

Influence of mating systems and selection intensity on the extent of inbreeding and genetic gain in the Slovak Pinzgau cattle

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ABSTRACT: The aim of the present paper was to simulate the scenarios for a maximum avoidance of inbreeding (MAI) mating strategy, and compare it with a random mating alternative, with the main focus on inbreeding and development of the genetic gain. The parameters of the simulation were based on the structure of the Slovak Pinzgau active population of 2868 animals (930 purebred cows). The selection under a total merit index (TMI) was simulated, covering the milk, survival, and live weight breeding value estimation results. The heritability of TMI ($h^2 = 0.09$) was estimated using a REML single trait animal model. Alternatives assumed a closed population structure, fixed number of mating per parent, and equal use of sires in insemination. Animals in generation 0 were set as founders without pedigree information. In separate simulation runs, the number of sires of sires was set at 2, 4, 5 or 10 mated with 40 dams of sires in all cases. The sex ratio of the offspring was assumed to be 50/50 male/female. Twenty consecutive generations were simulated for both random and maximum avoidance of inbreeding mating, which resulted in a total of 8 scenarios. Significant positive differences in genetic gain were observed in the MAI mating system with 2 (0.74**), 4 (0.24**), 5 (0.13**) or 10 (0.09**) sires in comparison to random mating design. When using MAI, significantly lower inbreeding was observed with 2 (5.44**), 4 (3.18**), 5 (2.43**) or 10 (1.16**) sires. Simulation results showed that the use of a maximum avoidance of inbreeding mating strategy would lead to significantly decreased rates of inbreeding while maintaining suitable levels of genetic gain in the Slovak Pinzgau population.

Keywords: Pinzgau breed; mating strategy; breeding program optimization

INTRODUCTION

Pinzgau cattle are traditionally bred in mountainous and sub-mountainous regions of Slovakia. Due to significant changes in the agricultural sector, the breed has become endangered. Whereas the total population of cows in Slovakia decreased by 25% in the last decade, the number of recorded Pinzgau cows under milk went down by 75% during the same period. The share of Pinzgau cows under milk recorded a decrease from 12 to 4%; the proportion

of purebred cows diminished from 3 to less than 1%, when looking at the total number of cows in Slovakia between 1997 and 2008 (Kasarda et al., 2008b). Despite its population size, the breed is still used commercially, but its breeding strategy needs to be changed in order to preserve internal breed diversity. For this reason the preferred mating strategy is the one that would keep inbreeding levels low, allowing genetic gain to accumulate over time.

According to Wright (1922), equal numbers of progeny per parent, avoidance of mating relatives,

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and mating of less related animals can decrease inbreeding in a population. Even if some programs lead to high genetic gain, they accumulate inbreeding as a result of a small group of frequently used individuals or sire families. Inbreeding is steadily increasing in most breeds, with possible economic losses, including depressions in growth, milk production, health traits, fertility, and longevity. An estimation of inbreeding tendencies in the breeding program designed for Slovak Pinzgau cattle was carried out by Kasarda and Kadlečík (2004), where a strategy of increasing the number of sires was proposed in order to decrease inbreeding below 1% per year. Kadlečík et al. (2004) proposed a change in the breeding goal, expanding the single recording of milk production to include recordings of multiple desirable traits which together serve as a basis for the total merit index proposed by Kasarda et al. (2008a). This index includes estimated breeding values (EBV) for milk production in kg (BS SR, 2009), for live weight at 210 days of age (Kasarda et al., 2009), and for functional length of production life (Mészáros et al., 2008). The economic importance of these traits was based on studies by Krupová et al. (2009).

