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Comparing inbreeding parameters in pigs: Drift, homozygosity, and IBD

K.R. Kelles[1,2]*, N.G. Leite[3], M. van Son[1,3], Y.C.J. Wientjes[4], E. Grindflek[1,3], P. Berg[2], and T.H.E. Meuwissen[2]

*[1]Norsvin, Hamar, Norway; [2]Norwegian University of Life Sciences, Ås, Norway; [3]Topigs Norsvin, 's-Hertogenbosch, Netherlands; [4]Wageningen University & Research, Wageningen, the Netherlands; *Corresponding author: kelvin.kelles@norsvin.no*

Introduction

Historically, the inbreeding coefficient was assessed solely from the numerator relationship matrix (**A**), derived from pedigree information. Nonetheless, advances in high-throughput genomic technologies have enabled the development of multiple genomic approaches to estimate inbreeding, making the selection and comparison of these methods a challenge for animal breeding programs.

Inbreeding methods can be grouped into three approaches: **1) Identity-by-Descent (IBD)** methods estimate the probability that alleles are identical due to common ancestry, including pedigree-based inbreeding (F_{PED}, assuming unrelated founders) and genomic linkage analysis (F_{GLA}, combining pedigree and marker data). **2) Drift-based** methods quantify deviations in allele frequencies from a base population using genomic relationship matrices (**G**) (VanRaden, 2008; Yang *et al*., 2010). They include F_{GVR1} (weighted toward intermediate alleles), F_{GVR2} (emphasizing rare alleles), and F_{GYANG}, which also gives greater weight to rare alleles. **3) Homozygosity-based (HOM)** methods estimate genome-wide homozygosity levels through runs of homozygosity (F_{ROH}, proportion of genome in homozygous segments), excess of homozygosity (F_{HOM}, deviation from Hardy-Weinberg equilibrium), and the **G** matrix with fixed allele frequencies of 0.5 ($F_{G0.5}$, measuring homozygosity relative to maximum expected heterozygosity).

Monitoring the rate of inbreeding (ΔF) is key to evaluating genetic diversity. ΔF reflects the change in inbreeding per generation or year and is affected by the selection strategy. Meuwissen *et al*. (2020) showed that drift- and homozygosity-based ΔF are equivalent under random mating, as allele-frequency changes are uncorrelated with initial frequencies. However, in breeding programs using optimum contribution selection (OCS) with genomic relationships to control inbreeding (GOCS), selection may create non-zero covariance, leading to F_{HOM} exceeding F_{drift} or *vice versa*.

The goal of this study was to investigate and compare estimates of inbreeding rates derived from pedigree and genomic data in a commercial pig breeding dam line. Three classes of approaches were evaluated: IBD, drift, and HOM-based estimates. Additionally, the study examines inbreeding rates derived from HOM- and drift-based approaches to determine whether OCS tends to increase one rate more than the other.

Materials & Methods

General dataset. The dataset includes purebred sires from artificial insemination centers and their genotyped relatives born between 2014 and 2024. The animals are part of a commercial breeding program, and genotyped individuals are a non-random subset, as genotyping mostly targets selection candidates. This selection resulted in 34,126 animals with genotype information. Animals were genotyped using various SNP panels and subsequently imputed to

medium- and high-density panels (50K and 660K). The complete pedigree tracing the ancestry of these 34,126 animals comprised 46,733 individuals.

Inbreeding estimates. Inbreeding coefficients were estimated for the 34,126 animals with imputed genotypes, enabling comparison between pedigree-based and genomic-based estimates. The coefficients were estimated using three different classes of approaches. IBD-based measures were obtained from the pedigree (F_{PED}) and the Genomic Relationship Matrix based on linkage analysis (F_{GLA}). The G_{LA} method determines whether marker alleles are inherited from the sire or dam to assess the probability of inheriting either the maternal or paternal allele at a locus, rather than assuming a 50/50 chance, as in F_{PED}. Drift-based measures were assessed through **G** constructed according to VanRaden (2008; methods 1 (F_{GVR1}) and 2 (F_{GVR2})) and Yang (F_{GYANG}) (Yang *et al*., 2010). HOM-based measures were estimated using Runs of Homozygosity (F_{ROH}), Excess of Homozygosity (F_{HOM}), and the **G** calculated using the VanRaden method 1 with allele frequencies fixed at 0.5 ($F_{G0.5}$). F_{ROH} and F_{HOM} were performed for both 50K and 660K SNP panels. F_{ROH} was calculated with a minimum segment length of 2 Mb, no heterozygous genotypes permitted within ROH, and window sizes of 60 SNPs (50K) or 100 SNPs (660K). However, due to computational constraints, a 50K marker panel was used for measurements based on the **G** matrix. The reference population for calculating allele frequencies was defined as animals born in 2014, as this was the first year with the largest number of genotyped individuals. This reference population was used for the F_{GVR1}, F_{GVR2}, F_{GYANG}, F_{HOM50}, and F_{HOM660} methods.

