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Inbreeding trends from 1991 to 2025 in > 1.1 million genotyped purebred beef and dairy cattle

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Introduction

Genomic selection has substantially changed cattle breeding. Widespread genotyping and more accurate genomic evaluations enable artificial insemination companies to identify genetically elite sires with more precision. This intense selection of bulls can reduce genetic diversity through overuse of a small number of elite sires. Higher selection intensity increases the risk of population-level inbreeding, which is associated with decreased performance in a host of growth, production, and fertility traits in beef and dairy cattle (Leroy, 2014); a phenomenon known as inbreeding depression.

One proposed mechanism of inbreeding depression is increased expression of deleterious recessive alleles (Falconer and Mackay, 1996). Under this model, inbreeding depression can be reduced or eliminated through purging of deleterious recessive alleles; this has been demonstrated in animal model studies in which inbreeding depression was reduced or eliminated with selective pressure (Swindell and Bouzat, 2006). Therefore, increased homozygosity is not necessarily an undesirable outcome of selective breeding. Negative consequences can arise if inbreeding is associated with a narrowing of selection such that the influence of genetic drift increases relative to the purging effects of selection.

In many national evaluations, inbreeding is measured using partial pedigree information (Cole, 2024). Estimates of inbreeding based on partial pedigree will identify inbreeding risk from closely related animals, but ignore inbreeding risk due to more distant co-ancestry. Such estimates of inbreeding may underestimate trends in the accumulation of inbreeding, especially given the changes genomic selection has brought to cattle breeding. Previous cattle studies have characterized the trends in inbreeding within the Irish population (McParland *et al.,* 2007), however, this was prior to the widespread adoption of genotyping and genomic selection in Ireland. The aim of the present study was to quantify the rate of inbreeding accumulation within purebred Irish beef and dairy populations over the past 30 years and compare pedigree-based and genomic estimates of inbreeding in contemporary purebred cattle populations.

Materials & Methods

Genotype data and pedigree records. Genotype data were available for >1.1 million purebred cattle. An animal was considered purebred if it was > 87.5% purebred per herd book records. Animals were genotyped on a range of medium-density (50K) single nucleotide polymorphism (SNP) arrays. Animals with a call-rate >90% were retained and then imputed to a common set of 50,855 SNPs (the SNP panel used for routine genomic evaluations) using the imputation software FImpute (Sargolzaei *et al.,* 2014). Only animals born in years with at least 100 genotyped purebred animals of the same breed were included. The longest time span analysed in the present study was from 1991 to 2025 (Holstein) and the shortest was from 2011 to 2025 (Friesian).

After edits, there were 120,220 genotyped Aberdeen Angus, 15,496 Aubrac, 154,351 Charolais, 18,578 Friesian, 59,101 Hereford, 336,987 Holstein, 315,383 Limousin, 15,980 Saler, 24,565 Shorthorn, and 62,789 Simmental. Pedigree records were available for all genotyped animals.

There were 369,678 pedigree records for Aberdeen Angus, 38,906 Aubrac, 840,628 Charolais, 497,051 Friesian, 195,249 Hereford, 7,366,723 Holstein, 1,068,593 Limousin, 45,493 Saler, 98,824 Shorthorn, and 733,600 Simmental. Only animals with both a genomic and a pedigree inbreeding estimate were retained.

Inbreeding and pedigree completeness metrics. Genomic inbreeding estimates (F_{ROH}) were calculated separately per animal based on runs of homozygosity (ROH) that were called from the imputed autosomal SNP data using plink v1.9 software (Purcell *et al.,* 2007). ROH were called using conservative parameters to avoid calling shorter ROH which are more likely to be identical by state or potentially influenced by imputation. The parameters for calling ROH were: a scanning window of 50 consecutive SNPs, a maximum of one heterozygous SNP, a minimum density of one SNP per 120kb, at least 100 SNPs per ROH, and a minimum genomic length of 1 Mb. No maximum length or maximum number of SNPs per ROH was specified. F_{ROH} was calculated per animal as the summed length of each ROH divided by the total length of all the autosomes. The length of each autosome was defined as the distance between the first and last SNP on the autosome. Pedigree information was not used in the calculation of F_{ROH}.
The pedigree-based inbreeding estimate (F_{PED}) was calculated within breed using the Meuwissen & Luo (1992) algorithm implemented in the Pedig software (Boichard, 2002). Pedig was also used to calculate complete generation equivalents (CGE) for each animal.
The relationship between effective pedigree depth and F_{PED} was examined in the set of 1,500 animals per breed that had the highest common CGE (within 0.25 of each other). The sample size of 1,500 was chosen to balance between accuracy in summary statistics and obtaining the deepest pedigree for analysis. The pedigree of the target animals was progressively truncated by removing one generation of ancestors at a time starting with the most distant ancestors. At each iteration F_{PED} and the CGE were recalculated for the target animals.
Finally, the effective population size, which is inversely related to the rate of accumulation of inbreeding (Hill, 1972) was also calculated separately within breed for F_{PED} and F_{ROH} as:

$$N_e = \frac{1}{2\Delta F_g L}$$

where ΔF_g was the annual rate of change in the inbreeding coefficient of newborn calves. Population-level inbreeding is expected to accumulate multiplicatively across generations (Falconer and Mackay, 1996); as such ΔF_g was calculated based on a multiplicative model of inbreeding accumulation as described in Hjorto *et al*. 2021. The average generation interval, denoted by L, was calculated within breed and ranged from 5.3 years (Holstein) and 6.7 years (Friesian).

Results & Discussion

Trends in inbreeding. For 2024-born calves, mean F_{PED} was between 0.92% (Shorthorn) and 5.92% (Holstein), whereas average F_{ROH} ranged from 2.65% (Limousin) to 7.41% (Holstein). The average annual rate of increase in F_{PED} was between 0.02% (Hereford) and 0.15% (Holstein), which corresponded to an effective population size of between 62 (Holstein) and 476 (Hereford). Trends in F_{ROH} accumulation were less consistent, with no observed increase for Aberdeen Angus, Hereford, and Shorthorn, so effective population size based on F_{ROH} could not be estimated for these three breeds. In the remaining breeds, the effective population size estimated from F_{ROH} ranged from 66 (Holstein) to 1,196 (Saler). This corresponded to an average increase in F_{ROH} of between 0.01% (Saler) and 0.14% (Holstein) per year, demonstrating substantial between-breed variation. The higher rates of inbreeding in Holsteins relative to the beef breeds was consistent with previous Irish studies and likely reflect higher

selection pressure and lower introgression of foreign genetics in the dairy herd (McParland *et al.,* 2007).

Trends in ROH length. The proportions of ROH < 5 Mb, 5-10 Mb, and >10 Mb reflect the relative contribution of distant versus recent co-ancestry to inbreeding. The proportions of ROH in the three aforementioned length categories were relatively consistent year-to-year in all breeds except for Holstein, Charolais, and Limousin. In the Charolais and Limousin, the proportion of ROH >10 Mb steadily increased from 0.20 to 0.27 and 0.25 to 0.31, respectively, accompanied by comparable decreases in the proportion of ROH <5 Mb and ROH between 5-10 Mb over the period from 2000 to 2025. In contrast, Holsteins showed a linear decline in the proportion of ROH >10 Mb from 0.42 to 0.35 balanced by an increase in the proportion of ROH between 5-10 Mb over the same period. Despite this decline, the Holsteins had one of the highest proportions of ROH >10 Mb for the 10 breeds analysed. These observations suggest that the level of inbreeding due to recent co-ancestry declined in Holsteins over the past two decades, but has remained high relative to the other breeds analysed in the present study.