Meuwissen and Sonesson (1998), and Williams et al. (1999) predicted long term genetic contributions and asymptotic genetic gains by including Bulmer equilibrium genetic parameters (Bulmer, 1971), a method suitable for mass, index, and BLUP selection. Ducrocq and Quaas (1988) presented a method for calculation of asymptotic genetic gain using the example of a dairy cattle breeding program utilizing a truncation selection scheme, based on theoretical outlines of the effects of overlapping generations on genetic gain (Bichard et al., 1973). Based on the theory of long-term contribution, it is possible to model multigeneration evolution in pedigrees (Sánchez et al., 2003). This assumption was confirmed by stochastic simulation. The optimization of contributions can be implemented using Lagrangian multipliers (Meuwissen and Luo, 1992; Wray and Goddard, 1994; Brisbane and Gibson, 1995; Colleau et al., 2004). This approach has been shown to offer substantial improvements in genetic gain. Kremer et al. (2006) developed software for stochastic simulation of animal selection and different mating strategies. It allows the optimization of conservation breeding schemes, applying truncation selection with avoidance of related individuals, and optimal selection based

on various means of constraining inbreeding (e.g., Wray and Goddard 1994; Meuwissen, 1997).

In selected populations, two basic forms of non-random mating are present. The first case is the mating of individuals with a common ancestor, which leads to an increased frequency of homozygous loci. This can be dangerous in a small population, due to loss of genetic variability and increased inbreeding. In the second case, individuals are mated according to their genotypes. Fernández et al. (2003) presented an alternative approach to control inbreeding in small populations, based on minimizing global co-ancestry. As presented by Meuwissen and Sonesson (1998), the main goal in breeding programs in small populations is maximizing genetic gain by constraining inbreeding. To maximize the genetic (breeding) value of selected animals in populations with overlapping generations, it is crucial to constrain the average relationship of the mated animals to avoid large increase of inbreeding, but not to maximize genetic gain in the current selection round, because inbreeding of future generations increases half of its average relatedness. Cyclic mating strategies to constrain increases in inbreeding have been described by Wright (1922), Cockerham (1970), and Windig and Engelsma (2008). Sørensen et al. (2005) analyzed factorial and hierarchical mating using long-term genetic contributions. Compensatory mating has been studied by Caballero et al. (1996) and Nomura (1999). Honda et al. (2004) analyzed a mating system based on a hierarchical structure of population with reduction of inbreeding. The crucial requirement is a higher number of sire lines compared to the number of sires in each line. Fluctuations in inbreeding levels within sire lines can be minimized by constraining the repeated usage of highly inbred lines. Wellmann et al. (2012) studied influence of historic migration on maximizing the gene diversity under optimum contribution selection, constraining breeding value of the offspring or inbreeding (Meuwissen, 1997).

The aim of the present work was to simulate a scenario of maximum avoidance of inbreeding (MAI) mating strategy and compare it with a random mating alternative, based on development of inbreeding and genetic gain.

MATERIAL AND METHODS

The parameters of the simulated database were based on the population structure of Pinzgau cattle in Slovakia, with an active population of 2868 animals (930 purebred cows). Basic parameters of the

Table 1. Statistical characteristics of parameters of total merit index (TMI)

EBV	\bar{x}	SD	X_{\min}	X_{\max}
Milk production	16.68	164.28	-740.90	1025.20
Length of productive life	0.04	0.14	-0.35	0.52
Live weight at 210 days	-0.16	8.61	-37.59	149.12
TMI	1.72	1.19	-24.45	45.71

EBV = estimated breeding value

EBV are given in Table 1. In reality, Pinzgau cattle are selected based on BLUP EBV for milk yield, without any specific mating strategy. Given that the Pinzgau was a dual purpose breed, animal selection based on a total merit index (TMI) would be beneficial, as envisaged by Kasarda et al. (2007). For this reason, our simulation was also based on a TMI scenario, so that practical selection can follow the new setup in the near future. For setting up the TMI, EBV for a 305-day milk production (BS SR, 2009), functional length of productive life (Mészáros et al., 2008) and live weight at 210 days of age (Kasarda et al., 2009) were used. As stated by Lin and Allaire (1977), the selection index is inherited. The heritability of the TMI was estimated by Kasarda (2010, unpublished) using a REML single trait animal model (Table 1). Increases in inbreeding and genetic gain were then studied over 20 consecutive generations applying maximum avoidance of inbreeding (MAI) method. Random mating design was used as the comparison method.

