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Inbreeding depression and its effect on sperm quality traits in Pietrain pigs

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Abstract

In most cases, inbreeding is expected to have unfavourable effects on traits in livestock. The consequences of inbreeding depression could be substantial, primarily in reproductive and sperm quality traits, and thus lead to decreased fertility. Therefore, the objectives of this study were (i) to compute inbreeding coefficients using pedigree (F_{PED}) and genomic data based on runs of homozygosity (ROH) in the genome (F_{ROH}) of Austrian Pietrain pigs, and (ii) to assess inbreeding depression on four sperm quality traits. In total, 74,734 ejaculate records from 1034 Pietrain boars were used for inbreeding depression analyses. Traits were regressed on inbreeding coefficients using repeatability animal models. Pedigree-based inbreeding coefficients were lower than ROH-based inbreeding values. The correlations between pedigree and ROH-based inbreeding coefficients ranged from 0.186 to 0.357. Pedigree-based inbreeding affected only sperm motility while ROH-based inbreeding affected semen volume, number of spermatozoa, and motility. For example, a 1% increase in pedigree inbreeding considering 10 ancestor generations (F_{PED10}) was significantly ($p < 0.05$) associated with a 0.231% decrease in sperm motility. Almost all estimated effects of inbreeding on the traits studied were unfavourable. It is advisable to properly manage the level of inbreeding to avoid high inbreeding depression in the future. Further, analysis of effects of inbreeding depression for other traits, including growth and litter size for the Austrian Pietrain population is strongly advised.

KEYWORDS

correlations, inbreeding, inbreeding depression, pedigree, Pietrain pigs, runs of homozygosity, sperm quality traits

1 | INTRODUCTION

Inbreeding is the probability that two alleles within an individual are identical by descent (IBD) as they are inherited from the same common ancestors (Cassell, 2009; Wakchaure & Ganguly, 2015). Inbreeding increases the overall homozygosity in an individual (Cassell, 2009; Silió et al., 2013). The inbreeding coefficient (F_{PED}) has traditionally been calculated from pedigree records based on the path coefficient method. However, pedigree information is often unreliable due to incomplete pedigree (Keller et al., 2011) and error in recording of ancestry (Martikainen et al., 2018).

Fortunately, advanced genomic tools allow genotyping of animals, and with the wide availability of dense single nucleotide polymorphism (SNP) data, inbreeding can also be calculated alternatively, based on runs of homozygosity (ROH). ROH are long stretches of homozygous genotypes (Szmatoła et al., 2020; Zhang et al., 2015), and are believed to have formed mainly due to mating between relatives (Mastrangelo et al., 2016; Szmatoła et al., 2019).

ROH along the genome can be used to measure individual homozygosity and to identify genes that are associated with traits of interest (Xu et al., 2019). Length of ROH can be related to the distance within the pedigree for their common ancestors (Bjelland et al., 2013). While longer ROH arise from recent inbreeding, short ROH are derived from ancient inbreeding in a population (Curik et al., 2014; Howrigan et al., 2011) as recombination interrupts long chromosome segments over time (Bjelland et al., 2013; Doekes et al., 2019). ROH, therefore, has become a common tool to estimate and characterize inbreeding (Mastrangelo et al., 2016; Szmatoła et al., 2019).

The inbreeding calculated based on ROH (F_{ROH}) makes it possible to differentiate specific IBD regions from homozygosity based on identity by state (IBS) (Silió et al., 2013; Zhang et al., 2015), although dependent on methodology used. In addition, F_{ROH} calculation does not depend on pedigree completeness and quality (Oliehoek & Bijma, 2009) and incorporates autozygosity arising from distant common ancestors (Keller et al., 2011).

Inbreeding may have a detrimental effect on certain traits, and this phenomenon is called inbreeding depression (Doekes et al., 2019). Inbreeding has been found to reduce the immune system function and thereby increases the susceptibility to infectious diseases (Acevedo-Whitehouse et al., 2003) and reduces the tolerance to extreme environmental conditions (Dahlgaard et al., 1995; Shikano et al., 2001). The increased homozygosity due to inbreeding can lead to an increased frequency of unfavourable genotypes (Howard et al., 2017). Moreover, inbreeding is believed to have detrimental effects on reproduction as it reduces the fertility of an inbred individual (Keller et al., 2011). It reduces fertility by lowering the reproductive efficiency due to a delay in sexual maturity (Fitzpatrick & Evans, 2009) and impairing certain parameters of sperm production and quality.

