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Pedigree analysis: estimation of genetic parameters and the effect of inbreeding on dairy traits in Simmental cattle

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The objectives of this study were (1) to evaluate the level of inbreeding by estimating inbreeding coefficients and (2) to estimate the effect of inbreeding on lactational milk traits in Polish Simmental cows. Two reference populations were defined for pedigree analysis: animals born between 1984 and 2009 (dataset A, n=20,827) and animals born between 2010 and 2020 (dataset B, n=19,554). Mean inbreeding coefficients for the analysed cows were generally low in both reference populations, however, approximately 72% of the inbred cows were born in the second studied decade. Notably, an increased number of ancestors did not result in an increase in genetic diversity. 7 founders exhibited the highest gene contribution. The principal ancestors with the highest gene contribution were 11 sires in dataset A and 15 animals in dataset B. The coefficients of regression on inbreeding were low and negative for milk yield and fat or protein content for all three lactations, whereas positive effects were observed for fat or protein percentage. Overall, the genetic variability of Polish Simmental cows is at a satisfactory level, nevertheless in young cows an increase in the number of inbred individuals is observed. Analysis of ancestral gene contributions indicates significant changes in the composition of ancestors in this younger population.

KEY WORDS: ancestors / founders / inbreeding depression / Simmental cows

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Inbreeding occurs when closely related animals are mated more frequently than the population average mating relatedness. This leads to a loss of genetic variability and an increased frequency of deleterious alleles. The consequences of inbreeding include genetic drift, reduced heterozygosity, and decreased genetic diversity. Additionally, inbreeding can cause reproductive and productivity problems in animals [Hinrichs and Thaller 2011, Howard *et al*. 2017, Strapáková and Strapák 2024]. An inbreeding trend can be detected and assessed through analyses of pedigree information.

The level of inbreeding in dairy cattle has received considerable attention for many years. Conventional breeding programs can achieve high rates of genetic progress but may also cause genetic erosion in selected populations [Stachowicz *et al*. 2011]. Rios Utrera *et al*. [2018] reported low inbreeding coefficients parallel to reduced genetic variability attributed to both the existing bottlenecks in pedigrees with 15 ancestors explaining about 20% of genetic diversity as well as to genetic drift. In Colombian Simmental cattle, Amaya et al. [2020] found that the average annual inbreeding rate decreased by nearly 50% over a period of more than 30 years following the introduction of new sires from Europe and North America. This intervention contributed to increased genetic diversity. In contrast, Melka *et al.* [2013] found a 7% decline in genetic diversity in the Brown Swiss cattle population over the last 40 years due to increased inbreeding.

Overall, literature reports cooccurrence of inbreeding and production challenges. Many studies indicate that accumulation of inbreeding and loss of genetic diversity are a real problem in modern dairy cattle breeds adversely affecting many traits important for breeders and, in extreme cases, leading to premature culling of animals. A high level of inbreeding can impair calf birth weight and survival, disease resistance, other calving traits, fertility, and milk yield [Thompson *et al.* 2000, McParland *et al.* 2007, Rokouei *et al.* 2010, Hinrichs and Thaller 2011, Fuerst-Waltl and Fuerst 2012, Maltecca *et al.* 2020]. Therefore, monitoring the genetic variability of dairy cattle populations is essential.

Several methods can be applied to prevent the loss of genetic variability. An effective way to control the level of inbreeding is to limit the number of closely related animals entering the cattle herd. Another approach is to analyse mate pedigrees to prevent close-kin matings. To mitigate the negative effects of inbreeding, responsible breeders and breed associations employ strategies such as maintaining diverse and well-managed breeding stock, implementing selection programs that emphasize genetic diversity, and periodically introducing unrelated genetic material through outcrossing. These measures contribute to the maintenance of genetic diversity and help ensure the long-term viability of a cattle population [Maltecca *et al*. 2020].

When juxtaposed with the most important breed in Poland, Polish Holstein-Friesian (HF) cattle, the population of Simmental cattle remains relatively small. As a dual-purpose breed for both meat and milk production, Simmental cattle breeding has historically been concentrated in southeastern regions of Poland. Reflecting the distribution, most population research in the country has traditionally focused on HF cattle, while Simmentals and other smaller breeds have received comparatively little scientific attention.

Recent years, however, have brought the onset of a new trend. Throughout the country, breeders maintaining herds consisting predominantly of HF cows have increasingly introduced small numbers of Simmental cows to evaluate their efficiency and productivity in farm conditions. Following favourable results, some breeders have chosen to modify the production profile of their herds. An example of such a trend is the Pępowo Stud Farm in Poznan Province, where both HF and Simmental cows are raised within the same production system. The Simmental cows from this farm have repeatedly achieved championship titles at the National Simmental Cattle Show in Rudawka Rymanowska.

The growing importance of Simmental cattle in Poland together with the intensification of semen imports from Simmental bulls, primarily from Germany, have highlighted the need to revise the existing Simmental cattle breeding programs. Therefore, a comprehensive genetic and population analysis of Simmental cattle in Poland is required. The objectives of this study were (1) to evaluate the level of inbreeding by estimating inbreeding coefficients based on pedigree information and (2) to assess the effect of inbreeding on milk production traits in Polish Simmental cows.

