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Estimation of inbreeding coefficient and generation interval in Pag Sheep – baseline for development of optimum contribution selection

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Summary

The aim of the study was to estimate coefficient of inbreeding (F_{PED}) and generation interval (GI) in the population of Pag sheep breed in order to provide a scientifically based background for implementation of optimum contribution selection. The average F_{PED} was 6%, with inconsistent trend in the last decade, and GI was estimated to be 4.44 years. The F_{PED} was higher than reported for majority of few well known European dairy breeds, while the GI was in line with the reports. The estimated F_{PED} calls for attention of the breeders to keep it as low as possible in the future, preferably by following the basic principles of the optimum contribution selection.

Keywords: Pag sheep, inbreeding, generation interval, selection

Introduction

The Pag sheep breed with an estimated population size of 30,000 animals has great economical, traditional, and cultural importance for residents of the Pag island. Dairy products of the breed have a tremendous market niche for long time now (milk ~1.7 €/L, cheese ~30 €/kg) which is the main reason why the breeders seek to permanently increase the milk production in their flocks via selection. Pedigree and performance recording in this population started about two decades ago in order to use BLUP in genetic evaluation for dairy traits (test-day repeatability animal model; Špehar et al., 2020.). Substantial part of the phenotyped population has been recently genotyped (50K SNP chip) for purpose of transition to genomic selection (single-step genomic BLUP; Legarra et al., 2009.). Inbreeding is inevitable in small populations, especially under severe selection pressure due to overuse of genetically superior animals. The rationale behind this claim relies on the fact that animals that share common genes, have similar breeding values, and therefore tendency to inter-mate. In order to control inbreeding while providing selection gain, future mating schemes should have a low expected inbreeding coefficient of the offspring, which is a consequence of the kinship between the parents (Legarra et al., 2009.). Generation interval (GI) represents an important population parameter for predicting response to selection and provides an indication about dynamics of generations change in the population under concern (Boichard et al., 1997.; Gutiérrez et al., 2003.). The shorter the GI, the faster selection gain is expected in the population. However, this is the true only under assumption that selection intensity remains the same, which cannot be obtained because these two parameters are tightly related to each other in undesirable manner. The optimum contribution selection seems to be the best possible selection strategy in the future for this population in order to provide selection gain while minimising loss of genetic variability. In the era of "genomics", the best possible solution seems to be the genomic selection. However, prior to transition to this complex strategy, numerous questions about existing state of the population need to be answered. The level and trend of inbreeding and GI are very important population parameters from this point of view so their estimation represents the main goals of this study.

Material and methods

Pedigree records were provided by the Croatian Ministry of Agriculture. Initial pedigree comprised of 281760 animals born from 1981 to 2019, but after comprehensive quality control of the pedigree, only subset of the animals with

sufficient pedigree information was used in estimation of coefficient of inbreeding and GI. Number of fully traced generations (NFG) represented the number of the last ancestral generation with known sire and dam. Number of equivalent generations (NEG) was obtained as the sum of the proportions of known ancestors of an individual over all traced generations as follows: . where was the number of ancestors of individual , and was the number of generations between individual and its ancestor i (Maignel et al., 1996.). In this way, 1/2 was added for each known parent, 1/4 for each known grandparent, 1/8 for each known great-grandparent and so on. Pedigree completeness index (PCI) or harmonic mean of the pedigree completeness of the parents was calculated using the following formula: with and being proportions of paternal and maternal ancestors estimated based on: where was the ratio of known to unknown ancestors in each generation and was the number of generations (MacCluer et al., 1983.). Completeness was calculated for individuals and for groups of individuals in each ancestral generation representing the proportion of known ancestors in each generation (Figure 1). Reference population was set to animals born after 2010 with constraint imposed on animals with *NEG*≥3. The generation interval was calculated as the average age of the parents at birth of their offspring, and coefficient of inbreeding (F_{PED}) as the probability that two alleles chosen at random from the maternal and paternal haplotypes are identical by descent. The pedigree analysis was conducted in the R programming environment (R Core Team, 2020.) using package "optiSel" (Wellmann, 2021.). Preparation of data, descriptive statistical analysis, and plotting of the results were carried out using "data.table" (Dowle and Srinivasan, 2021.), "tidyverse" (Wickham et al., 2019.), "pastecs" (Grosjean and Ibanez, 2018.), "descriptr" (Hebbali, 2020.) and "ggplot2" (Wickham, 2016.).

