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Population size and levels of inbreeding in the Icelandic goat breed – an update

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ABSTRACT

The Icelandic goat breed is a closed population consisting of 1875 animals kept in approximately 118 herds. The population has gone through several bottlenecks and has declined below 100 animals at least twice. A detailed analysis of the population was last reported in 2012, showing a 3% annual rate of inbreeding and an effective population size of only 5.1 animals. Here the genetic diversity of the breed was re-estimated using pedigree information of animals born 1962 to 2022, showing a rate of inbreeding per generation in 2016-2022 of 2.8% and an estimated effective population size of 18 animals. The results presented here show that the Icelandic goat population is steadily growing, the rate of inbreeding is decreasing, and the effective population size has increased substantially. Here we discuss some of the population management decisions that have brought about this positive change in a very small and inbred population.

Keywords: Icelandic goat, pedigree, pedigree completeness, inbreeding, effective population size, genetic contribution

YFIRLIT

Stofnstærð og staða skyldleikaræktar í íslenska geitfjárstofninum - endurmat

Íslenska geitféð er lokaður erfðahópur sem samanstendur af um 1875 gripum í 118 hjörðum. Vitað er að stofninn hefur gengið í gegnum nokkra flöskuhálsa og tvisvar hefur stofnstærð farið niður fyrir 100 dýr. Ítarleg rannsókn var gerð á stofninum 2012 sem sýndi að árleg aukning í skyldleikarækt var 3% og virk stofnstærð aðeins 5,1 dýr. Í þessari rannsókn var erfðabreytileiki endurmetinn og notast við öll tiltæk ættargögn frá 1962 til 2022. Niðurstöður sýna að aukning í skyldleikarækt yfir kynslóð hefur minnkað og er fyrir árin 2016-2022 metin 2,8% og virka stofnstærðin 18 dýr. Þær niðurstöður sem eru kynntar hér sýna að stofninn fer jafnt og þétt stækkandi og dregið hefur úr skyldleikarækt og virka stofnstærðin aukist töluvert. Hér verður fjallað um þær verndaraðgerðir sem hafa leitt til jákvæðs árangurs í verndun íslenska geitfjárstofnsins sem er lítill skyldleikaræktaður stofn.

INTRODUCTION

The importance of genetic diversity for species adaptability is well established and is considered one of three main pillars of biodiversity, along with species and ecosystem diversity (Hoban et al. 2020, DeWoody et al. 2021). Although this may seem especially important to wild species that can face rapidly changing environmental conditions, genetic diversity is in the long run no less important for domestic species that can face considerable environmental changes over time and suffer from inbreeding depression when genetic diversity within populations is rapidly depleted (Leroy 2014, Doekes et al. 2021). An important goal in the management of animal populations is therefore to conserve genetic diversity and reduce inbreeding (Fernández et al. 2005). Inbreeding is defined as the mating of individuals that are related to each other more closely than the average relationship within the population (Falconer & Mackay 1996). Effective population size (N_e) is the most used indicator to assess genetic diversity for conservation, computed from pedigree inbreeding (ΔF). It is highly dependent on the completeness of the pedigree data available (Cervantes et al. 2011).

During the past decades, hundreds of animal breeds identified by the Food and Agriculture Organization of the United Nations (FAO) have become extinct, including numerous goat breeds, with many more kept only in small numbers and close to extinction (Taberlet et al. 2008). The Icelandic goat (*Capra hircus*) is believed to have been brought to Iceland from Norway during the settlement period around 1100 years ago (Stefán Aðalsteinsson 1981). There is no evidence of later goat import to the country. Records from 1703 on, as well as archaeological remains, show that goats were kept in most parts of the country (McCooey 2021). The population is known to have gone through several bottlenecks and has at least twice, in the years 1885 and 1962, declined to under 100 animals. The population size has been less than 1000 animals most of the time, with the highest number, nearly 3000 animals, recorded in 1930 (Baldursdottir et al. 2012). The most recent bottleneck was in 1962 when the number of goats in Iceland fell to around 90 animals, which raised concerns that the population might go extinct. This led the Icelandic government to start paying conservation subsidies in 1965 for all registered goats, although from 1976 the subsidies were limited to 20 animals per herd. Since then, the population has grown steadily, although goats at that time were mostly kept without production aims. In 2012 a conservation plan was established for the goat breed with aims to increase the population size, utilization, and subsidies to minimize inbreeding (Birna Kristín Baldursdóttir & Jón Hallsteinn Hallsson 2012).

Before the 1990s little was known about the structure of the population or the levels of genetic diversity. The level of inbreeding and its effect on the fitness of the breed were estimated in 1994, showing an average inbreeding of 26% and only an insignificant effect of increases in inbreeding on fertility, litter size at birth, and number of kids born alive (Stefán Aðalsteinsson et al. 1994). Adding to the persistent problem of a small population size, Iceland has since the middle of the 20th century been divided into isolation zones aimed at controlling the spread of sheep diseases, which has led to the fragmentation of the goat population into sub-populations with limited flow between zones. Fragmentation is known to negatively affect levels of inbreeding and adaptability (Frankham et al. 2017).