Material and methods

Pedigree data for Simmental cows were obtained from FedInfo, the official Polish national recording system, and provided by the Polish Federation of Cattle Breeders and Dairy Farmers. To assess changes in the Simmental cattle population in Poland resulting from the import of sires, two reference populations were defined for pedigree analysis. The first reference population (dataset A) included animals born between 1984 and 2009, while dataset B included animals born between 2010 and 2020. Dataset A contained 20,827 animals, and dataset B contained 19,554. Dataset A represents earlier generations of Simmental cattle bred under previous selection objectives and management conditions, whereas dataset B reflects more recent breeding strategies, improved recording, and advances in herd management. This arrangement allows for the evaluation of genetic progress, changes in inbreeding trends, and shifts in population structure and selection intensity across decades.

The completeness of the pedigrees across generations is presented in Figure 1. The whole pedigree file contained information on 89,220 animals. The cows were the daughters of 3,033 sires and 30,140 dams. Only 109 cows lacked dam information. Most sires had between 1 and 10 recorded daughters. The structure of the Simmental dataset is summarised in Table 1.

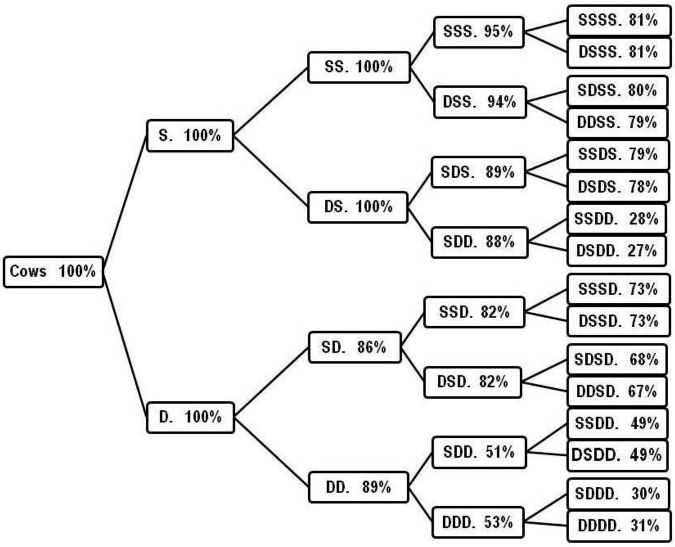

Fig. 1. Level of identification of ancestors up to 4 generations in pedigree of Simmental cows. S is sire and D is dam.

Table 1. Demographic structure of Simmental cattle population

Generation interval	No. of individuals	Mean (year)
Sire-son path for bulls	6,280	7.43
Sire-daughter path for cows	39,102	6.91
Dam-son path for bulls	5,358	4.99
Dam-daughter path for cows	31,779	4.81
Family size	maximum	mean
Cows per sire	488	12.23
Cows per dam	8	1.34

Pedigree-based analyses

Pedigree completeness was calculated as the mean equivalent of complete generations (EqG), as described by Boichard *et al.* [1997]:

where:

$$\mathrm{EqG} = \frac{1}{\mathrm{N}}\sum_{j=1}^{\mathrm{N}}\sum_{i=1}^{n_i}\frac{1}{2^{g_{ij}}}$$

EqG – mean equivalent of complete generations;

N – number of animals included in the analysis;

n_i – total number of ancestors of j-th animal in the population under study;

g_{ij} – number of generations between j-th animal and its i-th ancestor.

Higher the values of EqG indicate greater pedigree completeness and higher-quality pedigree information.

Individual inbreeding coefficients (F_x) for the animals were calculated according to Meuwissen and Luo [1992]. The effective population size (Ne) was estimated following Falconer [1996] as:

where:

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

Ne – effective population size;

ΔF – mean inbreeding rate.

The change in the mean inbreeding rate was defined as [Falconer 1996]:

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

where:

F_{t+1} – mean inbreeding coefficient in the next generation;

F_t – mean inbreeding coefficient in the current generation.

Founders were defined as animals with unknown parents. The contribution of a founder to a reference population depends on its use in the past; therefore, information given by the total number of founders was limited, so Lacy [1989] introduced the concept of the effective number of founders. This parameter represents the number of equally contributing founders expected to generate the same genetic diversity as observed in the studied population. The effective number of founders was calculated as:

$$f_e = \frac{1}{\sum_{k=1}^{f} q_k^2}$$

where:

f_e – effective number of founders;

f – total number of founders;

q_k – probability of gene origin from k-th founder.

The ratio f_e/f indicates the balance of the founder contributions to the reference population, with higher values reflecting more evenly distributed contributions among founders. However, when calculating the effective number of founders, pedigree bottlenecks are not accounted for. Therefore, Boichard et al. [1997] proposed the effective number of ancestors (f_a), which incorporates bottleneck effects by replacing the squared probability of gene origin from the k-th founder (q_k^2) in the original formula with the squared marginal contribution of the k-th ancestor (p_k^2).

Another parameter for the genetic diversity of a reference population is the effective number of founder genomes [Boichard *et al.* 1997]:

$$f_g = \frac{1}{\sum_{k=1}^{f} \frac{q_k^2}{r_k}}$$

where:

f_g – effective number of founder genomes;
f – total number of founders;
q_k – probability of gene origin from k-th founder;
r_k – expected proportion of founder alleles in the reference population.