Comparison of inbreeding measures. For each of the methods to estimate inbreeding coefficients, the rate of inbreeding (ΔF) was computed using the software R by multiplying the regression coefficient of the natural logarithm of (1- F) on the animal's year of birth by negative one (Doekes *et al*., 2018). Moreover, the associations between the different measures of inbreeding were evaluated using Pearson's correlation coefficient, and significance was evaluated using the corresponding *t*-test.

Results

Inbreeding estimates and rate of inbreeding.

Annual inbreeding coefficients, presented as mean ± SE (standard error), showed increasing trends over the 2014-2024 period, although with distinct magnitudes across methods (Fig. 1). Notably, negative values were observed in F_{GVR1}, F_{GVR2}, F_{GYANG}, F_{HOM50}, and F_{HOM660}, reflecting higher-than-expected heterozygosity relative to the reference population. In contrast, IBD-based methods and F_{ROH} coefficients are constrained to be non-negative because they represent probabilities or proportions. Regarding ΔF, drift-based approaches exhibited the highest rates, with F_{GVR2} reaching 0.92%, F_{GVR1} at 0.64%, and F_{GYANG} at 0.58% per year. IBD-based methods showed moderate and similar rates (F_{PED} = 0.38%; F_{GLA} = 0.43%). HOM-based methods varied considerably, ranging from 0.21% (F_{ROH50}) to 0.42% (F_{HOM50}).

Correlation between inbreeding measures. The inbreeding measures showed moderate to high correlations within each approach (Fig. 2). Among the IBD-based methods, F_{PED} and F_{GLA} showed a strong association (r = 0.84). Drift-based measures differed in their consistency: F_{GVR1} and F_{GVR2} were moderately correlated (0.68), while F_{GYANG} aligned more closely with F_{GVR1} (0.80) but showed weaker agreement with F_{GVR2} (0.46). Finally, the HOM-based methods ($F_{G0.5}$, F_{HOM50}, F_{HOM660}, F_{ROH50}, F_{ROH660}) were highly correlated with one another, with values ranging from 0.85 to 0.98. Across approaches, the correlations were generally moderate. IBD and drift-based methods showed modest agreement, with F_{PED} and F_{GLA} correlating weakly to moderately with F_{GVR1}, F_{GVR2}, and F_{GYANG} (0.17–0.50). The IBD and HOM-based

metrics showed slightly stronger consistency, with correlations ranging from 0.39 to 0.58. Drift- and HOM-based measures exhibited the widest range of relationships: F_{GVR1} and F_{GYANG} showed low to moderate correlations with HOM metrics (0.39–0.73), whereas F_{GVR2} showed minimal agreement, with values near zero or slightly negative.

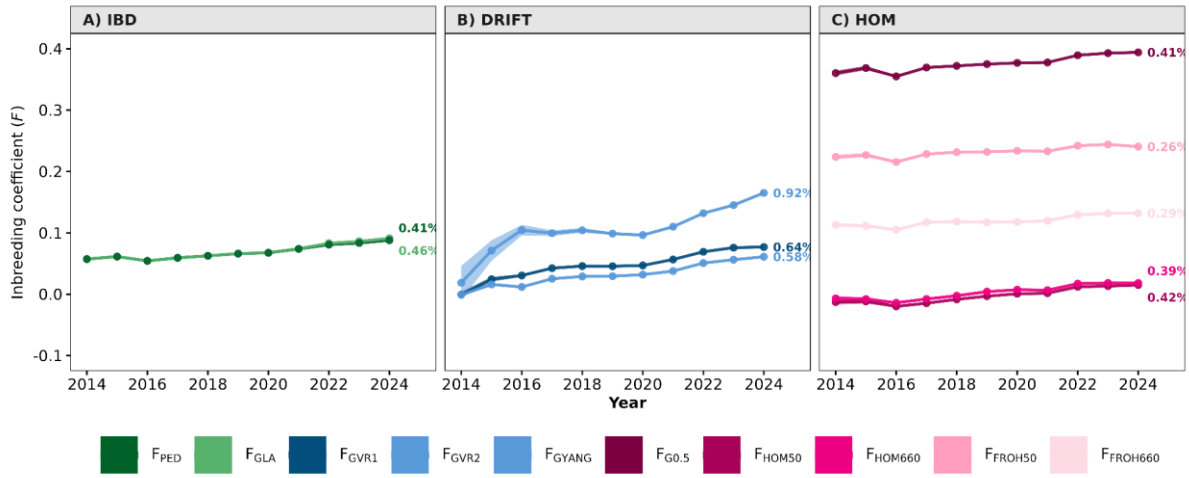

Figure 1. Temporal trends and rates of change (ΔF per year) of inbreeding coefficients estimated by different approaches

