term conservation of Finnsheep genetic resources (ex situ conservation of frozen semen; Meuwissen, 1999). Only the breeding rams and ewes born in 2000 or later were considered for this analysis. Data for 651 breeding rams and 6,897 breeding ewes were included in the calculations.

**RESULTS**

**Demographics**

Basic statistics for the total pedigree records and for the data used for the pedigree analysis (animals with $PEC \geq 0.6$) are in Table 1. Numbers of recorded Finnsheep with $PEC \geq 0.6$ were small from 1972 ($n = 0$) to 1988 ($n = 531$), but in 1989 there were more records ($n = 1,877$) than for all of the previous years combined. In addition, the animal registrations in 2007 were incomplete. Thus, 148,833 animals with $PEC \geq 0.6$ that were born in 1989 through 2006 were those used for subsequent analyses. During the last 16 yr, variation in the number of animals has been considerable. A rapid increase in the number from 1,877 to 13,251 annually was recorded up until its maximum in 1995. This was followed by a substantial drop of 55% over the subsequent 6 yr, and after 2001 it increased again. By 2006 there were 11,746 Finnsheep with $PEC \geq 0.6$.

The mean generation interval ($\bar{t}$) for animals born over the 1989 to 2006 interval was 2.85 yr. The generation intervals for the 4 pathways were $l_{mm} = 2.96$, $l_{mf} = 3.15$, $l_{fm} = 2.65$, and $l_{ff} = 2.49$ yr. The generation interval of the pathway from ram to progeny was 2.97 yr.
which is longer than the pathway from ewe to progeny of 2.72 yr.

**Pedigree Completeness and Trend in Inbreeding**

The pedigree completeness by birth year is given in Table 1 for animals with $PEC \geq 0.6$. Pedigree filling improved over time, with the most recent cohort of Finnsheep born in 2006 having pedigrees with up to 5 generations of known ancestors ($PEC \geq 0.9$). The pedigrees were quite complete, with $PEC \geq 0.8$, from 1995 onwards, whereas $PEC$ ranged from 0.66 to 0.77 for animals born in 1994 or before.

Average inbreeding coefficients by birth year are given in Figure 1 for all animals and for all breeding animals born between 1989 and 2005. The indices of both groups of animals increased, although they fluctuated. They reached their greatest levels in 2004, ranging from 1.1% in 1989 to 2.95% in 2004 for all animals, and from 0.63% in 1989 to 2.95% in 2004 for the breeding animals. During most of the time frame of this study the average level of inbreeding was less in the group of breeding animals than for all animals. From the linear regressions estimated, the average increase in inbreeding was 0.10% ($P < 0.001$) per annum in all animals, and 0.15% ($P < 0.001$) per annum in breeding animals.

**Relationship Coefficients**

Average relationship coefficients in breeding animals among rams, among ewes, and between rams and ewes, were plotted by birth year from 1989 to 2006 (Figure 2). The average relationship coefficient among rams was invariably greater than that for the other 2 relationships. In general, all 3 average relationships increased over the period studied. Variance (not shown) in average relationship coefficient was greater among rams than among ewes and than between rams and ewes. The 3 average coefficients varied slightly during 1989 to 1996, after which they increased at greater rates and reached 1.67, 1.45, and 1.46% in the 2005 cohort, respectively.

The scatter plot of average relationship coefficients of rams against those between rams and ewes is presented in Figure 3. With this analysis, we aimed at identifying rams with a low relationship coefficient to the current ram and ewe populations, which would be of value in conserving genetic diversity of Finnsheep. All of the average coefficients of both relationships were less than 0.03. A total of 137 rams were identified as having a relatively low relationship coefficient ($R \leq 0.01$), both with other rams and with ewes, whereas 60 rams had values between 0.02 and 0.03.

**Effective Population Size**

The rate of increase in inbreeding was 0.148% (derived from Table 1). Based on this value ($b = 0.148\%$) and 2.85 yr for $\bar{t}$, an effective population size of $N_e = 119$ animals was estimated for the Finnsheep population using the method of Gutiérrez et al. (2003). This estimate does not, however, account for overlapping generations. The other method of Gutiérrez et al. (2008) accounts for overlapping generations and gave an effective population size of 122.