A study carried out in 2012 on the Icelandic goat population, which at that time consisted of only 700 animals kept in 45 herds, showed the population to be highly fragmented with an average level of inbreeding for all animals in 2006 at 10.5%, an annual rate of inbreeding of 3%, and an effective population size of only 5.1 animals (Baldursdottir et al. 2012). This led to increased subsidies to farmers for all winter-fed animals, production of milk and fiber, more emphasis on registration, as well as the collection and freezing of semen as a way of reducing population fragmentation (Reglugerð um almennan stuðning við landbúnað nr. 430/2021).

The aim of the current study was to examine changes that have occurred in the Icelandic goat population since the last comprehensive population analysis in 2012. The results, such as the current level of inbreeding, average co-ancestry within cohorts, and effective population size, will serve as a valuable input into the ongoing conservation plan for the breed and will allow us to better understand the effects of the actions taken so far to minimize inbreeding, fragmentation, and loss of genetic diversity.

MATERIALS AND METHODS

Population and pedigree data

Pedigree data for Icelandic goats were obtained from 'HEIÐRÚN', an electronic herdbook established in 2015 and maintained by the Icelandic Agricultural Advisory Center (Ráðgjafamiðstöð landbúnaðarins). The pedigree data analyzed here includes information for a total of 11312 animals (compared to 2240 animals in 2012), the oldest born in 1962 and the youngest born in 2022. All animals registered in 'HEIÐRÚN' receive a composite ID number consisting of the year of birth (first four digits), sex (one digit; 1 = male, 2=female), farm number (seven digits), and a three-digit individual identifier. Information about the population size was gathered from Hagstofa Íslands (Statistics Iceland 2025) and from 'Forðagæsluskýrslur', reports made each year accounting for all livestock and available fodder in Iceland.

Pedigree completeness

Pedigree completeness (*PEC*) is important when estimating inbreeding through pedigree analysis, since incomplete pedigrees underestimate inbreeding (Miglior & Burnside 1995). To detect inbreeding, an animal must have at least both parents and one grandparent known (MacCluer et al. 1983), corresponding to a *PEC* value of 0.24.

In the EVA v. 3.0 inbred program (Berg et al. 2006) *PEC* values are calculated for each animal as:

$$PEC_{animal} = \frac{4(C_{sire} * C_{dam})}{C_{sire} + C_{dam}}$$

where C_{sire} and C_{dam} are contributions from the paternal and maternal lines, respectively (MacCluer et al. 1983) with the contributions computed as follows:

$$C = \frac{1}{d}\sum_{i=1}^{d} a_i$$

where a_i is the proportion of ancestors present in generation *i,* and *d* is the number of generations. Here, five ancestor generations were used (d = 5) and the *PEC* index referred to as *PEC5*. The average *PEC5* index was calculated according to birth year. Average inbreeding coefficient for animals with *PEC5* values of ≥0.24, ≥0.40, ≥0.60 and >0.80 were calculated to ascertain the extent to which the completeness of the pedigree affects the results.

Inbreeding coefficient

The EVA inbred program (Berg et al. 2006; Sørensen et al. 2008) was used to calculate individual inbreeding coefficients and average inbreeding coefficients within birth cohorts, using the algorithm of Meuwissen and Luo (1992). The trend in inbreeding was studied for all animals and for subgroups of animals with *PEC5* ≥0.24, ≥0.40, ≥0.60, and ≥0.80, the numbers in each group being 11312, 4788, 3637, 2247 and 960 animals, respectively.

Average co-ancestry

The average co-ancestry of animals within each cohort was calculated with the EVA inbred program (Berg et al. 2006; Sørensen et al. 2008), using the algorithm proposed by Colleau (2002). The trend in average relationship between all animals within each cohort was plotted for the cohorts from 1962 to 2022.

Generation length

The generation length (*L*), which is the average age of parents at the birth of their offspring, was calculated for the four gametic pathways: buck to son ($L_{f\text{-}s}$), buck to daughter ($L_{f\text{-}d}$), doe to son ($L_{m\text{-}s}$), and doe to daughter ($L_{m\text{-}d}$), from the difference between birth dates of animals and their parents using the Pedig software package (Boichard 2002). The average generation length was calculated as:

$$L = \frac{(L_{\mathrm{f-s}} + L_{\mathrm{f-d}} + L_{\mathrm{m-s}} + L_{\mathrm{m-d}})}{4}$$

Effective population size

The effective population size (N_e) is an estimate of the number of breeding animals that would produce the observed rate of inbreeding in the current generation under ideal conditions (Lacy 1995). The effective population size (N_e) was estimated from the rate of inbreeding per generation (ΔF), obtained by multiplying the annual rate of inbreeding (ΔF_y), with the generation length (L):

$$N_e = \frac{1}{2\Delta F}$$

Changes in F were obtained by regressing annual inbreeding coefficients on generation number as (Falconer & Mackay 1996):

$$\Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}} = \frac{1}{F_t}$$

The effective population size was estimated using the development in inbreeding of animals with *PEC5* ≥0.80 in the years 2016-2022 (two generation intervals). Fluctuations in population size and pedigree completeness made it necessary to study the increase in inbreeding over two generation intervals and with animals having the most complete pedigrees. The development in inbreeding was calculated with a regression model where the average inbreeding within a year was regressed against time. Using the estimated regression coefficient and assuming a generation interval of interval (L) is one way of estimating the rate of inbreeding per generation (Sørensen et al. 2005).