The effective number of founder genomes describes random losses of alleles caused by genetic drift during bottlenecks. The ratio f_g/f_e accounts for random genetic losses caused by genetic drift: if the value is closer to zero, the genetic losses caused by genetic drift are higher.

Genetic diversity (GD) representing losses of genetic variation due to genetic drift and unequal founder contributions was calculated as in Melka *et al.* [2013]:

$$GD = 1 - \frac{1}{2f_g}$$

When expressed as 1-GD, this parameter estimates the proportion of genetic diversity lost in the population since the founder generation as a result of pedigree bottlenecks and genetic drift. Genetic diversity representing the loss of genetic variation due to unequal founder contributions (GD*) was computed according to Melka *et al.* [2013] by replacing the effective number of founder genomes (f_g) with the effective number of founders (f_e). Similarly, the loss of genetic diversity due to unequal contributions of founders was estimated as 1-GD*. The loss of diversity by genetic drift was calculated as the difference between GD* and GD.

Estimation of genetic parameters and 1% inbreeding depression

The BLUPf90 package [Misztal *et al.* 2014] was used for the estimation of variance components and the 1% inbreeding depression on milk, fat and protein yields, as well as on fat and protein content in milk.

Dataset C was created to estimate genetic parameters for lactational milk, fat and protein yield, as well as fat and protein content in milk (Tab. 2). Lactation records from 57,848 first three lactations of 26,782 Simmental cows were analysed. There were 26,782, 19,109 and 13,286 cows from the first, second and third lactations, respectively. Cows with records in the second lactation were required to have records in the first one, and cows with records in the third lactation were required to have records in the two previous lactations. Lactation lengths for individual cows ranging from 200 to 1,200 days were included in the analysis. Because lactations of different lengths were

Table 2. Means with standard deviation (SD) for five whole-lactation milk traits of Simmental cows, by lactation

Lactation	Milk (kg)		Fat (kg)		Fat (%)		Protein (kg)		Protein (%)	
no.	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
1	6,193.83	2,321.71	258.51	101.43	4.17	0.44	215.26	86.34	3.45	0.24
2	6,675.91	2,389.00	278.33	104.13	4.17	0.47	233.86	87.73	3.49	0.24
3	6,889.15	2,331.87	286.71	102.24	4.16	0.47	238.56	85.03	3.45	0.24

included in the analysis, the traits presented in Table 1 showed considerable variability. As a result, the standard deviations of these traits were relatively high. Because the dataset covered a wide range of lactation lengths, a regression on lactation length was included in the Gibbs model for estimating genetic parameters. Adding lactation length as a covariate helped to reduce systematic variation, resulting in more accurate estimates of genetic and residual variances and, consequently, more precise heritability estimates.

Cows, daughters of 1,266 sires, calved from 2001 to 2022 at ages 18-48, 29-65 and 41-75 months, for the first, second and third times, respectively. Two seasons of calving were assumed (October-March and April-September). First, a restriction of a minimum of 3 daughters per sire was imposed; second, herd-year-season (HYS) subclasses were restricted to a minimum of 2 contemporaries. There were 9,320 HYS subclasses in the analysis.

A multi-trait animal model and a Bayesian method via Gibbs sampling were used to estimate (co)variance components. In matrix notation the model was:

$$\boldsymbol{y} = \boldsymbol{Hh} + \boldsymbol{Ll} + \boldsymbol{F_1 f} + \boldsymbol{F_2 f^2} + \boldsymbol{Za} + \boldsymbol{Ppe} + \boldsymbol{e}$$

where:

$\boldsymbol{y}$ – vector of observations including whole-lactation milk, fat, protein yield, and fat and protein content in milk in subsequent lactation;

$\boldsymbol{h}$ – vector of fixed herd-year-season effect;

$\boldsymbol{l}$ – vector of fixed regression coefficients for lactation length;

$\boldsymbol{f}$ – vector of fixed linear regression coefficients for inbreeding coefficient;

$\boldsymbol{f^2}$ – vector of fixed quadratic regression coefficients for inbreeding coefficient;

$\boldsymbol{a}$ – vector of random additive genetic effects;

$\boldsymbol{pe}$ – vector of random permanent environmental effects;

$\boldsymbol{e}$ – vector of residuals;

$\boldsymbol{H}, \boldsymbol{L}, \boldsymbol{F}_1, \boldsymbol{F}_2, \boldsymbol{Z}, \boldsymbol{P}$ – incidence matrices assigning observations to effects.

100,000 samples of (co)variance components were generated, and the first 20,000 samples were discarded as burn-in based on the plot of Gibbs samples. For further use, i.e. estimation of heritability and repeatability as well as standard deviations of these estimates, every 20th sample from 80,000 samples was saved. In summary, the genetic parameters were reported as the mean values of their posterior distributions.

Inbreeding depression was quantified using the linear and quadratic regression coefficients for inbreeding coefficients included in the above-mentioned model. The inbreeding depression was expressed as the marginal effect corresponds to the first derivative of the polynomial regression function and the errors were calculated using error-propagation methods. In addition, statistical significance of all fixed effects including level of inbreeding, was based on the F-test with PROC GLM in SAS [2014].