Results and discussion

The coefficient of inbreeding (F_{PED}) obtained from genealogical records is accurate insofar as the quality of the pedigree. Therefore, a thorough control of the pedigree completeness was carried out in order to establish a reference population with sufficient ancestral information. Rams and ewes had practically the same completeness of the pedigree (Figure 1). It is visible that 100% of individuals have known both ancestors in the first generation, almost 99% of them in the second, 85% in the third, 56% in the fourth and 31% in the fifth. The average NEG, NFG, NMG, and PCI in the reference population was 3.96, 2.48, 6.9, and 0.73, respectively (Table 1). The obtained quality control parameters of the pedigree kind of guarantee that F_{PED} and GI in this population was estimated with sufficient dose of certainty. The estimated average of F_{PED} in the reference population was 6% (Table 1) with three quarters of population having F_{PED} below 1% (Table 2). Different quality of the pedigree between different populations often poses huge limits to fair comparisons of estimates of F_{PED} obtained in different studies. Many studies on sheep breeds do not impose any restrictions based on the pedigree quality parameters while estimating F_{PED}, which often results with severe underestimation of the true value of F_{PED}. Our estimate might be to some extent comparable to F_{PED} obtained in Italian (Cortellari et al., 2022.), Spanish (Granado-Tajada et al., 2020.), and French (Rodríguez-Ramilo et al., 2019.) dairy sheep breeds. However, missingness of pedigree information in the two latter studies was tackled by using methodology proposed by VanRaden (1992.) which allows estimating inbreeding coefficients in populations with missing genealogy, by assuming that the F_{PED} of individuals with missing parents are equal to the mean of the inbreeding coefficients of those animals with known parents and born during the same year. The estimated F_{PED} for Delle Langhe, Comisana, Massese and Sarda was estimated at 6%, ~2%, ~4%, and ~9%; for Latxa Cara Negra from Euskadi, Latxa Cara Rubia, and Latxa Cara Negra from Navarre ~2%, ~2%, and ~2%; and for Basco-Béarnaise, Manech Tête Noire, Manech Tête Rousse, Lacaune Confederation, and Lacaune Ovitest ~3%, ~3%, ~2%, ~2%, and ~3%, respectively.
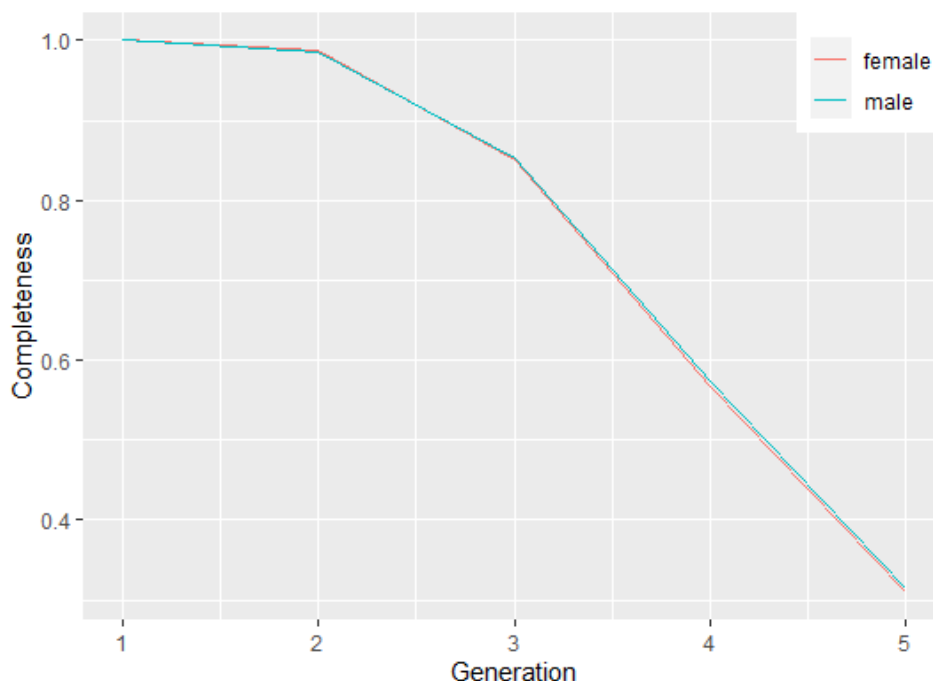
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Figure 1. Completeness of the pedigree in the reference population.