Ancestors with the highest contribution

As the rate of inbreeding in a population is directly related to the long term genetic contributions of ancestors to descendants and as large genetic contributions of few ancestors leads to increased inbreeding (Woolliams & Thompson 1994), identifying ancestors with large genetic contributions is of interest. Here, genetic contributions of individuals were calculated using the EVA inbred program (Berg 2006). Three birth cohorts with five-year intervals, 2010, 2015, and 2020, were selected for this calculation, as well as the 2022 birth cohort, which is the last year with available data.

RESULTS

Population size and number of herds

The Icelandic goat population has fluctuated considerably in size since the first census of farm animals was taken in 1703, reaching its largest size in the 1930s and falling rapidly in the following two decades. In 2006 the Icelandic goat population consisted of a total of 449 winterfed goats kept in 44 herds (Baldursdottir et al. 2012), but in 2022 the number of goats had risen to 1875, kept in 118 herds (Figures 1 and 2A). From 1963 to 1982 (including both years) a steady increase in population size of around 6 animals per year was seen, equal to a 5.1% growth rate in this period, with some minor year-by-year fluctuations. From 1983 to 2002 a similar growth was seen in the number of animals but with a lower relative growth rate of 2.8% in this period. In the next twenty-year period, from 2003 to 2022, a sharp increase was seen in the growth rate of around 8.5% per year (data not shown). This increase in population size was driven by both more herds (Figure 2A) and a rising number of goats per herd (Figure 2B).

Pedigree completeness and inbreeding

Registrations are extremely important for efficient population management, but unfortunately the registration of Icelandic goats in the 'HEIÐRÚN' herdbook remains relatively low and the pedigree completeness therefore incomplete. In 2022 the total number of goats in Iceland was 1875 (Statistics Iceland 2025), but only 67%, or 1254 goats, were registered in 'HEIÐRÚN'. The pedigree completeness (*PEC5*) for the population remained below 0.4 on average and was only 0.32 in 2022, with the highest value of 0.39 seen in 1997 (Figure 3A). Of the 1254 goats registered in 2022, only 77 had *PEC5* ≥0.8. The number of goats recorded with *PEC5* ≥0.24, ≥0.40, and ≥0.60, were 674, 555, and 292, respectively (Figure 3B).

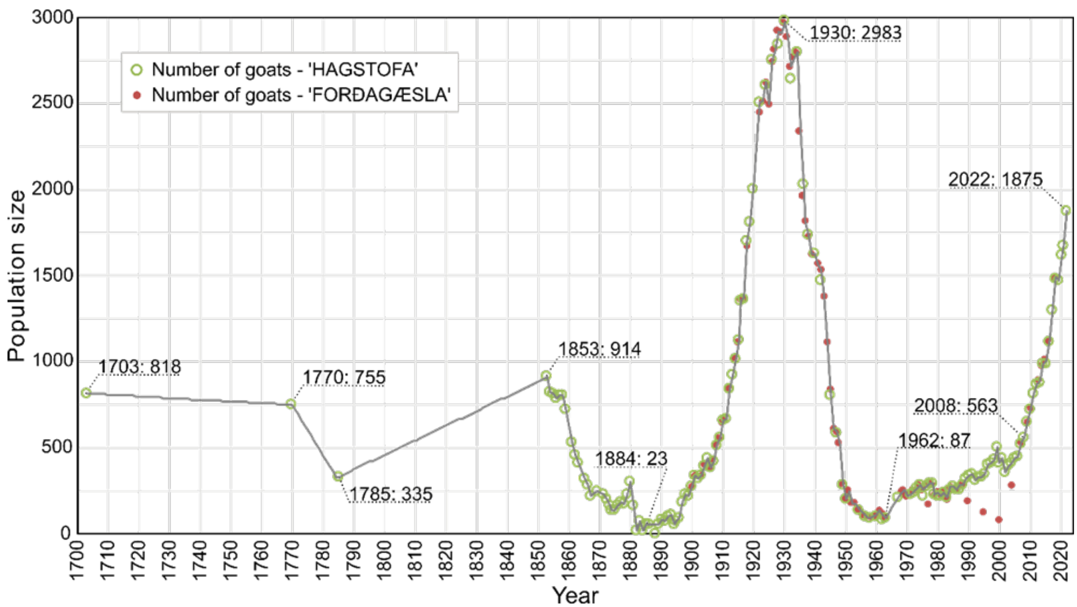

Figure 1: Populations size of the Icelandic goat population from 1703 to 2022. Since the earliest available population data for the Icelandic goat breed in 1703 to 2022 the population has gone through several severe bottlenecks, with the most severe bottleneck being in 1884 when the population went below 50 individuals. Open green circles represent information from 'Hagstofan' (e. Statistics Iceland) and red dots information from 'Forðagæsluskýrslur' (livestock owners are obligated to deliver information on herd size and available fodder every fall) (Lög um búfjárhald 38/ 2013). Where a discrepancy is seen between datasets the data from Statistics Iceland is used. Local maximums and minimums are indicated on the graph.