We conducted a stochastic simulation using the SixS software, Version 2 (Kremer et al., 2006). Both alternatives assumed a closed population structure, fixed number of mating per parent, and equal use of sires in insemination. Animals in generation 0 were set as founders without pedigree information.

In separate simulation runs, the number of sires of sires was set at 2, 4, 5 or 10 mated with 40 dams of sires in all cases. Number of mated animals represented individuals after the final step of the selection. The sex ratio of the offspring was assumed to be 50/50 male/female. Twenty consecutive generations were simulated for both random and maximum avoidance of inbreeding mating, which resulted in a total of 8 scenarios. Basic outlines of breeding scheme are present in Table 2.

Mating strategies used were as follows: alternative 1 – random mating – without control of

Table 2. Basic outlines of breeding program parameters

Parameter	
Active population	4000
Selection basis of bull mothers	500
No. of selected bull mothers	40
Intensity of selection of bull mothers (%)	8
Correction on length of calving period	0.8528
No. of progeny born	34
No. of bull calves born	17
Selection on growth (%)	60
Selection on AI station (%)	10
Test mating division (%)	70
Insemination index	2.2
No. of daughters per bull in test	120
No. of selected proven bulls	5
No. of sires of sires	2, 3, 4, 5
Intensity of selection of sires of sires (%)	12, 18, 24, 29
Pregnancy rate (%)	65
No. of daughters with lactation (%)	80
No. of daughters per proven sire	154, 103, 76, 61

AI = artificial insemination

inbreeding (Random) with selection based on BLUP EBV, alternative 2 – maximum avoidance of inbreeding (MAI) with selection based on BLUP EBV.

A truncation selection principle (Bichard et al., 1973; Ducrocq and Quaas, 1988) with avoidance of mating relatives (Wray and Goddard, 1994; Meuwissen, 1997) was used. The principle was to limit inbreeding by reducing increases in average relationships. If the relationship of an animal with itself is included, the average relationship is:

$$\bar{A} = I' \mathbf{A} I / n^2$$

where:

\mathbf{A} = matrix of additive genetic relationships

n = number of animals

I = vector of ones

In discrete generations, genetic gain can be maximized when constrained by the rate of inbreeding by obtaining a vector of mating proportions (c_t) for the current n candidates at time t to produce new progeny at time $t + 1$. The solution is obtained by maximizing the function:

$$I_t = c_t' g_t - \lambda_0 (c_t' \mathbf{A}_t c_t - C_t) - [c_t' \mathbf{Q} - (\frac{1}{2})'] \lambda$$

where:

g_t = vector of EBV of the selection candidates at time t

A_t = ($n \times n$) relationship matrix among n selection candidates

Q = known incidence matrix $n \times 2$ (with 1 = males, 0 = females in the first column and vice versa in the second column)

C_t = constraint on the rate of inbreeding

λ_0, λ = vectors of order 2 (Lagrangian multipliers)

However, when generations overlap, the flow of genes through a single cohort (sex and age class) is insufficient to describe all gene flow from an ancestor. Consequently, optimizing long-term contributions by looking at a single cohort in isolation will be insufficient to maximize gain and control the rate of inbreeding. The gene flow from an entire generation needs to be considered, using principles of the gene flow methodology by Hill (1974) applied to a population with overlapping generations. At any time (t), there are animals of different ages in a population with overlapping generations. The animals will be divided into age classes, and an age class is defined as the time period between two consecutive rounds of selection (usually 1 year). Where $m_t = [m_t(1) m_t(2) m_t(3) \dots]$

is a vector of average true breeding values of the age classes, 1, 2, 3, ..., in year t , $m_t(i)$ = average breeding value of age class i in year t . The following recursive relationship exists between m_t and m_{t+1} (Hill, 1974):

$$m_{t+1} = Pm_t + e_{t+1}$$

where:

P = matrix of gene flow between the age classes (see Hill, 1974 for details)

e_{t+1} = sampling deviation from the expected breeding values

The contributions of an entire generation at the time of selection need to be described. The numbers of previous cohorts are derived from maximum breeding age and then consequently. Weighting factors were applied to each cohort for the contributions of each individual summing to one. With this approach, the gene flow of an entire generation can be computed in a way analogous to $c'_t A_t c_t$ from the discrete case. One can derive weighting factors from the current age structure of the parents' weights for each cohort (Meuwissen and Sonesson, 1998; Sonesson and Meuwissen, 2000).

Table 3. Estimation of genetic gain (g) in total merit index after random mating with selection based on estimated breeding values

Generation	No. of sires							
	2		4		5		10	
	Δg	SD	Δg	SD	Δg	SD	Δg	SD
1	0.13	0.14	0.06	0.18	0.06	0.31	0.06	0.18
2	0.47	0.25	0.39	0.23	0.31	0.18	0.23	0.23
3	1.04	0.35	0.49	0.23	0.4	0.14	0.32	0.23
4	1.70	0.42	0.91	0.24	0.87	0.16	0.72	0.24
5	1.77	0.40	0.95	0.25	0.89	0.16	0.88	0.25
6	2.42	0.39	1.14	0.24	1.12	0.19	1.04	0.24
7	2.76	0.40	1.43	0.24	1.37	0.25	1.32	0.24
8	3.16	0.40	1.85	0.23	1.77	0.24	1.62	0.23
9	3.33	0.39	2.02	0.22	1.85	0.24	1.94	0.22
10	3.41	0.38	2.48	0.21	2.26	0.23	2.01	0.21
15	3.65	0.28	3.33	0.19	3.16	0.21	2.92	0.19
20	4.42	0.20	4.23	0.19	3.90	0.20	3.82	0.19
Average 1–20	3.04	0.31	2.47	0.21	2.28	0.21	2.13	0.21
Average 6–20	3.67	0.31	3.07	0.20	2.83	0.22	2.66	0.20
Average 10–20	3.93	0.28	3.56	0.19	3.26	0.21	3.05	0.19

RESULTS AND DISCUSSION

Intrapopulation diversity is an important part of the global diversity of farm animals. To prevent deterioration of genetic diversity, minimizing inbreeding in small populations is of prime importance (Grundy et al., 1998). The classical approach was to even out the numbers of sires and dams in the mating program. In contrast to the proposed approach, a low number of breeding animals and a high mating ratio are used in most commercial populations. There are also problems with keeping large numbers of mature breeding sires. Increased inbreeding also has an economic impact, as demonstrated by Kasarda and Kadlečík (2007). Inbreeding depressions of -8.95 kg for milk production, -0.37 kg for fat, and -0.36 kg for protein per 1% increase of inbreeding were found in the Pinzgau population in Slovakia.

The development of a pedigree structure was simulated in a population according to the two alternatives, i.e. without consideration for or maximum avoidance of inbreeding. The changes in inbreeding and genetic gain were then estimated based on a relationship matrix. A number of authors (Bulmer, 1971; Silvela and Diez-Barra, 1985;

Sánchez et al., 2003; Falconer and Mackay, 2004) have evaluated inbreeding in mating strategies considering selection based on BLUP EBV, while panmictic/random mating with phenotypic selection served as a basic scenario for comparison. As stated by Wellmann et al. (2012), optimum contribution strategy by maximizing gene diversity could eventually lead to the extinction of local breeds with historical migration because increased gene diversity would be achieved by maximizing migrant contributions. As there was a historical migration in Pinzgau cattle in Slovakia, simulation was conducted based on purebred population data and closed population structure. We simulated a population with random mating with selection based on BLUP EBV, in order to follow the current selection strategy in Slovakia. This was compared to the maximum avoidance of inbreeding scenario, to show the effect of inbreeding avoidance on the population development.