Results and discussion

Quality of pedigrees, and inbreeding coefficient

In the Polish Simmental pedigree, the level of identification of ancestors up to the fourth generation was satisfactory. However, less complete information was available along the dam line of pedigree (Fig. 1). Pedigree completeness for the analysed Simmental cow population, together with the number of animals by year of birth are presented in Figure 2. The mean equivalent of complete generations (EqG) for all cows was 3.53 in dataset A (cows born between 1984 and 2009) and 4.67 in dataset B (cows born between 2010 and 2020). For inbred cows, EqG values were 4.42 in dataset A and 5.03 in dataset B.

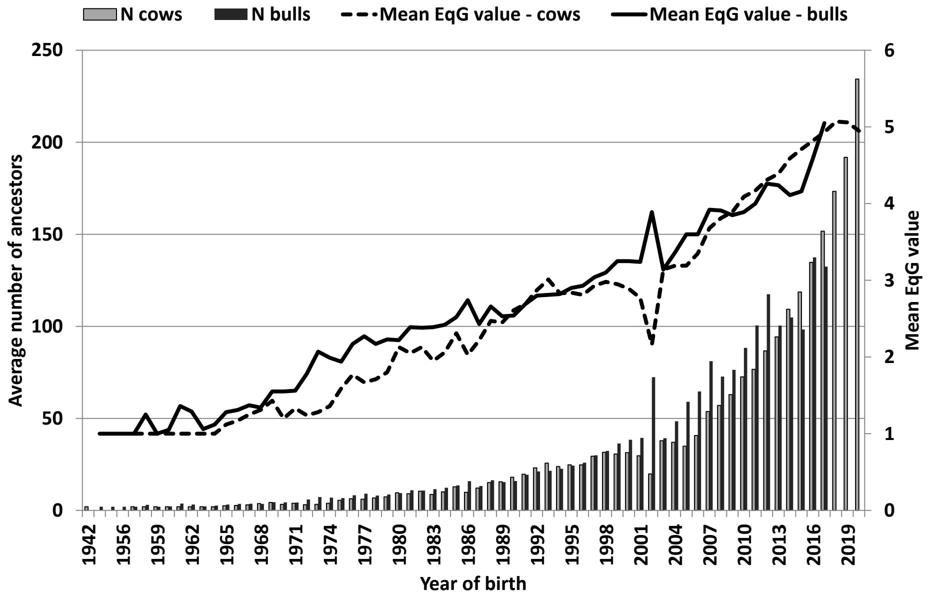

Fig. 2. Mean equivalent of complete generations (EqG) and number of animals in consecutive birth years for Simmental cows.

Analysis of changes in inbreeding levels provides insight into overall population trends and indicates that breeders are mating related animals more frequently. Mean inbreeding coefficients were generally low in both reference populations (Tab. 3 and Fig. 3). The highest inbreeding coefficient was 0.25 in dataset A and 0.32 in dataset B. Approximately 72% of inbred cows were born in the last 10 years. In dataset B,

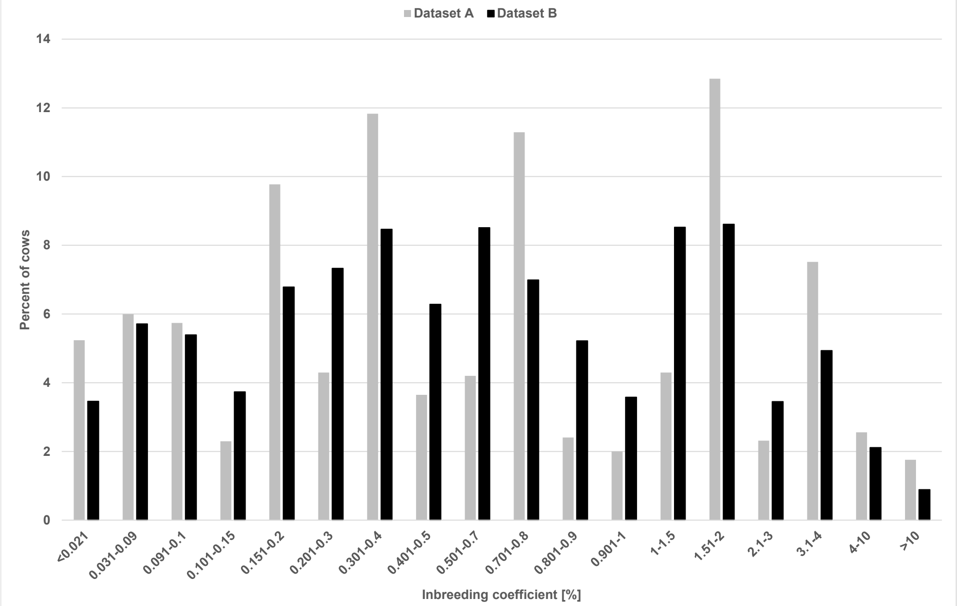

Fig. 3. Distribution of inbreeding coefficients for cows born between 1984 and 2009 (dataset A), and between 2010 and 2020 (dataset B). Only cows with an inbreeding coefficient greater than zero are included.