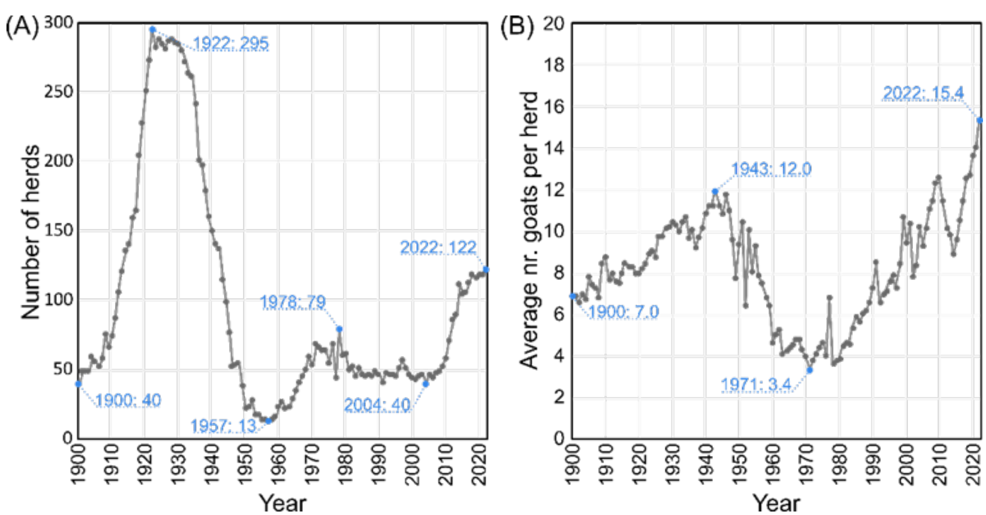

Figure 2: Number of goat herds and average number of goats per herd in Iceland in the period 1900-2022. (A) The number of goat herds in Iceland has fluctuated considerably in the twentieth century, from 40 at the beginning of the century to 122 herds in 2022, with the highest numbers of herds in 1922, and the lowest numbers of only 13 herds in 1957 and 40 herds in 2004. **(B)** The number of goats per herd has increased steadily from three goats per herd on average in 1971 to about 15 goats per herd in 2022. Local maximum and minimum values are indicated on the graph.

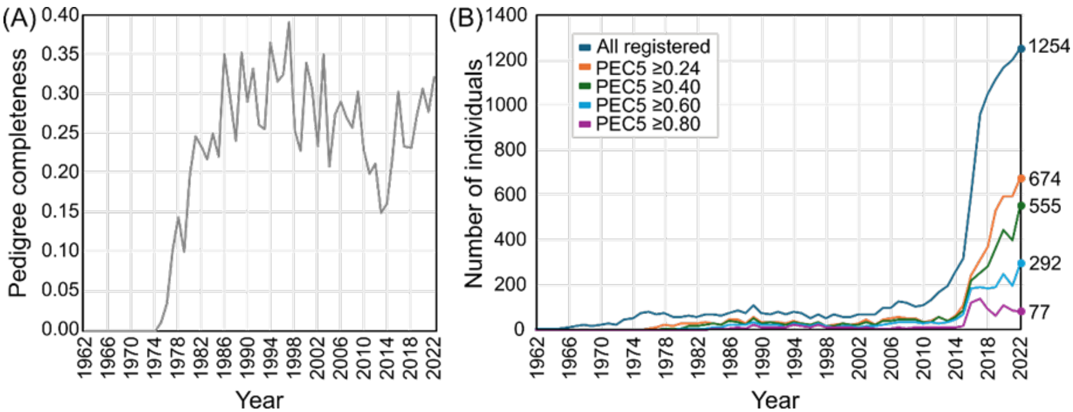

Figure 3: Pedigree completeness for the period 1962 to 2022. **(A)** Pedigree completeness (*PEC5*) in the period 1962 to 2022. **(B)** For 2022 the total number of individuals in the database was 1254; 674 individuals have a *PEC5* ≥0.24, but only 77 individuals have a *PEC5* ≥0.80.

The mean inbreeding coefficient (*F*) was calculated within birth years for all animals and for animals with different *PEC5* indices. The average level of inbreeding for all animals in 2022 was 4.2%. For *PEC5* ≥0.24, ≥0.40, ≥0.60, ≥0.80 the inbreeding was 6.9%, 7.2%, 9.1%, and 14.5%, respectively (Figure 4). Inbreeding was first detected in 1974 for all animals (0.5%) and for animals with *PEC5* ≥0.24 (25%), in 1978 for animals with *PEC5* ≥0.50 (18.8%), in 1981 for animals with *PEC5* ≥0.70 (21.5%) and in 1984 for *PEC5* ≥0.80 (45.8%). The highest inbreeding was calculated in 1985 with *PEC5* ≥0.80 (64.4%) (Figure 4).