Increased levels of inbreeding were found to affect several parameters of sperm production and quality in Shetland pony stallions (van Eldik et al., 2006), Friesian stallions (Boer, 2007), and Fleckvieh bulls (Ferenčaković et al., 2017; Maximini et al., 2011). A study on inbreeding depression analyses by Hinkson and Poo (2020) revealed compromised sperm quality in terms of motility, concentration, and viability in dusky gopher frogs. As spermatogenesis relies on highly regulated developmental genes, the appearance of deleterious alleles (increased homozygosity) may directly affect sperm quality (Ferenčaković et al., 2017). Sperm quality is one of the most important traits that defines the reproductive potential of male breeding animals (Dorado et al., 2015). Therefore, lowered sperm performance can have substantial negative consequences on the population due to decreased male fertilization success leading to lowered fertility in the female mates (Losdat et al., 2018).

Reduction of reproductive, fitness, and survival performance of an inbred individual would ultimately result in lowered profitability of livestock farming by decreasing the lifetime productivity, and also by increasing the management costs like insemination and veterinary costs (Martikainen et al., 2018). Inbreeding depression on reproductive traits, such as litter size was found in Austrian Landrace and Large White pigs by Köck et al. (2009). However, the effects of inbreeding on sperm quality and quantity traits in Austrian Pietrain boars have not been investigated yet. Accordingly, this study aims at providing insights on inbreeding and its association with four sperm quality traits of Austrian Pietrain boars maintained by the Austrian breeding organization, PIG Austria GmbH (PIG AT). The objectives of this study were (i) to compute pedigree-based and ROH-based inbreeding coefficients, and (ii) to assess inbreeding depression on four sperm quality traits of Austrian Pietrain boars.

2 | MATERIALS AND METHODS

Pedigree, genotype, and phenotype data were provided by PIG AT in collaboration with the University of Natural Resources and Life Sciences, Vienna, Austria.

2.1 | Pedigree data

The pedigree records comprised 87,525 Pietrain pigs born between 1971 and 2020. Pedigree-based inbreeding coefficients were calculated for the entire pedigree (F_{PED}), for 10 generations (F_{PED10}), and for 7 generations (F_{PED7}) using the program RelaX2 v1.65 as described by Strand (2014). The F_{PED10} and F_{PED7} were estimated to investigate the effect of (recent) pedigree inbreeding up to 10 and 7 generations, respectively. For computation of F_{PED}, all animals born between 2010 and 2020 were defined as the reference population whereas for F_{PED10} and F_{PED7} calculation, all animals born between 2016 and 2020 were used as reference population. In addition, to assess pedigree completeness, equivalent complete generations (ECG) and the proportion of animals with the number of complete generations known (NCG) were determined using Retriever v1.0, an inbreeding monitor software, as described by Windig et al. (2019). ECG was computed as the sum of

$(1/2)^n$ of all known ancestors of an individual, where n is the number of generations separating the individual from each known ancestor (Doekes et al., 2019; Windig, 2021).

2.2 | Genomic data

From a total of 2489 Austrian Pietrain pigs genotyped by PIG AT, 1770 pigs were genotyped with Illumina PorcineSNP60 BreadChip v2 (Illumina Inc., San Diego, CA, USA), and another 719 pigs were genotyped with Illumina PorcineSNP80 BreadChip v2 (Illumina Inc., San Diego, CA, USA). The two files were merged using the program PLINK v1.9 (Chang et al., 2015), a tool for handling SNP data. To prevent the unnecessary loss of animals due to SNP missingness, only the overlapping autosomal SNPs between the two chips were considered for further analyses. Due to the presence of mismatches of chromosome and base pair positions between the two data sets (60k and 80k files), the chromosome and SNP positions in the 60k map file were updated based on the 80k map file.

