

Original study

Pedigree analysis in White Shorthaired goat: First results

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Abstract

Pedigree records of 1 682 animals of the White Shorthaired goat in Slovakia were investigated. The reference population was defined as the animals born from 2008 to 2011 with at least one ancestor known in the second ancestral generation (670 animals kept in eight flocks). The numbers of founders (286), ancestors (256), effective founders (73), effective ancestors (45) and founder genome equivalents (32) were assessed. Fifteen ancestors were needed to explain 50 % of genetic variability. Marginal contributions of the ten most influential ancestors varied between 5.45 % and 2.47 % and accounted for 39.8 % of genetic variability. The mean values of inbreeding and co-ancestry were 0.69 % and 1.55 %, respectively. The effective population size was assessed to consist of 182 and 142 individuals, depending whether it was calculated from the individual increase in inbreeding or the individual increase in co-ancestry. The number of maximum generations traced, fully traced generations and equivalent complete generations traced were 5.62, 1.97 and 3.04, respectively. The first, second and third ancestral generation were 100 %, 83 % and 71 % complete, respectively. The completeness decreased to as low as 35 % and 11 % in the fourth and fifth generation. To be able to keep genetic links across generations in touch, the amount of pedigree information needs to be increased. This is a serious requirement for appropriate monitoring and management of genetic relations within the population.

Keywords: goats, genealogical information, founders, ancestors, founder genome equivalents, inbreeding, co-ancestry, effective population size

Archiv Tierzucht 56 (2013) 53, 547-554
doi: 10.7482/0003-9438-56-053

Received: 24 October 2012
Accepted: 1 March 2013
Online: 26 April 2013

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Introduction

The national goat population in Slovakia amounts to about 30 000 heads. The White Shorthaired breed predominates. Goat-farming is of minor importance and has features of self-subsistence. An extensive production system with one kidding per year is applied. In performance testing a few flocks of the White Shorthaired breed are included. Selection is performed under the guidance of the Sheep and Goats Breeders' Association and the Breeding Services of Slovakia. The recorded population involves 700 to 800 females at present. Breeding strategies are aimed at improvement of milk (selection on phenotypic values), prolificacy and exterior (selection on linear scores using a three-point and a twenty-point scale, respectively) and have an impact on evolution of the breed. These should take genetic diversity aspects into account since genetic diversity is the basis for genetic adaptability for all changes over time such as changes in climate, pollution and diseases (Baldursdóttir 2010). Information on inbreeding and co-ancestry is important when effort to prevent breeds from extinction is in place (Goyache *et al.* 2003, Gutiérrez *et al.* 2005). Information on probabilities of gene origin (founders, ancestors, effective founders, effective ancestors and founder genome equivalents) enables to provide an insight into the genetic history of the breed. A tool for assessment of these parameters is the pedigree analysis. With populations of small ruminants in Slovakia, it was recently completed with the Valachian breed (Oravcová & Krupa 2011, Oravcová & Margetín 2011). The genetic variability of goats has not been studied until now.

The objective of this study was to assess the parameters derived from probabilities of gene origin and identity-by-descent probabilities in a population of the White Shorthaired breed. The pedigree completeness was analysed.

Material and methods

Genealogical information on 1 682 animals (1 485 females and 197 males) of the White Shorthaired goat was investigated. In total, 971 animals with progeny and 711 animals without progeny were considered. For males, 136 sires and 95 grandsires were identified. For females, 835 dams and 503 grand-dams were identified. Due to only natural mating being applied, the ratio dams/sires in a pedigree was found to be low. The average number of descendants per sire was 10.2. The average number of descendants per dam was 1.6. Up to 70% of sires were individuals with 1 to 10 descendants. Less than 10% of sires had 40 and more descendants. No dams with more than 10 descendants were found. Up to 80% of all animals in the pedigree were animals with both parents known and 16% were animals with no parents known. The proportion of animals with one parent known was 4%.

To assess probabilities of gene origin and identity-by-descent probabilities, the population under study (reference population) was defined as the animals born from 2008 to 2011. Only animals with at least one ancestor known in the second ancestral generation were taken into account (670 individuals in eight flocks). Of these, 625 were females and 45 were males. Pedigree records were provided by the Breeding Services of Slovakia. The number of founders, the effective number of founders, the effective number of ancestors and the number of ancestors explaining 50% and 75% of genetic variability, as well as the founder genome equivalents were calculated. The mean values of coefficients of inbreeding and co-

ancestry were calculated by averaging respective values of all individuals in the reference population. The realized effective size was calculated taking into account (a) the individual increase in inbreeding and (b) the individual increase in co-ancestry. The programme ENDOG v.4.8 (Gutiérrez & Goyache 2005) and the SAS software (2009; SAS Institute Inc., Cary, NC, USA) were used for analyses.