Inbreeding was first detected for animals born in 1974 with 2% of animals being inbred (animals more closely related than the average relationship within the breed), whereas in 2006 that proportion had increased to 62.5%, or 35 out of 56 animals born in that year (Figure 5). The highest proportion of inbred individuals, 70.9%, was seen in the birth cohort of 1980 (39 inbred out of 55 individuals). The highest individual inbreeding observed was 71.1%, with the ten most highly inbred goats in the period 1962-2006 ranging from 56.1-71.1%. Two does born in 1986 and 1987 were 71.1% inbred and had a *PEC5* index of 0.93. All the ten most inbred goats had *PEC5* ≥ 0.87 (Baldursdottir et al. 2012).

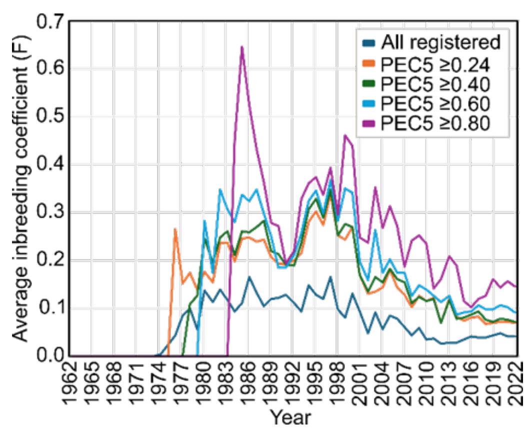

Figure 4: Development in inbreeding (F) for the period 1962 to 2022 calculated for all animals and four different PEC5 indices. Mean inbreeding coefficient (*F*) was calculated within birth years for all animals and animals with different *PEC5* indices. Color coding of *PEC5* indices the same as in Figure 3B.

Average co-ancestry and effective population size

The average co-ancestry between all animals within each cohort for the period 1962-2022 was calculated and shown to be decreasing over time, the average co-ancestry in the year 2000

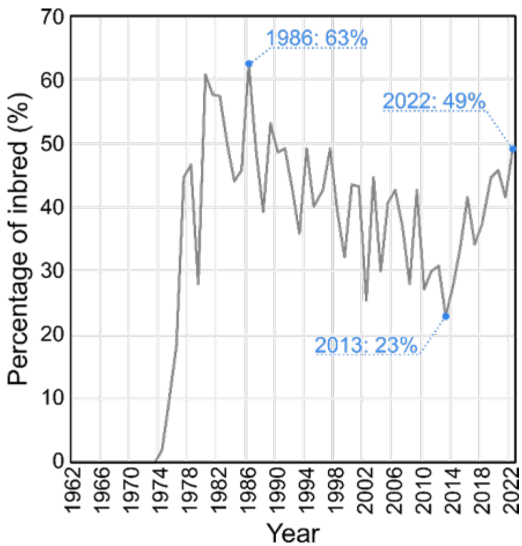

Figure 5: The percentage of inbred animals in the population in the period 1962 to 2022. The highest percentage of inbred individuals in the Icelandic goat population, 63% was seen in 1986, with the lowest percentage of 23% seen in 2013. In 2022 the percentage of inbred individuals in the Icelandic goat population was 49%. Maximum and minimum values are indicated on the graph.

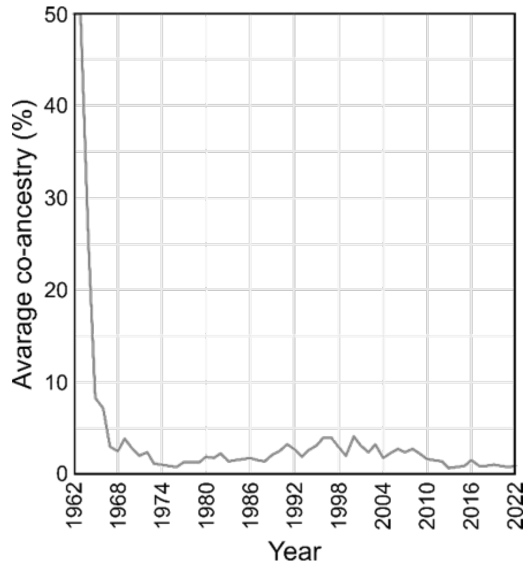

Figure 6: Average co-ancestry between all animals within each birth cohort. The trend in average co-ancestry shows lower average relationships per year. In 2010, 2015, 2020, and 2022 the average co-ancestry was 1.68%, 1.00%, 1.00% and 0.93%, respectively.

being 4.15% compared to 0.93% in the year 2022 (Figure 6).

The average generation length was 3.5 years, and the rate of annual increase in inbreeding for the years 2016 to 2022 was found to be $\Delta F_{year} = 0.8\%$ ($P < 0.001$) and per generation $\Delta F_{gen} = 2.8\%$ ($P < 0.001$). Based on these data, the effective population size (N_e) was estimated to be 18 animals for the last two generation intervals.