Table 3. Inbreeding level in the whole studied population of datasets A and B

Inbreeding coefficient	No. of animals		Dataset A			Dataset B		
	dataset A[1]	dataset B[1]	mean	SD	max	mean	SD	max
0	15,996	7,016						
(0, 0.015625)	3,887	10,397						
(0.015625, 0.03125)	579	1,355						
(0.03125, 0.0625)	220	540						
(0.0625, 0.125)	92	152						
(0.125, 0.25)	52	74						
(0.25, 0.3125)	4	17						
> 0.3125	0	3						
All cows in reference population (dataset A or B)			0.0032	0.014	0.2539	0.0068	0.017	0.3164
Only inbred cows			0.0136	0.027	0.2539	0.0106	0.020	0.3164
Rate of inbreeding change per year[2]			-0.002683			-0.000681		

[1] Dataset A (n = 20,827) includes cows born between 1984 and 2009 and dataset B (n = 19,554) includes cows born between 2010 and 2020.

[2] Rate of inbreeding change per year was defined as: $\Delta F = \frac{F_{t+1}-F_t}{1-F_t}$ where F_{t+1} is the mean inbreeding coefficient in the year $t + 1$ and F_t is the inbreeding coefficient in the year t.

12,538 of 19,554 cows (over 64%) and 4,834 of 20,827 cows (about 23%) in dataset A were inbred, with an average inbreeding coefficient of 0.02.

Effective population size (N_e) indicates the level of genetic diversity of a population. Lower N_e values reflect a higher relatedness among individuals, leading to a reduction in the overall gene pool. N_e was relatively low: 555.49 for cows in dataset A (born from 1984 to 2009) and 181.53 for cows in dataset B (born from 2010 to 2020).

The average inbreeding coefficients for male and female ancestors were low. Among 9,199, male ancestors the inbreeding coefficient was 0.0032 for all animals and 0.0135 for inbred animals (n = 2,162). For 39,640 female ancestors, the average inbreeding coefficient was 0.0004 for all animals and 0.0117 for inbred animals (n = 1,261). Male ancestors were inbred more than seven times as frequently as female ancestors (23.5% vs. 3.18%). The highest inbreeding coefficient observed was 0.25 for ancestors of both sexes.

Mean EqG was 2.34 for all male ancestors and 4.34 for inbred male ancestors. For female ancestors, EqG was 1.21 for all animals and 4.69 for inbred animals.

Slightly more than 30% of non-inbred cows were born from 2010 to 2020. In contrast, up to 62.3% of cows with an inbreeding coefficient higher than 0.0625 were born in the same period (dataset B), including three animals with an inbreeding level exceeding 0.3125 (Tab. 3).

Analysis of founder and ancestor gene contribution

The effective number of founders, ancestors, and founder genomes, together with the number of founders and ancestors accounting for 50% of the gene pool of datasets A and B, are summarized in Table 4. Although the use of imported animals increased the number of ancestors, this did not translate into higher genetic diversity in either dataset. The ratios f_a/f_e, f_e/f and f_g/f_e indicate that for cows born in the last decade (dataset B) founder contributions were less evenly distributed, while the loss attributable to the bottleneck effect was almost the same as in dataset A. Genetic losses resulting from genetic drift were slightly lower in dataset B than in dataset A, as reflected by the marginally lower f_g/f_e ratio. Notably, the effective number of founder genomes (f_g) in dataset B was three times lower than in dataset A indicating significant changes in the founder composition.

The genetic diversity lost since the founder generation due to bottlenecks and genetic drift (1-GD), the loss of genetic diversity due to unequal contributions of founders (1-GD*) as well as the loss due to genetic drift (GD*-GD) were all lower in dataset A than in dataset B (Tab. 5). The contributions of genetic drift to overall genetic variability loss was 54% for cows born from 1984 to 2009 (dataset A) and 67.8% for cows born from 2010 to 2020 (dataset B). In contrast, the effect of unequal founder contribution on genetic diversity accounted for 46% and 32.2% in datasets A and B, respectively.

Table 4. Effective number of founders, ancestors and founder genomes, and number of founders and ancestors accounting for 50% of the gene pool of datasets A and B

Item	Dataset A[1]	Dataset B[1]
Number of founders (f)	23,780	20,185
Effective number of founders (f_e)	467	234
Number of ancestors	11,103	18,965
Effective number of ancestors (f_a)	217	110
Effective number of founder genomes (f_g) with standard deviation (SD)	214.6 (17.9)	75.3 (9.0)
f_a/f_e ratio	0.465	0.470
f_e/f ratio	0.020	0.010
f_g/f_e ratio	0.460	0.314
Number of founders explaining 50% of gene pool	219	122
Number of ancestors explaining 50% of gene pool	103	58
Maximum value of founder gene contribution	0.015	0.023
Maximum value of ancestor gene contribution	0.027	0.047

[1] Dataset A (n = 20,827) includes cows born between 1984 and 2009 and dataset B (n = 19,554) includes cows born between 2010 and 2020.

Table 5. Genetic diversity lost in the population since the founder generation due to bottlenecks and genetic drift (1-GD), loss of genetic diversity due to unequal contributions of founders (1-GD*), and loss of diversity due to genetic drift (GD*-GD) in datasets A and B

Item	Dataset A[1]	Dataset B[1]
1-GD	0.00233	0.00660
1-GD*	0.00110	0.00210
GD*-GD	0.00130	0.00450

[1] Dataset A (n = 20,827) includes cows born between 1984 and 2009 and dataset B (n = 19,554) includes cows born between 2010 and 2020.