The pedigree completeness was evaluated by the index of pedigree completeness (MacCluer *et al.* 1983) taking into account contributions from the maternal and paternal lines. In addition, the number of maximum generations traced, fully traced generations and equivalent complete generations traced (Maignel *et al.* 1996, Gutiérrez & Goyache 2005) were calculated. The number of fully traced generations was defined as generations separating the offspring from the furthest generation where 2^n ancestors are known (generation 0 are ancestors with unknown parents). The number of maximum generations traced was defined as generations separating the offspring from the furthest ancestor. The number of equivalent complete generations traced was defined as the sum of $(1/2)^n$ where n is the number of generations separating the offspring from each known ancestor (parent=1, grandparent=2 etc.).

Among parameters of probabilities of gene origin, the number of founders (f) was defined as animals with one or two unknown parents. The effective number of founders (f_e) was defined as the number of equally contributing founders that would produce the same genetic diversity in the population under study (Lacy 1989) and was calculated as

$$f_e = 1 / \sum_{k=1}^f q_k^2 \quad (1)$$

where q_k is the expected proportional genetic contribution of founder k . The ancestors (founders or not) were identified using the method proposed by Boichard *et al.* (1997). The effective number of ancestors (f_a) was defined as the minimum number of ancestors explaining the genetic diversity of the population under study (Boichard *et al.* 1997) and was calculated as

$$f_a = 1 / \sum_{j=1}^a q_j \quad (2)$$

where q_j is the marginal contribution of ancestor j not explained by any other ancestor chosen before (contribution independent of the contributions of the other ancestors). The number of founder genome equivalents (f_g) was defined as the number of founders producing the same genetic diversity in the population under study if the founders were equally represented and no loss of alleles occurred (Lacy 1989). The number of founder genome equivalents was obtained by the inverse of twice the average co-ancestry of the individuals in the reference population (Caballero & Torro 2000).

Among parameters of identity-by-descent probabilities, the coefficient of co-ancestry was defined as the probability that any two alleles sampled at random (one from each individual) are identical copies of an ancestral allele (Malécot 1948 as cited by Ghafouri-Kesbi 2010). The individual coefficient of inbreeding was defined as the probability that an individual has two identical alleles by descent and was calculated following Meuwissen & Luo (1992). The coefficient of individual increase in inbreeding (Gutiérrez & Goyache 2005) was calculated

from the individual coefficient of inbreeding F_i taking the number of equivalent complete generations t into account:

$$\Delta F_i = 1 - \sqrt[t-1]{1 - F_i} \quad (3)$$

The coefficient of individual increase in co-ancestry between any pair of individual j and individual k was calculated as

$$\Delta c_{jk} = 1 - \sqrt{\frac{g_j + g_k}{2} \sqrt{1 - c_{jk}}} \quad (4)$$

where c_{jk} is the inbreeding of a descendant from both and g_j and g_k are the equivalent complete generations for the parents (Cervantes *et al.*, 2011). By averaging the individual increase in inbreeding

$$\overline{N}_e = \frac{1}{2\Delta F} \quad (5)$$

(Gutiérrez *et al.* 2008) and the individual increase in co-ancestry

$$\overline{N}_{ec} = \frac{1}{2\Delta c} \quad (6)$$

(Cervantes *et al.* 2011), the realized effective population size can be estimated.