Random mating in a population selected based on BLUP EBV led to higher values of genetic gain after 20 generations (Tables 3 and 4) compared to MAI.

Significant differences were observed in designs with 2 (0.74**), 4 (0.24**), 5 (0.13**) or 10 (0.09**) sires.

Table 4. Estimation of genetic gain (g) in total merit index after maximum avoidance of inbreeding with selection based on estimated breeding values

Generation	No. of sires							
	2		4		5		10	
	Δg	SD	Δg	SD	Δg	SD	Δg	SD
1	0.06	0.14	0.06	0.16	0.07	0.17	0.06	0.18
2	0.31	0.14	0.3	0.17	0.26	0.17	0.23	0.14
3	0.48	0.15	0.47	0.17	0.41	0.18	0.25	0.12
4	0.64	0.16	0.81	0.2	0.8	0.19	0.46	0.14
5	0.95	0.17	0.89	0.22	0.84	0.19	0.88	0.16
6	1.36	0.16	1.13	0.21	1.04	0.21	1.13	0.17
7	1.53	0.19	1.4	0.20	1.37	0.22	1.20	0.18
8	1.77	0.21	1.73	0.19	1.70	0.21	1.45	0.18
9	2.10	0.22	2.08	0.19	1.94	0.22	1.70	0.18
10	2.19	0.23	2.18	0.18	2.10	0.22	1.94	0.21
15	3.01	0.22	2.95	0.18	2.93	0.2	2.91	0.21
20	4.38	0.23	4.10	0.21	4.06	0.2	3.73	0.20
Average 1–20	2.31	0.21	2.23	0.19	2.14	0.2	2.04	0.19
Average 6–20	2.87	0.22	2.77	0.19	2.66	0.21	2.56	0.02
Average 10–20	3.27	0.23	3.16	0.19	3.04	0.2	2.96	0.21

Table 5. Estimation of increase in inbreeding (% per year) after random mating (Random) and maximum avoidance of inbreeding (MAI) with selection based on estimated breeding values

Generation	No. of sires								
	2		4		5		10		
	Random	MAI	Random	MAI	Random	MAI	Random	MAI	
1	0	0	0	0	0	0	0	0	0
2	3.44	3.82	1.66	0	2.01	0	0.17	0	
3	4.18	3.95	2.39	1.79	2.10	1.02	0.76	0.05	
4	5.00	3.55	3.71	2.05	2.80	1.78	1.15	0.24	
5	5.40	4.67	3.60	2.60	3.05	2.11	1.37	0.59	
6	5.97	4.89	3.63	2.92	3.08	2.23	1.43	0.81	
7	6.52	5.14	3.60	3.14	3.07	2.44	1.51	1.02	
8	6.93	5.52	3.52	3.34	3.04	2.59	1.58	1.12	
9	6.60	5.82	3.48	3.65	3.07	2.75	1.54	1.22	
10	6.99	5.97	3.60	3.74	3.30	2.87	1.55	1.29	
15	7.20	6.42	4.14	3.89	3.83	3.03	1.78	1.64	
20	7.26	6.72	5.05	4.13	4.12	3.12	2.05	1.73	
Average 1–20	6.20	5.44	3.50	3.18	3.25	2.43	1.50	1.16	
Average 6–20	7.01	6.14	3.88	3.78	3.65	2.89	1.75	1.46	
Average 10–20	7.18	6.40	3.98	3.95	3.84	3.02	1.83	1.60	

sires in comparison to MAI. Differences in genetic gain between the alternatives tended to decrease with the increasing number of sires, as a result of using MAI as the mating strategy. Decrease of genetic gain within particular design with an increased number of sires was a result of decreased intensity of selection. Variance of the genetic gain between separate simulation runs was 7–10%, both under random or MAI mating strategy. Trend of

genetic gains after random mating with the use of 2, 4, 5, and 10 sires was non-linear over generations with the tendency of culmination to asymptotic values (Figure 1), confirming the results of Bulmer (1971) and Woolliams et al. (1999). In contrary to Bulmer (1971), asymptotic values were not reached between 6–10 generations. Trends of genetic gain after MAI with the use of 2, 4, 5, and 10 sires were almost linear over generations.