Only autosomal SNPs assigned to a chromosome were kept, sex chromosomes, and unplaced SNPs were excluded. In addition, individuals and SNPs with more than 10% missing genotypes were removed from further analysis. Hardy–Weinberg Equilibrium (HWE) was set to 0.0000001. As recommended by Meyermans et al. (2020), minor allele frequency (MAF) and linkage disequilibrium (LD) pruning were skipped because this may result in missed ROH and affect the proper detection of homozygosity. Finally, 48,096 variants and 2480 samples (1817 males and 672 females) passed the quality control.

2.2.1 | Identification of runs of homozygosity (ROH)

The software PLINK v1.9 (Chang et al., 2015) was used to detect ROH. A default window size of 50 SNPs was used. The criteria used by Ferenčaković et al. (2012) were set to define a ROH: a minimum number of SNPs required to declare a segment as ROH was set to 15, and a maximum physical gap between consecutive homozygous SNPs was set to 1 Mb. Five different ROH lengths were defined with minimum lengths of 1, 2, 4, 8, and 16 Mb. By setting a minimum threshold for ROH lengths, distance to the base population where all ancestors are assumed unrelated might be determined (Doekes et al., 2019; Howrigan et al., 2011) and can help exclude common ROHs that may not be due to inbreeding (Ceballos et al., 2018). Additionally, different numbers of missing SNPs and heterozygous SNPs were allowed depending on the cut-off length of ROH. For ROH lengths of 1 Mb and 2 Mb, no missing SNPs were allowed. However, a maximum of 1 missing SNP for 4 Mb, 2 missing SNPs for 8 Mb, and 4 missing SNPs for 16 Mb were allowed. Likewise, a maximum of 1 heterozygous SNP in the run was allowed for 16 Mb length, because in long ROH, some heterozygous genotypes might arise from genotyping errors (Ferenčaković et al., 2012; Meuwissen et al., 2020).

2.2.2 | ROH-based inbreeding calculation

After defining ROH segments, the inbreeding coefficients (F_{ROH}) were calculated for each individual using the equation proposed by McQuillan et al. (2008): $F_{\mathrm{ROH}_i} = \frac{\Sigma L_{\mathrm{ROH}_i}}{L_{\mathrm{AUTOSOME}}}$ where the $L_{\mathrm{ROH}i}$ is the total length of ROH_i of genotyped individual i, and L_{AUTOSOME} is the overall length of the autosomal genome (chromosome 1–18) covered by SNPs. L_{AUTOSOME} was computed as the length between the first SNP and the last SNP per chromosome for all autosomal chromosomes and was 2,445,928 kb in this study.

Spearman correlation between different inbreeding categories was computed. A total of 2393 pigs that had both pedigree and genomic individual inbreeding coefficients were included for computing correlations.

2.3 | Phenotypic data

Initially, the phenotype dataset consisted of 115,121 ejaculate records from 1764 boars born between 2002 and 2020. For each ejaculate, traits recorded were semen volume, density, motility, and number of spermatozoa. Besides, the interval between two successive semen collections and the age of the boar at each semen collection were available. Since not all animals with phenotypes were genotyped and vice-versa, after merging phenotype and inbreeding datasets, 74,734 ejaculate records from 1034 Pietrain boars born between 2009 and 2020 remained for inbreeding depression analyses. Those records were from three different artificial insemination (AI) stations in Austria: AI station 1 ($n = 13{,}498$; from 87 boars collected between 2017 and 2020), AI station 2 ($n = 20{,}634$; from 255 boars collected between 2017 and 2020), and AI station 3 ($n = 40{,}602$; from 692 boars collected between 2012 and 2020).

Extreme values for each variable were excluded by setting a threshold: For the traits sperm density and number of spermatozoa, the values that lie between >0 and $\leq$ mean + 3 standard deviations (SD) were retained. The number of spermatozoa was calculated as a product of semen volume and density. Values lower than 0.1% of the quantile were excluded from the analyses for the motility trait. Ejaculate volumes lower than 30 mL and higher than 650 mL were also excluded.