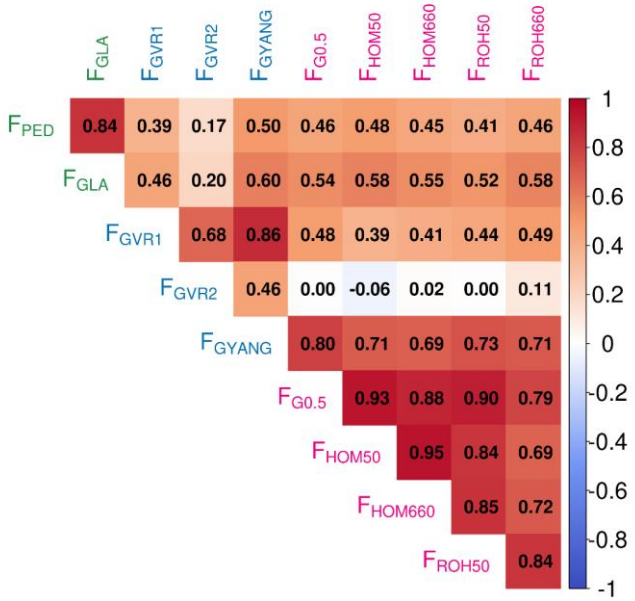

Figure 2. Pearson correlations among different measures of inbreeding. All correlations were significant different from 0 ($p < 0.01$), except for F_{GVR2} with $F_{G0.5}$ and F_{ROH50}.

Discussion

The correlation patterns indicate moderate to strong agreement within approaches, but weaker concordance across approaches, reflecting that each captures different aspects of inbreeding. IBD-based methods estimate expected relatedness from shared ancestry, homozygosity-based metrics quantify realized autozygosity through excess homozygosity or extended ROH segments, and drift-based estimators capture population-level allele frequency changes relative to a base population. The low correlation between F_{GVR2} (Drift) and IBD or HOM measure may indicate a difference related to the weight of rare alleles, since F_{GVR2} emphasizes rare variants. However, F_{GYANG} also assigns more weight to rare alleles and shows a high

correlation. This suggests that differences in correlation across approaches mainly reflect the distinct biological and statistical definitions of inbreeding that the measures target, rather than differences in the contribution of common or rare variants. These complementary perspectives underscore that no single metric fully captures the complexity of inbreeding, and combining approaches provides a more comprehensive assessment for breeding program management.
OCS is widely used to manage genetic diversity in breeding programs. Although different relationship matrices can be applied, such as pedigree-based (POCS) and genomic (GOCS), the present study relies on empirical data from an active breeding program and therefore reports results only from the pedigree matrix used by the breeding company. In this dataset, ΔF_{DRIFT} exceeded ΔFHOM, indicating that selection tended to move allele frequencies toward intermediate values, thereby generating genetic drift and maintaining high heterozygosity (low F_{HOM}). In contrast, Gautason *et al*. (2023) reported the opposite pattern ($\Delta F_{DRIFT} < \Delta F_{HOM}$) when GOCS is applied. As explained by Meuwissen *et al*. (2020) and de Beukelaer *et al*. (2017), covariance between initial allele frequencies and changes in allele frequency drives these differences in ΔF. GOCS minimizes changes in allele frequencies by penalizing deviations from initial values through the genomic relationship matrix. This constraint creates a positive covariance between initial frequencies and their changes, pushing alleles toward fixation or loss. However, the pattern observed in this study suggests negative covariance: rare alleles tend to increase in frequency toward moderate levels. This preserves diversity at the allele level (low ΔF_{HOM}) but increases random drift across the genome (high ΔF_{DRIFT}). Additionally, in POCS, the inbreeding management restriction part is based on pedigree and thus does not directly affect allele frequencies. Therefore, the observed allele frequency changes are due to genomic selection within the breeding program.

Conclusions

Different approaches to estimate inbreeding capture different information. Pedigree and genomic approaches estimate distinct properties, with further differentiation among genomic measures themselves. For instance, measures of homozygosity do not effectively capture information about drift, and vice versa. Under optimal contribution selection with the pedigree matrix, drift-based inbreeding exceeded homozygosity rates, indicating that allele frequency changes were non-neutral and attributable to the selection component of the breeding program.

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