Seven animals (three sires and four dams) were identified as the founders with the highest gene contribution, over 0.01 in dataset B. These individuals were also the principal founders in dataset A, although their contributions were lower. Founders and ancestors with the highest gene contributions to both datasets of cows are shown in Figure 4. The vast majority of founders in both reference populations had very low gene contributions (below 0.001), comprising 14,575 and 20,630 founders in datasets A and B, respectively. Gene contributions between 0.005 and 0.01 were observed for 19 founders (0.13%) in dataset A and 26 founders (0.11%) in dataset B.

In dataset A (cows born between 1984 and 2009), 11 sires were identified as the main ancestors, with the individual gene contribution exceeding 0.01. Of these, five sires were not among the major ancestors in dataset B (cows born from 2010 to 2020). In contrast, dataset B included 15 principal ancestors (13 sires and 2 dams). Six sires were the main ancestors common to both datasets. The vast majority of ancestors in both reference populations had low gene contributions of less than 0.001, totalling 10,966 and 18,813 ancestors in datasets A and B, respectively. Gene contributions

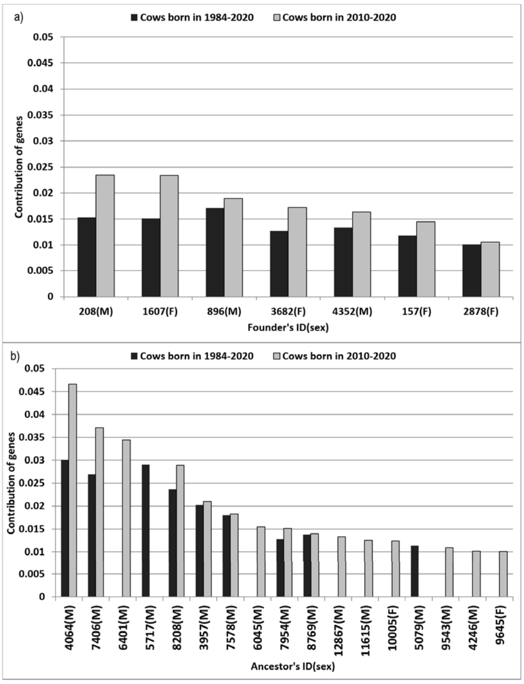

Fig. 4. Founders (a) and ancestors (b) with the highest gene contributions in both reference populations of Simmental cows.

between 0.005 and 0.01 were recorded for 17 ancestors (about 0.15%) in dataset A and 17 ancestors (about 0.09%) in dataset B. Although the ancestor composition of the younger cow population changed significantly and included new sires, but this did not result in a significant increase of the genetic variability.

Genetic parameters estimation

Table 6 presents the estimates of heritability and repeatability for milk, fat and protein yield per lactation, as well as for milk fat and protein content, together with their standard deviations and 95% highest posterior density (HPD) intervals. Heritability estimates were highest for fat content (0.49) and protein content (0.51), suggesting a strong genetic determination of milk composition traits. In contrast, lower heritability traits were obtained for milk yield (0.23), fat yield (0.23), and protein yield (0.21), reflecting a greater influence of environmental factors on production level.

Repeatability estimates followed a similar pattern. The lowest repeatability was observed for fat yield (0.39), whereas the highest estimate was recorded for fat content (0.61). These results suggest that milk composition traits are not only more heritable but also more consistent across successive lactations compared to yield traits, for which a larger proportion of variability arises from environmental influences.

Table 6. Heritabilities and repeatabilities of milk yield and composition traits in Simmental cows

Trait	Heritability				Repeatability			
	solution	SD	95% HPD interval		solution	SD	95% HPD interval	
Milk (kg)	0.232	0.012	0.219	0.244	0.414	0.0062	0.391	0.435
Fat (kg)	0.235	0.012	0.222	0.246	0.394	0.0062	0.369	0.415
Fat (%)	0.494	0.014	0.492	0.497	0.614	0.0047	0.594	0.630
Protein (kg)	0.206	0.012	0.192	0.219	0.402	0.0063	0.378	0.423
Protein (%)	0.505	0.014	0.504	0.508	0.592	0.0049	0.573	0.610

SD – standard deviation.
95% HPD interval – 95% Highest Posterior Density interval.

The standard deviations and 95% highest posterior density (HPD) intervals presented in Table 6 confirm the high precision of the estimates. For heritability, standard deviations were low, i.e. about 0.012 for milk, fat, and protein yields, and approximately 0.014 for fat and protein content. Repeatability estimates exhibited similarly small standard deviations ranging from 0.0047 to 0.0063. The corresponding 95% HPD intervals for both heritability and repeatability were narrow, further demonstrating the robustness and precision of the obtained estimates.

Inbreeding depression for total milk yield measures

Inbreeding depression, expressed as the change in expected phenotype per 1% increase in inbreeding coefficient, is presented in Table 7. In most cases the estimated linear and quadratic regression coefficients were significant ($p<0.01$), indicating a clear detrimental effect of increasing inbreeding. The quadratic regression coefficient for fat content in milk was the only non-significant effect ($p = 0.19$). A 1% increase in the inbreeding coefficient was associated with a reduction of approximately 70 kg in milk yield, 2.6 kg in fat yield, and 2.3 kg in protein yield per lactation. In contrast, the effects of a 1% increase in inbreeding on fat and protein content in milk were negligible.