Table 1. Quality control parameters of the pedigree, coefficient of inbreeding, and generation interval estimated in the reference population of Pag sheep breed

	NEG	NFG	NMG	PCI	F_{PED}	GI
min	3.00	1.00	3.00	0.32	0	1
max	6.43	5.00	11.00	1.00	0.44	14.5
average	3.96	2.48	6.9	0.73	0.06	4.44

NEG - number of equivalent generations; NFG - number of fully traced generations; NMG - number of maximum known generations; PCI - pedigree completeness index, F_{PED} – coefficient of inbreeding, GI – generational interval

Table 2. Distribution of the coefficient of inbreeding (F_{PED}) in the reference population

Class of F_{PED}	Frequency	Percent (%)
0.0000-0.0875	12323	76.43
0.0875-0.1750	2760	17.12
0.1750-0.2625	682	4.23
0.2625-0.3500	339	2.10
0.3500-0.4375	19	0.12
Total	16123	100

Trend of inbreeding in the examined period was not completely conclusive, since it actually decreased up to 2016, and thereafter increased (Figure 2). However, this small increase of the F_{PED} in the last five years does not represent a serious issue, since it did not exceed the 6.25% which is considered as an acceptable level of inbreeding in small populations undergoing selection. From all these results pertaining to F_{PED}, it seems that inbreeding in this population has been in acceptable level regardless of selection on the milk production. Breeders in this population are aware of potentially negative impacts of inbreeding (inbreeding depression) and they make efforts to avoid close inbreeding in their flocks by replacing their sires from other, usually neighbouring flocks (unofficial circulation of the rams). According to some preliminary results obtained in this sheep populations, it looks that inbreeding does not directly

threaten to the main selection goal in this population (milk production). However, there are serious indications that it has a substantial impact on birth weight, which can indirectly impact profitability of this breed. Regardless of being based on comprehensive and deep statistical analysis, these statements still need to be proven under the framework of genetic animal model level prior to generalisation.
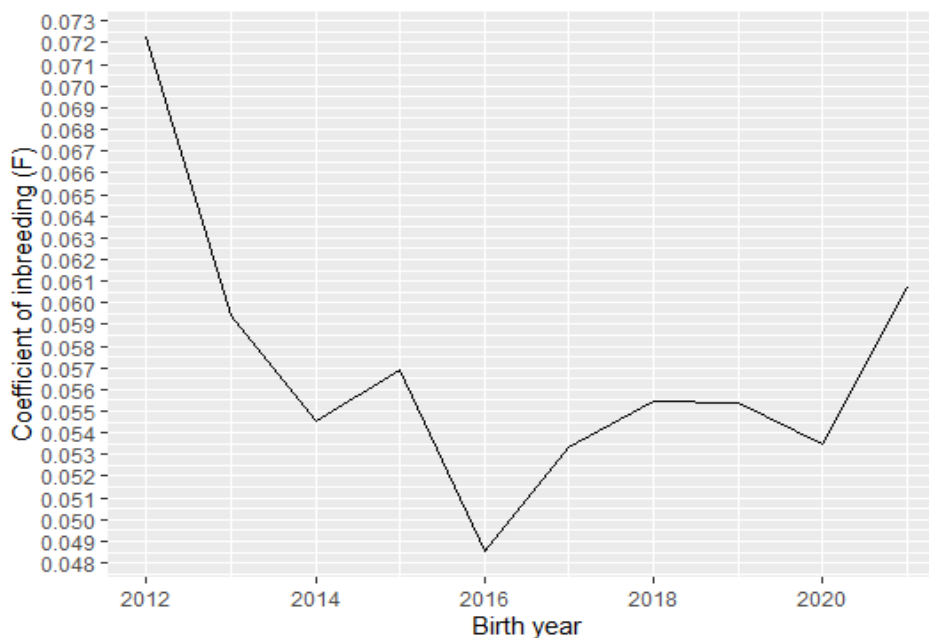

Figure 2. Trend of inbreeding in the reference population of Pag sheep.