The age of the boar at each semen collection was recorded in days, and records with age less than 200 days were excluded. Records with intervals between semen collections with less than 1 or more than 30 days were also excluded.

Besides, the generation interval (L), which is defined as the average age of parents at the time of birth of the offspring (Doekes et al., 2018), was also computed with Retriever v1.0 as described by Windig et al. (2019).

2.4 | Calculation of inbreeding rate

To understand the inbreeding trend in the Austrian Pietrain population, the rate of inbreeding (ΔF) per year was calculated as illustrated in the formula: $\Delta F = \frac{(F_t - F_{t-1})}{(1 - F_{t-1})}$ where F_t is the average inbreeding level in the current year, F_{t-1} is the average inbreeding level in the previous year. This inbreeding rate per year was multiplied with the generation interval to express the change per generation.

2.5 | Statistical analysis

Effects of inbreeding were estimated by regressing phenotypes on inbreeding coefficients using single-trait repeatability animal models. Different models were applied for different traits based on fixed effects that explained significant variability for each trait. Model 1 (full model) without inbreeding effect was used to estimate narrow sense heritability (h^2) for each trait. For semen volume and number of spermatozoa, model 2 was considered. Model 3 was applied for sperm density and motility traits. All traits were adjusted for random effects in the model. While the age of boar at semen collection and collection interval were used as covariates with linear and quadratic terms, the other fixed effects were used as categorical variables. Inbreeding coefficients calculated from pedigree and from ROH were used as covariates.

$$y_{ijklmno} = \mu + \text{breeder}_i + \text{birth}S_j + \text{cym}_k{}^*\text{station}_l + b_1(\text{CI}) + b_2(\text{CI})^2 + b_3(\text{age}) + b_4(\text{age})^2 + \text{Boar}_m + \text{PE}_n + e_{ijklmno} \quad (1)$$

$$y_{jklmno} = \mu + \text{birthS}_j + \text{cym}_k{}^*\text{station}_l + b_1(\text{CI}) + b_2(\text{CI})^2 + b_3(\text{age}) + b_4(\text{age})^2 + b_5\,(F) + \text{Boar}_\text{m} + \text{PE}_n + e_{ijkmno} \quad (2)$$

$$y_{iklmno} = \mu + \text{breeder}_i + \text{cym}_k{}^*\text{station}_l + b_1(\text{CI}) + b_2(\text{CI})^2 + b_3(\text{age}) + b_4(F) + \text{Boar}_m + \text{PE}_n + e_{iklmno} \quad (3)$$

where $y_{(i)(j)klmno}$ is the value of the given semen quality trait; μ is the overall mean; breeder$_i$ is the breeder of the boar at l^{th} boar station (i = 1–4); birthS$_j$ is the fixed effect of birth season (j = 1–4); cym$_k$, is fixed effect of semen collection-year-month (k = 1–108); station$_l$ is the fixed effect of boar station (l = 1–3), where cym$_k$*station$_l$ is the interaction of kth collection-year-month and lth station; CI is the collection interval in days between two successive semen collections; age is the age of the boar at each semen collection; Boar$_m$ is the random genetic effect of mth boar; PE$_n$ is the permanent environmental effect of boar; b_1–b_5 are the regression coefficients. F is the inbreeding coefficient that includes all various measures of inbreeding; $e_{(i)(j)klmno}$ is the random error. The boar effect was assumed to follow $N(0, \text{A}\sigma_a^2)$, where A was the numerator relationship matrix and σ_a^2 the additive genetic variance.

All analyses were performed in ASReml 4.1 as described by Gilmour et al. (2015). It allows to account for family relations for large data sets and corrects for additive genetic relationships. Estimated effects and corresponding standard errors (SE) were obtained from the corresponding output file. Besides, p-values of Wald F-test obtained from output files were used to check for the significance of inbreeding depression on traits.

3 | RESULTS AND DISCUSSION

3.1 | Descriptive statistics and heritability estimates for phenotypes

Descriptive statistics and heritability estimates for sperm quality traits are presented in Table 1. The average number of ejaculates collected per boar was 71.5 ± 63.3. The number of semen collections per boar ranged from 1 to as high as 456 collections.