**DISCUSSION**

There have been numerous previous studies on pedigree analysis of domesticated animal species, including cattle (Kearney et al., 2004; Sørensen et al., 2005; Mc Parland et al., 2007), pigs (Fernández et al., 2002; Toro et al., 2002), dogs (Hamann et al., 2003; Cole et al., 2004), and horses (MacCluer et al., 1983; Sevinga et al., 2004), as well as in other species, such as blue fox (Peu-
ra et al., 2007; Strandén and Peura, 2007), and a few such studies on sheep population pedigrees have also been published (Goyache et al., 2003; Huby et al., 2003; Maiwashe and Blackburn, 2004; Norberg and Sørensen, 2007; Álvarez et al., 2008). Our analyses provide comprehensive information on the Finnsheep breed during the past 2 decades.

Several factors caused the dramatic fluctuations observed in the records for the Finnsheep population during 1989 to 2006. Political decisions influence the price of sheep products (mainly meat) and thus can be regarded as being the principal cause for the changes. The first turning point in 1995 was due to Finland joining the European Union. Immediately after the liberation

![Figure 2](image1.png)

**Figure 2.** Average relationship coefficient by birth year in breeding animals calculated among rams (thick solid line), among ewes (dashed line), and between rams and ewes (thick solid line with dots).

![Figure 3](image2.png)

**Figure 3.** Average relationship coefficients among rams against average relationship coefficients between rams and ewes in breeding animals born in 2000 or later.
of sheep meat import restrictions in 1995, considerable importation of mutton at decreased prices compared with other European Union countries and New Zealand decreased profits in the sheep sector in Finland. Hence, Finnish farmers scaled down sheep production. The decline continued until the second turning point toward resurgence in 2001. The policies on farm subsidies and new market exploration for sheep products contributed to the restoration of the census size of the Finnsheep population between 2001 and 2006.

The average generation interval of the Finnsheep population (2.85 yr) in the current study was somewhat less than has been observed for some other breeds. Blair and Garrick (2007) reported generation intervals of 3 to 4 yr in New Zealand breeds, whereas, for Egyptian breeds, intervals of 4.29 yr (Rahmani) and 4.34 yr (Ossini; Shaat et al., 2004), and 4.4 yr (Barki; Mansour et al., 1977) have been reported. One possible explanation for the shorter generation interval may be the more extensive use of a few elite breeding animals within the Finnsheep population, but particularly that the Finnsheep matures earlier (7 to 8 mo; Maji, 1996). The slightly shorter intervals of the ewe-progeny pathways compared with the ram-progeny pathways in this study are in contrast to reports for French Merino sheep (Prod'Homme and Lauvergne, 1993), where ewe-progeny generation intervals were longer. In the Finnsheep population, the slightly increased generation intervals in the 2 ram pathways are probably attributable to the fact that the prominent rams, compared with ewes, have usually been employed for more years to produce progeny.

Previous studies showed that the completeness of pedigree information has an effect on the estimates for inbreeding coefficients within a breed (Sigurdsson and Jonmundsson, 1995; Lutaaya et al., 1999; Cassell et al., 2003). A large fraction of missing parents in a pedigree may cause serious underestimation of the inbreeding level and the associated losses arising from inbreeding (Boichard et al., 1997; Lutaaya et al., 1999). Average PEC of the selected animals in the Finnsheep population is quite acceptable. In the whole population, PEC seems quite good after 1995, being above 0.6. The proportion of animals with PEC ≥ 0.6 increased from 14.7% in 1989 to 83.2% in 2006. It was more than 58% from 1993 onward and was 72.8% in 2004 and 77.5% in 2005. The increase of pedigree quality is due to increasingly complete recording practices, the computerized animal recording system, and extensive distribution of breeding animals with good pedigree records, particularly during the most recent years.

In the Finnsheep population, the present inbreeding coefficients were low. More than 80% of the animals with PEC greater than 0.6, born in 2000 or later, had an inbreeding coefficient of less than 3.125%. The proportion of animals having inbreeding coefficients greater than 6.25%, which is the level reached by cousin mating, was 13.1%. This is also a critical maximum that is not exceeded when mating principles are applied on many farms. Similar low levels of inbreeding in the Finnsheep population were also recorded in previous studies based on microsatellite and blood protein loci in the broad context of north European sheep breeds (Tapio et al., 2003, 2005).