A mating strategy with MAI (Wray and Goddard, 1994; Meuwissen, 1997) led to a decrease in inbreeding after 20 generations (Table 5). Due to building up a pedigree structure at the beginning of the simulation, tendencies in the development of inbreeding were non-linear, with tendency to culminate to asymptotic values. Significantly lower inbreeding was observed when the MAI strategy was used, either with 2 (5.44**), 4 (3.18**), 5 (2.43**) or 10 (1.16**) sires, confirming the results of Meuwissen and Sonesson (1998) and Sonesson and Meuwissen (2000). With a higher number of selected sires, the intensity of selection decreases, which consequently has an influence on inbreeding after 20 generations. To use maximum avoidance of inbreeding is more effective because it leads to significantly smaller increases in inbreeding. This

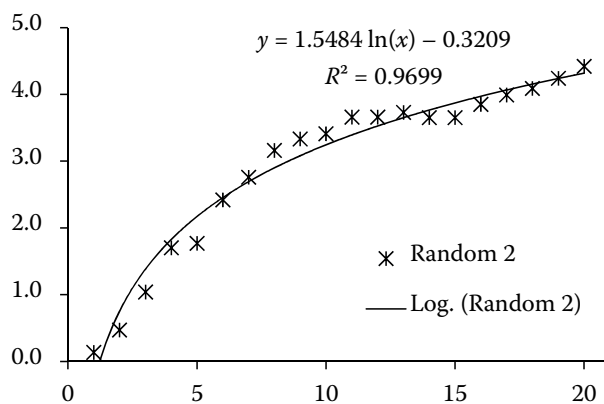


Figure 1. Trend of genetic gain of total merit index after random mating of two sires with selection based on estimated breeding values

attribute of MAI is very important in small/ endangered populations such as Slovak Pinzgau cattle.

Strategies similar to our case, selection based on BLUP EBV, were applied by Caballero et al. (1996), Meuwissen and Sonesson (1998), Fernández et al. (2003), and Windig and Engelsma (2008). They have shown that in a breeding program it is possible to decrease inbreeding in comparison with random mating by applying a specific mating strategy. Phenotypic selection leads to significantly less inbreeding, as proposed by Falconer and Mackay (2004). An average increase in inbreeding of 5.66% per generation was estimated by Kasarda and Kadlečík (2010) using phenotypic selection and random mating when only 2 sires were used. By increasing the number of sires to 5, inbreeding decreased to 2.99% per generation. Similar results were obtained by other authors when comparing random mating with MAI (Silvela and Diez-Barra, 1985; Sánchez et al., 2003), with assortative mating (Caballero et al., 1996; Nomura, 1999; Honda et al., 2004; Sørensen et al., 2005), or with factorial mating, with respect to avoiding mating animals with a common ancestor (Sánchez et al., 2003; Sørensen et al., 2005).

CONCLUSION

The Slovak Pinzgau is a dual purpose endangered cattle breed in which selection is currently based on BLUP EBV. The genetic gain increases along with the inbreeding coefficient, which may cause problems due to its small population size. Minimizing inbreeding is very important in order to safeguard genetic diversity in the Pinzgau population. Maximum avoidance of inbreeding is an effective strategy using BLUP selection, resulting in similar genetic gains in comparison to random mating, as long as the number of sires used is large enough. In comparison to random mating, maximum avoidance of inbreeding leads to significantly lower increase in inbreeding per generation. Simulations based on the current Slovak Pinzgau population show that the use of a maximum avoidance of inbreeding mating strategy would lead to favourable results. With 10, 5, and 4 selected sires, the predicted inbreeding after 20 generations was lower (1.16, 2.43, and 3.18% per generation) compared to the random mating scenario (1.50, 3.25, 3.5%). This meets the recommendations of the FAO global strategy (< 4% per generation).

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