The heritability estimates obtained in this study were close to the estimates reported in the literature. For instance, Li et al. (2019) found heritabilities of 0.25 ± 0.02 for semen volume in Duroc and 0.23 ± 0.03 for sperm density in Landrace in southern China. Marques et al. (2017) reported heritabilities of 0.15 ± 0.03 for sperm motility and 0.18 ± 0.02 for the number of spermatozoa in Dutch Pietrain pigs. The heritability is, however, population-specific and may vary depending on population in a specific environment (Kim et al., 2015). Heritability being a fraction of phenotypic variance attributable to genetic variation, can provide important information about the genetic basis of a trait (Ge et al., 2017). In general, the somewhat lower heritability for the composite traits could be due to the uncertainty of component traits and dependency on the genetic architecture around them (Knap & Doeschl-Wilson, 2020).

TABLE 1 Number of ejaculates (N), mean, standard deviation (SD), additive genetic variance (σ_a^2), phenotypic variance (σ_p^2), and heritability (h^2) with standard error (SE, in parentheses) for four boar semen quality traits.

Semen traits[a]	N	Mean	SD	σ_a^2	σ_p^2	h^2
Volume	73,928	262.52	98.95	2090.00	7609.00	$0.27_{(0.04)}$
Density	73,392	0.33	0.14	0.004	0.017	$0.26_{(0.04)}$
Spermatozoa	73,973	80.87	29.57	132.4	742.5	$0.18_{(0.03)}$
Motility	73,974	86.75	8.64	5.69	41.64	$0.14_{(0.03)}$

[a]Volume: semen volume in ml per ejaculate; density: sperm density in million per ml; spermatozoa: number of spermatozoa in billion per ejaculate; Motility: sperm motility in percentage.

TABLE 2 Summary statistics for the different inbreeding coefficients of Austrian Pietrain pigs.

Inbreeding[a]	N	Minimum	Maximum	Mean	SD	Median
F_{PED}	2393	0.00	16.83	3.21	1.61	2.99
F_{PED10}	2393	0.00	16.56	2.88	1.63	2.65
F_{PED7}	2276	0.00	15.64	1.97	1.54	1.72
F_{ROH1}	2393	0.50	14.93	7.33	1.84	7.33
F_{ROH2}	2393	0.35	14.85	7.16	1.84	7.05
F_{ROH4}	2392	0.18	12.99	5.28	1.80	5.04
F_{ROH8}	2368	0.33	11.24	3.05	1.65	2.83
F_{ROH16}	1884	0.65	10.18	2.16	1.39	1.82

[a]Number of animals: N; standard deviation: SD; F_{PED}, F_{PED10}, F_{PED7}: pedigree inbreeding coefficients based on all, 10 and 7 generations, respectively; F_{ROH1}, F_{ROH2}, F_{ROH4}, F_{ROH8}, and F_{ROH16}: inbreeding coefficients calculated from the sum of all ROH segments greater than 1, 2, 4, 8, 16 Mb, respectively.

3.2 | Pedigree completeness

The average ECG increased from 3.0 in 1971 to 16.9 in 2020, and was 8.4 when calculated across all years. The proportion of animals with a number of complete generations (NCG) above 5 has increased from 0% in 1971 to 99.0% in 2020. In cattle populations, Ferenčaković et al. (2012) considered an average ECG of 7.31 to 9.02 as an indication of good pedigree depth and completeness. Checking pedigree quality is important as it influences the estimates of inbreeding coefficients (Vostry et al., 2018).

3.3 | Descriptive statistics for inbreeding measures

Descriptive statistics for pedigree-based and ROH-based inbreeding coefficients are shown in Table 2. For all inbreeding categories, the mean was higher than the median which indicates the right-skewness of the underlying data distributions.