The estimated GI in this population was 4.44 years (Figure 3), which goes in line with reports of the studies conducted on the above discussed Spanish and French dairy sheep breeds. On the other side, the GI was notably above reports for sheep meat breeds worldwide, where the average GI generally range between 2.0 and 3.8 years (e.g. Rafter et al., 2022.; Hashemi and Ghavi Hossein-Zadeh, 2020.). The obtained GI in Pag sheep breed was expected for us by taking into consideration that ewes in this dairy orientated sheep population stay in production as long as possible, in some flocks practically until they die (it is not unusual that ewes reach 10-12 years of age). The culling rate in this population is generally obviously low, which can be considered as a flaw from selection point of view, but this is tricky, and it does not automatically imply lower selection gain, because lower culling rate leaves "more room" for higher selection intensity. To be more precise, by simply looking at the breeder's equation it can be superficially concluded that lower GI automatically and unconditionally leads to the faster genetic gain. Since selection gain depends also on selection intensity, you always need to think of that by lowering GI you automatically pose restrictions to selection intensity. Therefore, it is necessary to find a balance between GI and selection intensity that will result with maximal response to selection in this population which will be one of our goals in the future along with the finding solutions to maximally reduce loss of genetic variation by following the principals of optimum contribution selection. Since the products of this sheep population has an extraordinary market niche, investments to genomic selection seems to be reasonable and economically justified. By using genomic information with all historical data collected in this population, selection gain could be achieved much faster, particularly via more efficient selection of replacement sires that have been sub-optimally selected as confirmed by Kasap et al. (2022.).
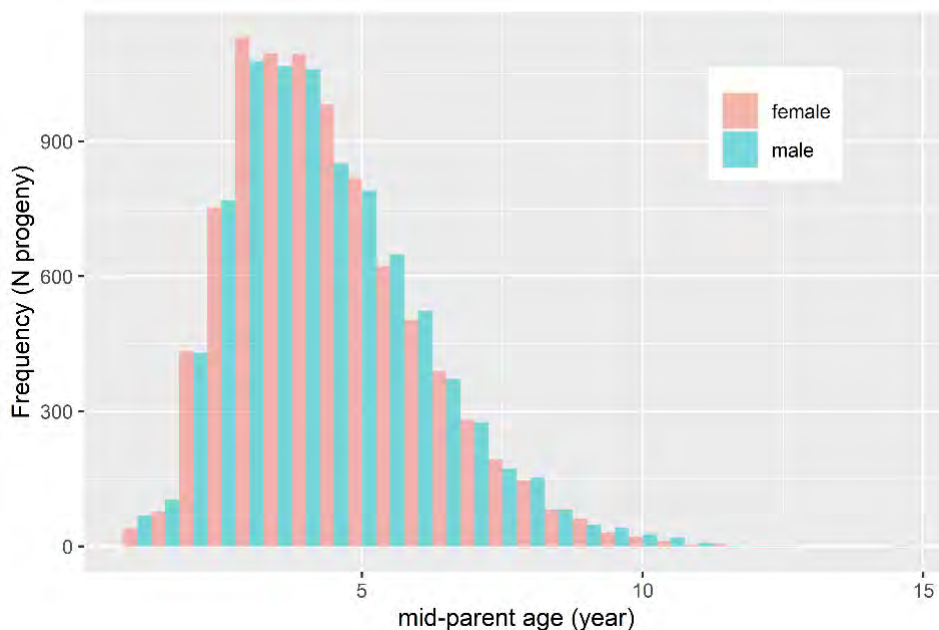
Figure 3. Distribution of mid-parent age in the reference population (n_{female}=8770, n_{male}= 8585)

Conclusion

The results represent an important scientific background about past breeding activities in the Pag sheep breed, and should serve as a baseline to upgrade the existing breeding program. The estimated inbreeding coefficient calls for attention of the breeders to keep it as low as possible in the future. The optimum contribution selection is the most appropriate selection strategy for populations under selection in order to balance selection gain with minimal loss of genetic variability, so we advocate hereby its usage in the future for this very important indigenous sheep breed.