Table 7. Estimates of the linear and quadratic regression coefficients describing the effect of inbreeding on milk, fat, and protein yield, as well as fat and protein content, together with the expected change in phenotype per 1% increase in inbreeding

Trait	Linear regression				Quadratic regression				1% change	
	coefficient	SD	F	p-value	coefficient	SD	F	p-value	solution	SD
Milk (kg)	-7,325.54	1,084.04	59.04	<0.0001	26,191.87	5,865.58	30.48	<0.0001	-70.448	10.986
Fat (kg)	-269.90	46.16	37.39	<0.0001	953.29	250.89	23.15	<0.0001	-2.597	0.468
Fat (%)	0.53	0.30	7.65	0.0057	-1.94	1.63	1.69	0.1930	0.005	0.003
Protein (kg)	-239.86	38.76	47.41	<0.0001	800.67	209.89	21.58	<0.0001	-2.313	0.393
Protein (%)	0.24	0.15	10.32	0.0013	-1.46	0.81	8.09	0.0044	0.002	0.002

SD – standard deviation
A p-value below 0.05 indicated that the regression coefficient was significant.

Pedigree-based analyses

The generation intervals were about 7 years along the sire progeny path and about 5 years along the dam progeny path (Tab. 1). These values reflect the typical breeding structure observed in dual-purpose Simmental populations, in which bulls are often used across multiple years and cows generally enter reproduction at an earlier age.

Similar or longer generation intervals have been reported in previous studies of Simmental cattle [Rios Utrera *et al.* 2018, Amaya *et al.* 2020] indicating that such values are common in herds where artificial insemination is used in combination with natural service. In contrast, Araujo Neto *et al*. [2020] reported shorter generation intervals along both paternal paths, likely due to more intensive replacement strategies and higher selection pressure on young bulls.

Pedigree quality in datasets A and B of cows, measured as the mean equivalent of complete generations (EqG), was satisfactory indicating reliable pedigree depth and sufficient genealogical information for accurate estimation of genetic parameters. The EqG values obtained in this study were consistent with the results from previous studies [Melka *et al*. 2013, Rios Utrera *et al*. 2018, Araujo Neto *et al*. 2020], supporting the robustness of the genetic evaluation and the consistency of data recording practices.

In recent years, an increasing inbreeding trend has been observed in cattle populations. In the present study, average inbreeding coefficient increased slightly, by 0.3% in dataset A and 0.7% in dataset B of Polish Simmental cows (Tab. 3). At present, this level of increase does not pose a serious concern, however, the observed trend should be monitored. Strapáková and Strapák [2024] reported a similar trend in the Slovak Simmental population, where inbreeding increased by 1.11% from 2003 to 2021. The authors concluded that increased inbreeding adversely affects reproductive and production traits, leading to a reduction of the productive lifespan of cows and negatively influencing farm economics. Similarly, Fuerst-Waltl and Fuerst [2012] reported an average inbreeding level of 5% in the Brown Swiss population, with 98% of animals exhibiting inbreeding coefficients ranging from 0 to 18.75%. High levels of inbreeding were associated with increased calf or heifer mortality, resulting in higher breeding costs and limited selection opportunities.

Slightly over 30% of non-inbred cows were born in the last decade. In contrast, up to 62.3% of cows with inbreeding coefficients (F_x) greater than 0.0625, including three animals with F_x exceeding 0.3125, were born between 2010 and 2020 (dataset B; Tab. 3). A similar F_x distribution was reported by Araujo Neto *et al.* [2020] for Brazilian Simmental cattle, where most animals exhibited inbreeding coefficients below 10%, which is generally considered as favourable.

The maximum gene contribution of founders to Polish Simmental cows was 1.5% in dataset A and 2.3% in dataset B, while the corresponding value for ancestors was 2.7% and 4.7% (Tab. 4). In this study, the same 7 founders (3 sires and 4 dams) made substantial genetic contributions to both reference populations. In dataset A, there were 11 ancestors (sires). In dataset B, 15 animals (13 sires and 2 dams) constituted the principal ancestors with the highest gene contribution. The same 6 sires were common major ancestors in both reference populations.

Comparable maximum gene contribution of major ancestors was reported by Rios Utrera *et al.* [2018] for Mexican Simmental cattle. A slightly higher maximum gene contribution of the leading ancestor (approximately 9%) was reported by Wirth *et al.* [2021] for German Brown cattle.

Parameters that provide information about the genetic diversity of a population are the effective number of founders (f_e), ancestors (f_a), and founder genomes (f_g). Hinrichs and Thaller [2011] reported effective numbers of founders of 111 and 92 for German Holstein cows, which are lower than the corresponding values in the present paper (467 and 234). Similarly, Araujo Neto et al. [2020] reported a lower effective number of founders ($f_e = 163$) than those observed in both reference populations in this study, while the effective number of ancestors (132) they presented exceeded the f_a for cows born between 2010 and 2020 ($f_a = 110$). Stachowicz *et al.* [2011] reported effective number of founders of 323 for Canadian Holsteins and 75 for Jerseys in Canada with corresponding effective numbers of ancestors at 16 and 18.6, respectively. The f_e, f_a, and f_g values estimated for Polish Simmental cows were comparable to or higher than those reported in the cited studies, indicating a good level of genetic diversity in the studied population.