As expected, the average ROH-based coefficients were higher than the average pedigree-based coefficients. For instance, F_{ROH1} was more than two times higher than F_{PED}. Similarly, F_{ROH4} was nearly two times higher than the corresponding pedigree-based F_{PED10}. In general, slight differences can be expected between ROH-based and pedigree-based coefficients either due to errors in ancestry recording or incomplete pedigree information, especially for distant generations (Forutan et al., 2018). Since the pedigree-based inbreeding estimate depends on pedigree depth, the mean inbreeding decreases as a smaller number of generations were captured for inbreeding calculation. Similarly, the mean ROH-based inbreeding coefficient decreases with increasing minimum ROH length (see Table 2). When the minimum length of the ROH is increased, the results obtained would be more related to recent inbreeding because long ROH is expected to arise from recent common ancestors (Bjelland et al., 2013).

The correlations within each inbreeding measure were high with values ranging from 0.609 to 0.996 for ROH-based and 0.982 to 0.989 for pedigree-based inbreeding (Table 3). However, the correlations between the genomic and pedigree inbreeding measures were unexpectedly low, ranging from 0.186 to 0.357. Although the exact reason for this low correlation is unknown, one of the reasons could be incomplete pedigree. Nevertheless, similar correlation coefficients between pedigree and different ROH-based inbreeding were reported in Italian pig populations by Schiavo et al. (2020). Shi et al. (2020) reported correlations ranging from 0.18 to 0.37 in a Large White population.

3.4 | Estimated effects of inbreeding

Inbreeding depression was present for each inbreeding category (F_{PED}, F_{PED10}, F_{PED7}, F_{ROH1}, F_{ROH2}, F_{ROH4}, F_{ROH8}, and F_{ROH16}) and the estimated effects were significant

TABLE 3 Spearman correlation coefficients between different inbreeding coefficients (pedigree-based and ROH-based) in Austrian Pietrain pigs ($n = 2392$).

Inbreeding[a]	F_{PED10}	F_{PED7}	F_{ROH1}	F_{ROH2}	F_{ROH4}	F_{ROH8}	F_{ROH16}
F_{PED}	0.989	0.984	0.334	0.332	0.346	0.328	0.186
F_{PED10}		0.982	0.332	0.330	0.344	0.327	0.188
F_{PED7}			0.345	0.342	0.357	0.339	0.199
F_{ROH1}				0.996	0.925	0.848	0.609
F_{ROH2}					0.926	0.847	0.611
F_{ROH4}						0.908	0.669
F_{ROH8}							0.732

[a]F_{PED}: inbreeding based on entire pedigree; F_{PED10}: inbreeding based on 10 generations; F_{PED7}: inbreeding based 7 generations; F_{ROH1}, F_{ROH2}, F_{ROH4}, F_{ROH8}, and F_{ROH16}: runs of homozygosity (ROH) inbreeding coefficients calculated from the sum of all ROH segments >1, 2, 4, 8, 16 Mb, respectively.

TABLE 4 Inbreeding rates per year and generation (Gen) for Austrian Pietrain pigs. The genotypic information was available from 2004 onwards. The Pietrain boars with phenotypes on sperm quality traits were born and genotyped from around 2009 onwards. The rates are shown in percentage (%).

	Period			
	1986–2003		2004–2020	
Inbreeding rate[a]	Year	Gen	Year	Gen
ΔF_{PED}	0.09	0.21	0.13	0.3
ΔF_{PED10}	0.07	0.16	0.12	0.27
ΔF_{ROH1}	–	–	0.31	0.72
ΔF_{ROH4}	–	–	0.44	1.02

[a]F_{PED}: inbreeding based on entire pedigree; F_{PED10}: inbreeding based on 10 generations; F_{ROH1} and F_{ROH4}: runs of homozygosity (ROH) inbreeding coefficients calculated from the sum of all ROH segments >1 and 4 Mb, respectively. The average generation interval computed across the entire period was 2.33 years for sire and dams combined.

($p \leq 0.05$) for either one or more sperm traits analysed. All categories of pedigree inbreeding showed significant effects ($p \leq 0.05$) for sperm motility and non-significant effects for the remaining traits (Table 5).