Acknowledgment

Literature

Boichard D., Maignel L., Verrier E. (1997). The value of using probabilities of gene origin to measure genetic variability in a population. Genetics Selection Evolution. 29 (1): 5–23.

Cortellari M., Negro A., Bionda A., Grande S., Cesarani A., Carta A., Macciotta N., Biffani S., Crepaldi P. (2022). Using Pedigree and Genomic Data toward Better Management of Inbreeding in Italian Dairy Sheep and Goat Breeds. Animals. 12 (20): 2828.

Dowle M., Srinivasan A. (2021). data.table: Extension of `data.frame`. R package version 1.14.2. https://CRAN.R-project.org/package=data.table

Granado-Tajada I., Rodríguez-Ramilo S.T., Legarra A., Ugarte E. (2020). Inbreeding, effective population size, and coancestry in the Latxa dairy sheep breed. Journal of Dairy Science. 103 (6): 5215–5226.

Grosjean P., Ibanez F. (2018). pastecs: Package for Analysis of Space-Time Ecological Series. R package version 1.3.21. https://CRAN.R-project.org/package=pastecs

Gutiérrez J.P., Altarriba J., Diaz C., Quintanilla R., Canon J., Piedrafita J. (2003). Pedigree analysis of eight Spanish beef cattle breeds. Genetics Selection Evolution. 35 (1): 43–63.

Hashemi M., Ghavi Hossein-Zadeh N. (2020). Population genetic structure analysis of Shall sheep using pedigree information and effect of inbreeding on growth traits. Italian Journal of Animal

Science. 19 (1): 1195–1203.

Hebbali A. (2020). Descriptr. Available at: https://github.com/rsquaredacademy/descriptr (Accessed December 2, 2022).

Kasap A., Božulić L., Ramljak J., Mioč B., Špehar M. (2022). Partition of genetic trend for milk yield by gender and flock in Pag sheep. In Proceeding of the 57th Croatian & 17th International Symposium on Agriculture. Majić I., Antunović Z. (ed.), 462-466. Vodice, Croatia: Josip Juraj Strossmayer University of Osijek, Faculty of Agrobiotechnical Sciences Osijek.

Legarra A., Aguilar I., Misztal I. (2009). A relationship matrix including full pedigree and genomic information. Journal of Dairy Science. 92(9):4656–4663.

MacCluer J.W., Boyce A.J., Dyke B., Weitkamp L.R., Pfennig D.W., Parsons C.J. (1983). Inbreeding and pedigree structure in Standardbred horses. Heredity. 74: 394–399.

Maignel L., Boichard D., Verrier E. (1996). Genetic variability of French dairy breeds estimated from pedigree information. Interbull Bulletin. 14: 49–54.

Rafter P., McHugh N., Pabiou T., Berry D.P. (2022). Inbreeding trends and genetic diversity in purebred sheep populations. Animal. 16 (8):100604.

R Core Team. (2020). R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org

Rodríguez-Ramilo S.T., Elsen J.M., Legarra A. (2019). Inbreeding and effective population size in French dairy sheep: Comparison between genomic and pedigree estimates. Journal of Dairy Science. 102 (5): 4227–4237.

Špehar M., Mulc D., Barać Z., Mioč B., Kasap A. (2020). Estimation of genetic parameters for dairy traits in Pag sheep with single and multi-trait test–day models. Small Ruminant Research. 183: 106029.

VanRaden P.M. (1992). Accounting for inbreeding and crossbreeding in genetic evaluation of large populations. Journal of Dairy Science. 75: 3136–3144.

Wellmann R(2021). optiSel: Optimum Contribution Selection and Population Genetics. R package version 2.0.5. https://CRAN.R-project.org/package=optiSel

Wickham H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wickham H., Averick M., Bryan J., Chang W., D'Agostino McGowan L., François R., Grolemund G., Hayer A., Henry L., Hester J., Kuhn M., Lin Pedersen T., Miller E., Milton Bache S., Müller K., Ooms J., Robinson D., Paige Seidel D., Spinu V., Takakashi K., Vaughan D., Wikle C., Woo K., Yutai H. (2019). Welcome to the tidyverse. Journal of Open Source Software. 4 (43): 1686.