Results and discussion

Table 1 shows the following indicators of the pedigree completeness level assessed for the reference population of White Shorthaired goat (animals born from 2008 to 2011 with at least one ancestor known in the second ancestral generation): 5.62 maximum generations traced, 1.97 fully traced generations and 3.04 equivalent complete generations. The first, second and third ancestral generation was 100%, 83% and 71% complete, respectively. The completeness decreased to as low as 35% and 11% in the fourth and fifth generation. No more than 3% completeness was found from the sixth to ninth generation. The large proportion of missing parents in a pedigree may cause underestimation of inbreeding (Boichard *et al.* 1997). Therefore, limited knowledge of pedigree should be taken into account when looking at the results of pedigree analysis in White Shorthaired goat. To the best knowledge of this study's author, only a single study has investigated the pedigree completeness in goats (Baldursdóttir 2010). With genealogical information of 2240 Icelandic goat individuals, the pedigree completeness in the fifth generation was found to be between 25% and 39% for the youngest animals. Comparisons with Valachian sheep (Oravcová & Krupa 2011) and Improved Valachian and Tsigai sheep (unpublished data) showed more complete pedigree records in Slovakian sheep than in goats (3.71 and 5 vs. 3.04 equivalent complete generations). In contrast, pedigree quality of Zandi sheep (3.15 equivalent complete generations) reported by Ghafouri-Kesbi (2010) was similar to pedigree quality found in White Shorthaired goat. Huby *et al.* (2003) reported 4.1 to 6.7 equivalent complete generations with exception of one breed. Moreover, Danchin-Burge *et al.* (2010) reported 4.6 to 10.5 equivalent complete generations in various French sheep breeds.

The parameters of probabilities of gene origin derived for the reference population of White Shorthaired goat are given in Table 1. The number of founders and the effective number of founders were 286 and 73, respectively. The more balanced the expected contributions of founders, the higher the effective number of founders. Consequently, the smaller number of effective founders compared to the number of founders indicates the excessive use of some animals as parents or a disequilibrium between the founder contributions (Goyache *et al.* 2003, Ghafouri-Kesbi 2010). The ratio f_e/f was 0.26 and was almost the same as the ratio f_e/f (0.25) in Xalda sheep (Goyache *et al.* 2003) with genealogical information of 561 animals investigated (329 founders and 81 effective founders). In contrast, the ratio f_e/f was 0.14 in Zandi sheep (Ghafouri-Kesbi 2010) with genealogical information of 2566 animals investigated (615 founders and 86 effective founders).

The number of ancestors contributing to the reference population of White Shorthaired goat was assessed 256 and was about 90% of the founder animals (vs. 72% and 97% in Xalda and Zandi sheep, respectively). This relatively high number of ancestors is typical for populations lacking long historical pedigrees by showing a short period of time between the youngest generations and the founders (Gutiérrez *et al.* 2003). The effective number of ancestors, defined as the minimum number of ancestors necessary to explain the complete genetic diversity of a population (considering the contribution of an ancestor not yet accounted for by other ancestors), was smaller (45) and was 16% of the founder animals. A small effective number of ancestors accounts for the loss of genetic variability from parent to offspring due to bottleneck (Álvarez *et al.* 2010) and is a result of the fact that selection increases representation of some animals in a pedigree (Goyache *et al.* 2003). In White Shorthaired goat, selection in the early 1990s allowed only pulled animals to be accepted for breeding. The ratio f_e/f_a in White Shorthaired goat was 1.6. The higher the value of this ratio, the higher the bottleneck effect resulting from the decrease of the number of reproducers over the generations (de Oliveira *et al.* 2012). When the ratio f_e/f_a is close to unity, the population is stable in terms of effectively contributing ancestors and the bottleneck has not played a significant role in the population (Fair *et al.* 2012). The effective number of ancestors in White Shorthaired goat was similar to that in Xalda sheep (40 effective ancestors) and the ratio f_e/f_a was smaller than that reported by Goyache *et al.* (2003) for Xalda sheep (1.6 vs. 2).

The calculation of f_a involves assessment of marginal contribution of each ancestor to the genetic variability of the reference population starting from the contribution of the most influential ancestor (Ghafouri-Kesbi 2010). Marginal contributions of the ten most influential ancestors varied between 5.45% and 2.47% and accounted for 39.8% of the genetic variability of the reference population of White Shorthaired goat. The most influential ancestors were nine males with 69 to 20 descendants per buck and one female with nine descendants. Fifty percent of the genetic variability of the reference population was explained by marginal contributions of 15 ancestors. Seventy-five percent of the genetic variability of the reference population was explained by marginal contributions of 43 ancestors (Table 1).

In contrast to the effective number of ancestors, the number of founder genome equivalents accounts for all random losses of genes during segregations and consequently provides a smaller number than f_e and f_a (Boichard *et al.* 1997). It was assessed 32 for the reference population of White Shorthaired goat (Table 1).