Doekes et al. (2021) while performing meta-analysis on inbreeding depression estimates found lower p-values of inbreeding depression estimates for ROH_based inbreeding measure than for pedigree-based inbreeding. However, in this study, no consistent differences in p-values and effect sizes were observed between inbreeding depression estimates for pedigree-based and ROH-based measures, although in some cases, p-values were smaller for ROH-based inbreeding measures (Tables 4 and 5). Usually, inbreeding measures with smaller p-values of inbreeding depression estimates can be suggestive of more power to detect inbreeding depression (Doekes et al., 2021).

Based on the information on ROH length, the number of generations for inbreeding events is inferred. The ROH due to ancient inbreeding tends to be shorter (for example, F_{ROH1}, F_{ROH2}) while the longer ROH are expected to represent more recent inbreeding (F_{ROH8}, F_{ROH16}). Given 1 centimorgan (cM) is approximately 1 Mb, and the average length of $1/(2G)$ Morgan for ROH derived from a common ancestor G generations ago (Fisher, 1954), the ROH length of 1, 2, 4, 8 and 16 Mb is expected to capture IBD segments from about 50, 25, 12, 6, and 3 generations, respectively. The ancient inbreeding is expected to have larger effects compared to old inbreeding. Ancient inbreeding is expected to be less harmful than the recent inbreeding due to purging of deleterious recessive alleles in each generation as a result of either natural or artificial selection (Baumung et al., 2015; Doekes et al., 2019; Gulisija & Crow, 2007). Purging can occur in the presence of strong selection pressure and a slow rate of increase in inbreeding levels over time (Hedrick & Garcia-Dorado, 2016). In the present study, pedigree-based inbreeding showed clear trends indicating that the effects of recent breeding are more severe than ancient inbreeding, especially on semen volume and sperm motility traits. For example, the effect of F_{PED7} was nearly five times higher than F_{PED} on semen volume. Doekes et al. (2021) also found stronger effects of recent pedigree inbreeding than ancient inbreeding on milk yield traits in dairy cattle. For ROH-based inbreeding, although there were indications for some traits that recent ROH-based inbreeding is more severe than ancient inbreeding (for example, the effects of F_{ROH8} were 1.6 times higher than F_{ROH4}), the trends were not consistent.

As the pedigree depth more relevant for the breeding organization was up to 10 generations, inbreeding calculated with a minimum ROH length of 4 Mb (F_{ROH4}) can be more appropriately chosen to match the pedigree inbreeding for the last 10 generations (F_{PED10}). A 1% increase in F_{PED10} was significantly ($p \leq 0.05$) associated with a reduction in sperm motility of 0.231%. This implies that on average, a boar with F_{PED10} of 10% is expected to have 2.31% less sperm motility than a non-inbred boar. Estimated effects of F_{PED10} on semen volume, density, and the number of spermatozoa were also unfavourable. Likewise,

TABLE 5 Estimated effects of pedigree-based inbreeding (per 1%) with standard error (SE) on four sperm quality traits evaluated.

Inbreeding[a]	Volume	Density	Spermatozoa	Motility
F_{PED}	$-0.183_{(1.571)}$	$-4.067_{(2.454)}$	$-0.611_{(0.453)}$	$-0.217_{(0.112)}^{*}$
F_{PED10}	$-0.235_{(1.587)}$	$-3.946_{(2.479)}$	$-0.551_{(0.458)}$	$-0.231_{(0.113)}^{*}$
F_{PED7}	$-0.838_{(1.654)}$	$-4.135_{(2.557)}$	$-0.808_{(0.478)}$	$-0.254_{(0.117)}^{*}$
F_{ROH1}	$-2.051_{(1.071)}$	$-0.797_{(1.650)}$	$-0.707_{(0.322)}^{*}$	$-0.188_{(0.078)}^{*}$
F_{ROH2}	$-2.128_{(1.072)}^{*}$	$-0.636_{(1.656)}$	$-0.692_{(0.322)}^{*}$	$-0.181_{(0.078)}^{*}$
F_{ROH4}	$-1.990_{(1.096)}$	$-0.473_{(1.687)}$	$-0.660_{(0.329)}^{*}$	$-0.126_{(0.080)}$
F_{ROH8}	$-3.233_{(1.191)}^{*}$	$2.041_{(1.834)}$	$-0.558_{(0.357)}$	$-0.102_{(0.087)}$
F_{ROH16}	$-0.814_{(1.471)}$	$-2.339_{(2.286)}$	$-0.979_{(0.449)}^{*}$	$-0.147_{(0.112)}$