Ancestors with the highest contribution

Genetic contributions of ancestors to the population were calculated for individuals born in 2010, 2015, 2020, and 2022 (Figure 7A). Individual 200811346461001 (Hávaði from Háafell) contributed the most in 2010 (6.3%), individual 199411682791120 (Hnokki from Háafell) contributed the most in 2015 (4.9%), and individual 199911346461100 (Heimir from Háafell) contributed the most in 2020 (4.6%) and 2022 (4.4%), Four individuals are on the top ten lists for both years (Table 1). Average genetic contributions of the ancestors with the highest genetic contribution in 2010, 2015, 2020 and 2022 have been slowly decreasing (Figure 7B).

DISCUSSION

Studies have shown that, when a large proportion of pedigree information is missing, the resulting calculations may underestimate the level of inbreeding and overestimate the effective population size (Boichard et al. 1997, Rodríguez-Ramilo et al. 2019). Therefore, pedigree completeness and quality are important. The amount of pedigree data available for the Icelandic goat population is low for all years, with considerable fluctuations. For example,

Table 1: The genetic contributions of top ten contributors for the years 2002, 2006 (Baldursdottir et al. 2012), 2010, 2015, 2020, and 2022, with averages for each year as well as minimum and maximum genetic contributions of the top ten ancestors.

Name	Farm	Identification (Id)	Sex	2002	2006	2010	2015	2020	2022
Ása	Vorsabæ	1999-2-1665021-082	F			3.3%			
Baugalín	Háafell	2003-2-1346461-037	F		8.3%				
Bogi	Fjallalækjarsel	1983-1-1545381-001	M	5.8%					
Bæringur	Háafell	2006-1-1346461-109	M			5.3%	4.0%	3.6%	3.4%
Dagur	Fjallalækjarsel	1984-1-1545381-002	M	7.7%					
Dreki	Fjallalækjarsel	1978-1-1545381-001	M	7.2%					
Dreki	Háafell	2010-1-1346461-103	M				3.0%		
Embla	Sólheimar	1997-2-1682791-120	F			2.9%		2.3%	2.2%
Glanni	Háafell	2004-1-1346461-001	M		16.5%	5.0%	3.3%	3.6%	3.3%
Hávaði	Háafell	2008-1-1346461-001	M			6.3%	3.0%	2.6%	2.4%
Heimir	Háafell	1999-1-1346461-100	M	7.7%	7.5%	5.8%	4.7%	4.6%	4.4%
Hlunkur	Háafell	2001-1-1346461-100	M		6.6%	3.5%			
Hnokki	Sólheimar	1994-1-1682791-120	M		4.9%	5.5%	4.9%	4.5%	4.3%
Hólmur	Háafell	2016-1-9700501-991	M						2.5%
Höttur	Fjallalækjarsel	1992-1-1545381-001	M	6.2%					
Keisara	Vorsabær	1978-2-1665021-080	F		6.0%				
Lína	Háafell	2001-2-1346461-007	F			3.4%			
Nói	Háafell	2017-1-1346461-048	M					3.0%	
Prins	Háafell	2000-1-1346461-100	M	5.1%					
Prins	Möðrudalur	2012-1-1589531-001	M				2.5%		
Rjómalind	Fjallalækjarsel	1973-2-1545381-001	F	6.3%					
Rjúpa	Fjallalækjarsel	1977-2-1545381-001	F	6.1%					
Slembi	Vorsabær	1987-1-1665021-080	M		6.2%				
Stóra Hatta	Sólheimar	1990-2-1682791-120	F						2.1%
Surtur	Háafell	2012-1-1346461-101	M				4.4%	2.6%	2.8%
Veiga	Sólheimar	1994-2-1682791-120	F	9.5%	9.5%				
Þokki	Háafell	2011-1-1346461-075	M				2.5%	2.4%	
Þorri	Sólheimar	1990-1-1682791-120	M	7.8%	9.0%	4.1%	3.5%	3.3%	3.1%
Örn	Þorbergstaðir	2003-1-1375921-100	M		5.4%				
			Average	6.9%	8.0%	4.5%	3.6%	3.3%	3.1%
			Max	9.5%	16.5%	6.3%	4.9%	4.6%	4.4%
			Min	5.1%	4.9%	2.9%	2.5%	2.3%	2.1%