Table 1
Parameters of pedigree completeness, probabilities of gene origin and identity-by-descent probabilities

Parameter	Reference population
No. of maximum generations, mean value	5.62
No. of fully traced generations, mean value	1.97
No. of equivalent complete generations, mean value	3.04
Pedigree completeness in 1st generation of ancestors	100
Pedigree completeness in 2nd generation of ancestors	83
Pedigree completeness in 3rd generation of ancestors	71
Pedigree completeness in 4th generation of ancestors	35
Pedigree completeness in 5th generation of ancestors	11
Pedigree completeness in 6th to 9th generation of ancestors	≤3
No. of founder animals	286
No. of ancestors	256
Effective No. of founders (f_e)	73
Effective No. of ancestors (f_a)	45
NA ₅₀	15
NA ₇₅	43
Founder genome equivalents (f_g)	32
Inbreeding, mean value (F %)	0.69
Co-ancestry, mean value (\bar{c} %)	1.55
\bar{N}_e (from increase in inbreeding)	182
\bar{N}_{ec} (from increase in co-ancestry)	142

NA₅₀ – No. of ancestors explaining 50 % of genetic variability, NA₇₅ – No. of ancestors explaining 75 % of genetic variability, \bar{N}_e , \bar{N}_{ec} – Effective population size

The parameters of identity-by-descent probabilities derived for the reference population of White Shorthaired goat are shown in Table 1. The mean values of coefficients of inbreeding and co-ancestry were assessed 0.69 % and 1.55 %, respectively. In total, 0.30 % matings between half sibs and 0.24 % matings between parent-offspring were identified. The low inbreeding level may be a result of insufficient pedigree completeness as well as a result of the breeders' intention to avoid mating of related animals. In contrast, the mean values of coefficients of inbreeding and co-ancestry in Zandi sheep assessed at 1.46 % and 1.21 % were reported by Ghafouri-Kesbi (2010). The co-ancestry describes the amount of relations among individuals in a breeding programme and the effectiveness of a selection programme. The opposite of co-ancestry may be considered as diversity according to Ghafouri-Kesbi (2010). The higher the co-ancestry, the lower is the genetic diversity. For effective selection, the co-ancestry needs to be managed.

The parameters \bar{N}_e and \bar{N}_{ec} (effective population size assessed from the individual increase in inbreeding and the individual increase in co-ancestry, respectively) are assumed to be the measure of the same cumulated drift processes in a population (Cervantes *et al.* 2011). A difference between \bar{N}_e and \bar{N}_{ec} would characterize the influence of preferential matings in a

population. It is not easy to interpret a difference between $\overline{N_e}$ and $\overline{N_{ec}}$ found in the population of White Shorthaired goat because similar values of $\overline{N_e}$ and $\overline{N_{ec}}$ may result from a shallow pedigree. The value of $\overline{N_{ec}}$ was found to be smaller than the value of $\overline{N_e}$ (142 vs. 182) which is in contrast to findings of Cervantes *et al.* (2011) who referred opposite relationship between $\overline{N_e}$ and $\overline{N_{ec}}$ in Spanish horse breeds.

No clear relationship between the results provided from calculations of parameters of probabilities of gene origin and parameters of identity-by-descent probabilities in White Shorthaired goat can be found. The parameters of probabilities of gene origin indicated a decrease in genetic diversity between the founders and the reference population (comparisons between founders and ancestors and between effective founders and effective ancestors as well as founder genome equivalents). This situation, however, is typical for populations lacking long historical pedigrees by showing a short period of time between the youngest generations and the founders (Gutiérrez *et al.* 2003). No genetic diversity issues were indicated by the values of effective population size. Findings presented in this study need to be interpreted with caution due to a limited history of a pedigree. Incomplete pedigree records with only one third and one tenth of ancestors known in the fourth and fifth ancestral generation may cause underestimation of inbreeding and increase in inbreeding as well (according to Cervantes *et al.* 2008, increase in inbreeding tends to stabilize with about five equivalent complete generations). The high number of the founders and ancestors and the disequilibrium between effective founders and effective ancestors may, in addition to preferential use of some animals and weak bottleneck effects, also be due to insufficient pedigree information.

In conclusion, the study shows the first results of a pedigree analysis in White Shorthaired goat in Slovakia. There were found small numbers of effective founders, effective ancestors and founder genome equivalents (in comparison to founders and ancestors), whereas the values of effective population size were assessed relatively high. Starting with the fourth generation of ancestors, the pedigree completeness was extremely low. To be able to keep genetic links across generations in touch, the amount of pedigree information needs to be increased. This is a serious requirement for appropriate monitoring and management of genetic relations within the population.

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