Average inbreeding coefficient in the Finnsheep population can be considered to be below critical levels. However, in contrast with the current inbreeding coefficient, the rate of inbreeding is an essential population variable. Moreover, as pointed out above, the inbreeding coefficients for animals are very sensitive to the quality of available pedigree information, and thus absolute inbreeding coefficient levels provide less information for comparative purposes than the average rate of increase per generation per annum. According to FAO guidelines (FAO, 1998) and the recommendation by Bijma (2000), a rate of inbreeding of more than 1% per generation should be avoided to maintain fitness in a breed. The rates of inbreeding recorded for the Finnsheep population (approximately 0.3% per generation for all of the animals and 0.45% per generation for the breeding animals) are less than this level and less than the levels reported in Danish populations of Texel (1.1% per generation), Shropshire (1.1% per generation), and Oxford Down (1.0% per generation; Norberg and Sorensen, 2007). The low levels indicate maintained potential for continued genetic gain. The estimated levels and rates of inbreeding for the Finnsheep population, considered alone, do not justify major changes to current breeding practices. These typically involve selection decisions done on Finnsheep farms and typically the mating of 1 ram to 10 to 50 ewes. Artificial insemination is not used, and Finnsheep lack a centralized breeding program.

A greater selection intensity in rams than in ewes may be responsible for the greater average relationship coefficients among rams than among ewes. The smaller number of selected rams than ewes could also explain the greater variation observed in the average relationship coefficients among rams when the population size has changed in time. A greater increase in rates of the 3 relationships since 1996 could be due to scaling down of the Finnsheep production during 1996 to 2001. Although the population size has resurged since 2001, no demographic bottleneck effect has been indicated in the variations of present average coefficients of the 3 paired relationships, as shown in Figure 2. This finding could be due to the fact that the number of elite breeding ewes and rams remained the same. In addition, a large amount of molecular variation was observed within the Finnsheep breed at microsatellite and blood protein loci (Tapio et al., 2003, 2005), indicating no trace of a genetic bottleneck.

An effective population size of 50 animals is a critical level for an animal breeding population according to FAO (1998). However, a recommendation by Meuwissen (1999) is to maintain a Ne of at least 50 to 100 to take into account mutation and drift. He also suggested that a Ne below 100 animals leads to a decrease in popula-
tion fitness. The estimates of $N_e = 119$ and 122 for the Finnsheep population are somewhat above the interval of 50 to 100. As noted by Sørensen et al. (2005), the recommendations are by no means magic numbers, but have been derived from theoretical arguments, where natural selection counteracts inbreeding depression. When the variation of selection response due to random genetic drift is used as a criterion, a much larger effective population size (order of several hundreds) is required to reduce the variation to an acceptable level (Nicholas, 1989; Grundy et al., 2000; Nomura et al., 2001). Our estimate of $N_e$ is comparable with those of other livestock breeds. For example, most of the estimates for cattle breeds are below 100, and they are essentially independent of the actual (census) size of the breed population (Taberlet et al., 2007). However, if the annual change in mean inbreeding coefficient increases in the Finnsheep population (for example, as a result of intensive use of a few rams), maintenance of genetic variability would become more difficult, and sound action would consequently be needed.

Different interventions can be suggested according to the demonstrated relationship coefficient information. Finnsheep is an indigenous sheep breed and forms a closed population where the management of inbreeding and genetic variation cannot be based on imports of genetic material from other breeds. The breeding rams presently identified with a decreased average relationship coefficient ($R \leq 0.01$) may have the greatest potential for future breeding purposes aimed at monitoring the increase in inbreeding in the Finnsheep population. Currently, the decreased values for rams could be due to their limited breeding use in only one or a few flocks. Given the ownership and flock sizes, an in situ conservation activity may be quite viable for them. In addition, as suggested by Mawashe and Blackburn (2004), collection of samples from the pedigree population for an animal genebank can be based on the least level of known genetic relationship. Development of germplasm cryoreserves to reintroduce genetic diversity at a later juncture could be also adopted to preserve genetic material of these animals for future utilization. Thus, the combination of an in situ live and cryoconservation scheme is advisable to reduce genetic drift and allow the population to evolve, and provide animals and breeding material to farmers over the longer term.

In conclusion, pedigree analysis was useful in monitoring changes in population structure and gathering key demographic parameters for the Finnsheep population. Average inbreeding coefficient by birth year in the Finnsheep population has increased over time, although current estimates of rate of inbreeding and effective population size are not in the range of critical levels. It seems that current mating practices to avoid inbreeding in the Finnsheep population work well and strategies to minimize inbreeding are not of immediate concern. For long-term maintenance of genetic diversity and dynamics of the breed, minimization of genetic relationships between candidate breeding animals is the most promising approach. Moreover, with the aid of knowledge from molecular and genealogical analyses, development of viable conservation programs such as in situ or ex situ live conservation populations and germplasm cryo-genebanks should be considered.

**LITERATURE CITED**


Pedigree analysis of Finnsheep