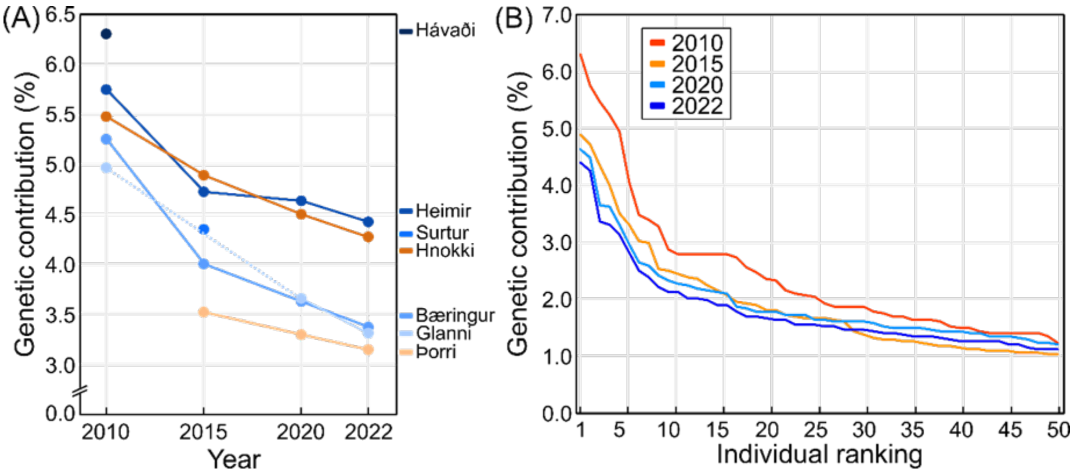

Figure 7: Genetic contribution of the most successful goats at four time points. (A) The genetic contribution of the top five most successful bucks in the population for 2010, 2015, 2020, and 2022. The results show a clear trend towards lower genetic contribution to the total population for the most successful bucks. The results are color coded by farm, with blue lines representing bucks from the farm 'Háafell' and orange lines representing bucks from the farm 'Sólheimar'. The strong effect of the farm 'Háafell' is explained by the herd size; there are approximately 200 goats at that farm or about 10% of the total population. (B) Genetic contribution of the 50 most successful goats at four time points. The genetic contribution was calculated for the top 50 most successful goats in the population for 2010, 2015, 2020, and 2022. A flatter line suggests less contribution of the most successful individuals to future generations and therefore a more equal chance of genetic material being passed from one generation to the next. The trend seen here is that most successful individuals are contributing less to each new generation, from 6.3% for Hávaði (Háafell) in 2010 to only 4.4% for Heimir (Háafelli) in 2022.

PEC5 was only 38.7% in 2006 (Baldursdottir et al. 2012) (Figure 3) and 32% in 2022. With only nine animals in the whole data set (a total of 1254 individuals) having a complete pedigree for five generations. This means that the levels of inbreeding calculated here are most likely underestimated, although it is difficult to say to what extent. This is supported by the facts that increased inbreeding is associated with more complete pedigree data (Figure 3) and that the animals with the highest inbreeding coefficients all had relatively high levels of pedigree completeness (*PEC5* ≥0.8), suggesting that more complete pedigree data would reveal even higher levels of overall inbreeding than seen here. When the effective population size was estimated, the increase in inbreeding for animals with *PEC5* ≥ 0.8 was used. This was done because this group of animals had the most stable development in inbreeding overtime and to avoid the effects of missing pedigree information affecting the result.

What might explain fluctuations observed in the pedigree completeness (Figure 3A) and the percentage of inbred animals (Figure 5) is difficult to say, but one problem facing the Icelandic goat population is a high turnover of breeders. Herds are often stable for only a few years at each farm (unpublished data), which might affect the quality of pedigree records.

The proportion of inbred animals in the population was estimated at 62.5% in 2006, and the increase in inbreeding per generation, ΔF equal to 9.9% ($P < 0.001$), was tenfold that recommended by FAO. In 2006 the inbreeding coefficient calculated for animals with *PEC5* ≥ 0.70 was 30.5% (Baldursdottir et al. 2012), compared to 26% in the period 1977-1992

(Stefán Aðalsteinsson et al. 1994). Previous results for the Icelandic goat breed have shown that a 10% increase in F resulted in a 2.8% decrease in fertility, a 0.8% decrease in total number of kids born, and a 2.6% decrease in the number of kids born alive, underlining the necessity of reducing the rate of inbreeding in the Icelandic goat population (Stefán Aðalsteinsson et al. 1994).

Threatened populations are vulnerable to the effects of both genetic drift and inbreeding, particularly when gene flow is low and the effective population size is small. Estimates of N_e provide important information on the status of endangered populations and serve as indicators of genetic diversity (Cervantes et al. 2011). Breeds with an inbreeding rate per generation > 1%, equivalent to a N_e < 50 individuals, are considered to be in a critical state (Scherf & Pilling 2015). It has been suggested that N_e should be ≥50 to prevent inbreeding depression from becoming a serious problem and that N_e should be in the range of 500-5000 to retain genetic diversity and thereby the long term evolutionary potential of the population (Franklin & Frankham 1998, Scherf & Pilling 2015). Simulation studies have revealed that N_e should be ≥70 to avoid inbreeding depression in the short-term (Caballero et al. 2017). The N_e estimate of 18 animals for the Icelandic goat population, based on pedigree data, underlines the breed's long-term problems with population size. For conservation, the socio-cultural background and the history of breeds are also important when assessing the endangerment level (Bahmani et al. 2024). Pedigree based inbreeding in White Shorthaired goats in Slovakia reported that N_e = 182, using pedigree data of 1682 animals with pedigree completeness of 35% and 11% in the fourth and fifth generation, respectively (Oravcová 2013). Girgentana goats in Italy underwent a drastic bottleneck when population size dropped from 30000 animals in 1983 to 252 animals in 2001, and inbreeding per generation was estimated in 2004 at 0.13% and effective population size at 380 (Portolano et al. 2004). Five native Norwegian cattle breeds have a similar status as the Icelandic goat breed with small population sizes, ranging from 233 to 1806 breeding females and effective population size between 36 to 123 in 2020 (Holene et al. 2021).