[a]Volume: semen volume in ml per ejaculate; density: sperm density in million per ml; spermatozoa: number of spermatozoa in billion per ejaculate; Motility: sperm motility in percentage; F_{PED}, F_{PED10}, F_{PED7}: pedigree inbreeding coefficients based on entire pedigree information, for 10 generations, and for 7 generations, respectively. F_{ROH1}, F_{ROH2}, F_{ROH4}, F_{ROH8}, and F_{ROH16}: runs of homozygosity (ROH) inbreeding coefficients calculated from the sum of all ROH segments greater than 1, 4, 8, 16 Mb, respectively. Significance for non-nullity is indicated by stars (*$p \leq 0.05$).

a 1% increase in F_{ROH4} was related to a decline in sperm motility of 0.126%. On average, a boar with F_{ROH4} of 10% is expected to have 19.90 mL less ejaculate volume and 6.60×10^9 less number of spermatozoa per ejaculate than a non-inbred boar. Sperm density was found to decline by 0.473×10^6 per ml per 1% increase in F_{ROH4}. Negative effects of inbreeding on sperm motility have been reported in horses (Boer, 2007; van Eldik et al., 2006), cattle (Maximini et al., 2011), and Mexican grey wolves (Asa et al., 2007). On the contrary, Losdat et al. (2018) found no evidence of inbreeding depression in sperm motility in a song sparrow (*Melospiza melodia*) population and concluded that moderate inbreeding would not necessarily constrain sperm performance.

The number of insemination doses that can be obtained from each ejaculate depends on semen quality and quantity (Frangež et al., 2005). Thus, the inbreeding depression with lowered semen quality and quantity has economic consequences. In the present study, the pedigree inbreeding has increased from 0.44% in 1986 to 3.86% in 2020, and the estimated effect of F_{PED} on semen volume was −0.183 mL per ejaculate. This would imply an average reduction of about 0.63 mL (-0.183×3.42) per ejaculate due to increased F_{PED} between 1986 and 2020. Similarly, the cumulative average reduction was 2.09×10^9 for a number of spermatozoa per ejaculate, 13.91×10^6 per ml for sperm density, and 0.74% for sperm motility. The depression seems small when only one particular trait is considered. However, the overall impact would probably be larger when such small effects on many other traits are considered (Doekes et al., 2019; Leroy, 2014). It is also important to realize that traits other than sperm quality that are not covered in this study might be compromised due to inbreeding. In many species, inbreeding was found to affect their lifetime performance (Yadav et al., 2019). Thus, minimizing the increase of inbreeding in the population is crucial from an economic point of view (Do et al., 2015). Usually, inbreeding depression can be reduced in a population by minimizing inbreeding or mean kinship based on pedigree information or genomic information when available (Hedrick & Garcia-Dorado, 2016; Kardos et al., 2015).

4 | CONCLUSIONS

In this study, we investigated inbreeding depression on four sperm quality traits in Austrian Pietrain boars. Inbreeding depression was observed for semen volume, a number of spermatozoa, and sperm motility percent. ROH-based inbreeding captured more inbreeding depression compared with pedigree-based inbreeding, except for the motility trait. All estimated effects, except the non-significant effect of F_{ROH8} on semen density were unfavourable. If the level of inbreeding is not properly managed, it might become substantial enough to cause significant inbreeding depression in the future. The long-term solution is to maintain inbreeding at low rate in the population. In the future, analysis of the effects of inbreeding depression for other traits, including growth and litter size, for the Austrian Pietrain population is strongly advised.

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CONFLICT OF INTEREST STATEMENT

Johann Sölkner, a co-author of this article is an Editorial Board member of Journal of Animal Breeding and Genetics. To minimize bias, he was excluded from all editorial decision-making related to the acceptance of this article for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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