The parameters f_a, f_e and f_g are highly sensitive to the population subset used for estimation. Consequently, the ratios f_a/f_e, f_e/f and f_g/f_e are more informative for evaluating population structure. For cows from dataset B, founder contributions were less evenly distributed (f_e/f of 0.01 for young cows and 0.02 for older cows). In contrast, genetic losses attributable to the bottleneck effect were almost the same in datasets A and B (f_a/f_e: 0.470 and 0.465, respectively). Losses due to random genetic drift in dataset B were slightly lower (f_g/f_e: 0.314 and 0.460, respectively).

The effective number of founder genomes (f_g) in dataset B (75.3) of young cows was almost threefold lower than that observed in dataset A (214.6), evidencing substantial changes in the founder composition of these two reference populations. Stachowicz *et al.* [2011] reported markedly lower f_g for Holstein (7.7) and for Jerseys (8.4) cattle populations. Similarly, the f_g results reported by Amaya *et al.* [2020] in the Simmental population (from 30 to 32, depending on year of birth), were much lower than those for Polish Simmental cows. In contrast, Rios Utrera et al. [2018] reported f_g comparable or higher than those observed in the present study, ranging from 107.8 to 179.3 in the Mexican Simmental cattle, depending on the reference population.

The genetic diversity lost since the founders' generation due to the bottleneck effect and genetic drift (1-GD) was 0.00233 in dataset A and 0.0066 in dataset B. Loss of genetic diversity attributable to unequal contributions of founders (1-GD*) was 0.0011 and 0.0021 in datasets A and B, respectively. Losses due to genetic drift (GD*-GD) were estimated at 0.0013 for dataset A and 0.0045 for dataset B. Higher losses due to genetic drift than the one reported in this study were observed by Stachowicz et al. [2011], who concluded that the main driver of genetic diversity loss in Canadian Holsteins and Jerseys was genetic drift accumulated over non-founder generations.

Almost all parameters analysed in this study indicate a decline in genetic variability among young Simmental cows. This pattern may be attributable to the importation of the sires without sufficiently accounting for their genetic relatedness to the animals already present in the Polish Simmental cattle population. Consequently, breeders should be encouraged to check the pedigrees of imported sires more carefully.

Genetic parameters estimation

The heritability of lactational milk yield obtained in this paper is similar to the estimates in Scheper *et al.* [2021] and Wei *et al.* [2021] (0.23). Scheper *et al.* [2021] reported highest heritabilities for fat (0.27) and protein yield (0.41), whereas Wei *et al.* [2021] obtained lower heritability estimates for both fat (0.13) and protein yield (0.10). Higher heritability for milk yield (0.49), and much higher for fat yield (0.46) were reported by Pantelić *et al.* [2011].

Importantly, most of the mentioned authors used a random regression test-day model for genetic parameter estimations and analysed test-day milk yield rather than 305-day or whole-lactation milk yield. Furthermore, their methodology for estimating genetic parameters differs from the methodology in this study limiting direct comparability.

Inbreeding depression for total milk yield measures

In the Holstein population, Smith *et al.* [1998] reported lower heritability estimated at 0.13 for milk, fat and protein yields, with higher values of inbreeding depression per 1% increase of inbreeding (-177.17 kg for milk yield, -6.01 kg for fat yield, and -5.45 kg for protein yield). In Holstein cows with a high inbreeding level, Thompson et al. [2000] observed a slightly positive effect of low inbreeding level on daily milk production; however, they reported that a high inbreeding levels resulted in substantial decreases in milk (-707.78 kg), fat (-23.33 kg) and protein (-19.93 kg) yield. Their estimates of inbreeding depression were higher than for the Simmental cows in this study.

Rokouei *et al*. [2010] reported that inbreeding depression in lactational milk yield ranged from -27.4 kg in the third lactation to -16.2 kg in the second lactation. They also calculated the inbreeding depression for fat yield to range from -0.69 kg (third lactation) to -0.37 kg (second lactation) and for protein yield from -0.67 kg (third lactation) to -0.43 kg (second lactation). For lactational milk yield these values were higher than those estimated for Simmental cows, whereas for other yield traits they were similar or lower. Overall, these findings indicate that, despite relatively low inbreeding values for Polish Simmental cows, inbreeding depression exerts a slight effect on dairy traits.

Conclusions

The genetic variability of Polish Simmental cows is at a satisfactory level overall. However, an increasing proportion of inbred individuals was observed in the youngest cows born between 2010 and 2020, including animals with inbreeding coefficients exceeding 30%.

Analysis of founder and, in particular, ancestral gene contributions indicate marked changes in the composition of ancestors in young cows. These changes may be partly attributable to the recent importation of these ancestors whose genetic relatedness to the existing Polish Simmental population was not sufficiently accounted for. Such practices likely contributed to the increase in inbreeding in the period from 2010 to 2020.

The cows included in the analysis were characterised by predominantly low to moderate levels of inbreeding, with only a relatively small proportion of individuals exhibiting inbreeding coefficients above 6%. This distribution indicates that inbreeding in the studied population has not yet reached critically high levels. Nevertheless, even within this moderate range, accumulated level of inbreeding was sufficient to produce a detectable, generally small inbreeding depression in the analysed dairy traits. These findings highlight the importance of implementing breeding strategies that limit further accumulation of inbreeding in th population.

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Conflict of interest

The authors declare that they have no conflicts of interest.

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