A previous study of the Icelandic goat population demonstrated a considerable fragmentation of the metapopulation (Baldursdottir et al. 2012). With this fragmentation, there are some highly inbred individuals within different subgroups. If only the trend in inbreeding is studied, the genetic diversity between different subgroups remains unaccounted for. Therefore, we calculated the average co-ancestry among all animals within each cohort. As this parameter is a predictor of the average inbreeding in the next generation, assuming random mating, the trend in average co-ancestry should be an indicator of development in genetic diversity that is insensitive to the fragmentation of the population. This trend in average co-ancestry for the Icelandic goat breed shows a lower average relationship per year; the average co-ancestry in 2000 was 4.15% and 0.93% in 2022 (Figure 6). The expected inbreeding within a year was also calculated based on average co-ancestry, assuming random mating. Although these calculations demonstrated that inbreeding can still be lowered in the population, as expected inbreeding is lower than observed for all the years (data not shown). The difference between expected and observed inbreeding is getting lower over time, showing that the breed is on the right track in regards to the management of genetic diversity.

The high genetic contribution of a few ancestors leads to increased inbreeding and is detrimental to the long term viability of a population (Woolliams & Thompson 1994). The high contribution of buck 2004136001 in 2006 was the result of his extensive use in the years 2005 and 2006, when he fathered 17% and 19.2% of the kids born, respectively (Table 1). The buck 2004136001 comes from the biggest herd, a herd that counted over 100 females. This underlines two of the problems facing those involved in goat breeding in Iceland: the lack of breeding advice and the lack of options when selecting bucks for the next generation. It has been pointed out that the sire breeding part of a population largely governs the rate of inbreeding (Goddard & Smith 1990, Rochambeau et al. 2000). Simulation studies have shown that breeding schemes that use more sires result in a lower rate of inbreeding (Korpiaho et al. 2002). Bottlenecks can increase demographic stochasticity, inbreeding, loss of genetic diversity and fixation of deleterious alleles, and thereby increase the probability of population extinction (Frankham 2005). The Icelandic goat population is known to have experienced at least two serious bottlenecks, one in 1885 and another in 1962, when the population was reduced to 62 and 87 animals, respectively. Methods based on heterozygosity excess did not reveal evidence of recent bottlenecks despite the breed's population history (Baldursdottir et al. 2012). This might be explained by substructures within the population due to the fragmentation (Cornuet & Luikart 1996). Studies of *Capra ibex* with known bottlenecks gave similar results, but when the population was separated into two geographic sub-populations the results showed a significant bottleneck signature (Maudet et al. 2002).

Although the importance of purging in protecting small endangered populations from extinction is debated (Frankham et al. 2001), the results presented here raise the question whether purging of deleterious alleles, probably occurring in many small inbred herds, may have left the Icelandic goat breed protected to some extent from the deleterious effects of inbreeding.

In the light of ever decreasing global genetic diversity of domestic animals, it is of great importance to protect unique breeds such as the Icelandic goat from further genetic erosion, in order to secure a sustainable future for this population that is believed to have existed in isolation for over 1100 years.

In view of the results presented here and in previous analyses of the Icelandic goat breed, which show high levels of inbreeding, population fragmentation, and low levels of genetic diversity as seen with molecular markers (Baldursdottir et al. 2012), an important step in protecting the breed would be to improve the pedigree records to better monitor the rate of inbreeding and to direct the breeding efforts in the right direction. Another possibility would be to use more markers, preferably high-density SNP arrays or whole genome sequencing, to resolve the genetic relationship between individuals, both within and among regions. Also, mating programs aimed at selecting the best suited parents to the next generation to minimize the level of inbreeding should be applied. This requires increased effort from the breeders to record pedigree data with more precision, as well as dedication from those institutions that can advise on breeding strategies. The breeding population should include all animals; the isolation of subgroups needs to be broken. This could possibly be done through an increased emphasis on semen collection and the use of artificial insemination to better steer the breeding effort. This would additionally open the possibility of semen storage as a backup for genetic material for future generations, which would give breeders more choices in their breeding work.

Further studies to evaluate the genetic diversity of the goat breed are necessary, preferably relying on high-density markers, but better pedigree records are also needed for an ongoing revitalization of the Icelandic breed. Such work should be done in the context of a long-term conservation plan based on a detailed population viability analysis. As a follow up to the work presented here, the first steps have been taken towards long term semen storage, artificial insemination and collecting more dense pedigree data. Despite the welcome increase in population size that the Icelandic goat breed has experienced in the last decade and the positive signs of a possible commercial utilization, it is important to increase the population size even further. A larger population is needed for product utilization and to sustain increased emphasis on product development, as discussed in the conservation plan for the breed (Birna Kristín Baldursdóttir & Jón Hallsteinn Hallsson 2012). In addition, while the future direction of utilization of the Icelandic goat breed is in the hands of Icelandic farmers, it is important that they have access to advice on how to avoid inbreeding.

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