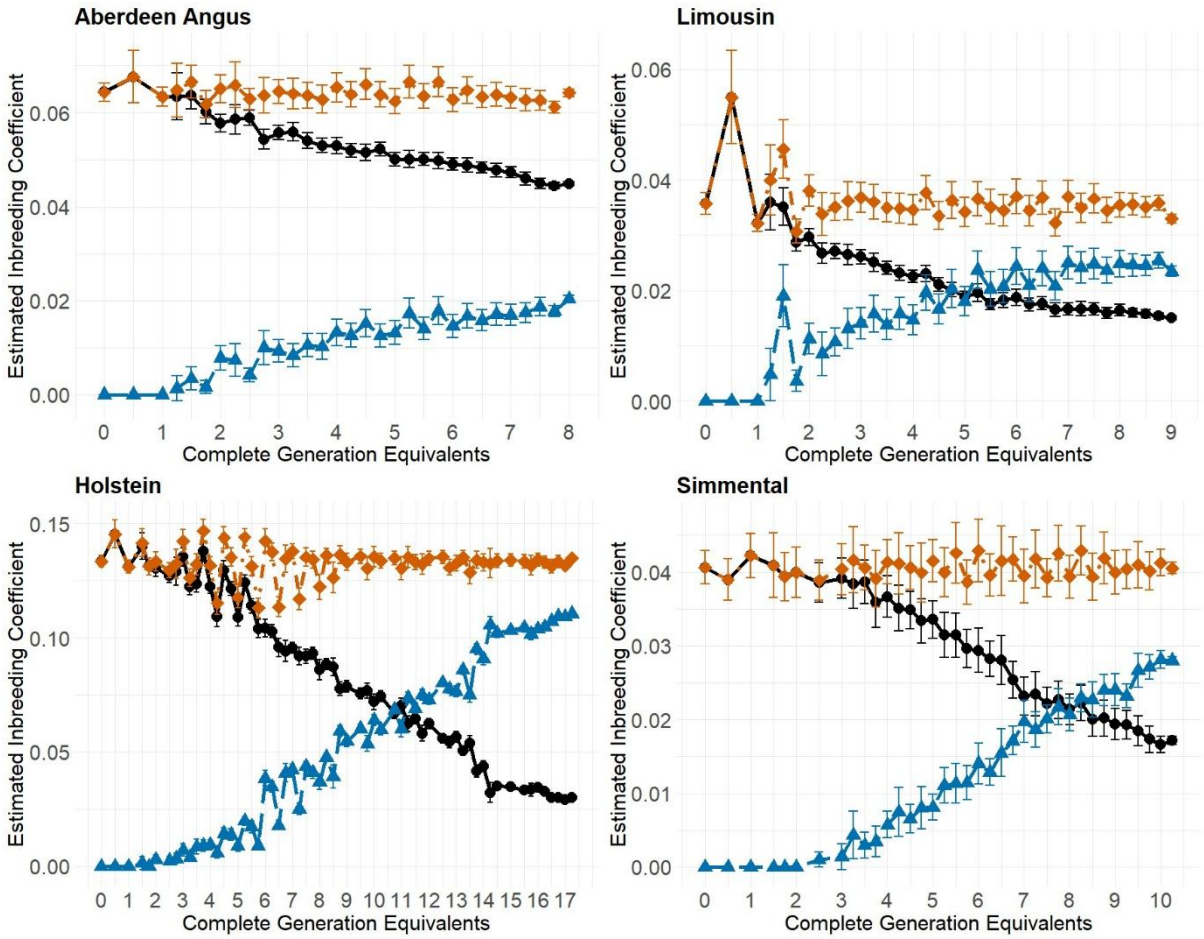

Figure 1: Plots of the genomic estimate of inbreeding (F_{ROH}; orange points and dotted line), pedigree estimate of inbreeding (F_{PED}; blue points and dashed line), and their difference (black points and solid line) plotted against complete generation equivalents for a target population of 1,500 animals per breed. For brevity, the results for Aubrac, Charolais, Friesian, Hereford, Saler, and Shorthorn are not shown.

Convergence of F_{ROH} and F_{PED}. F_{ROH} was always greater than the F_{PED}. This is to be expected since F_{PED} is likely an underestimate due to the assumption that founders are unrelated. With

each additional complete generation of pedigree data this bias may drop by up to 50% depending on the pedigree structure and relatedness of the founders.
For each of the 10 breeds analysed in the present study F_{PED} increased with increasing CGE and approached, although never reached, F_{ROH} indicating that additional pedigree depth was required to eliminate bias in F_{PED}. The difference between F_{ROH} and F_{PED} reached a minimum at approximately 1.6% in the Limousins and Simmentals (Figure 1). Even after accounting for pedigree depth, the difference between F_{ROH} and F_{PED} was inconsistent across and within breeds (Figure 1). For example, in the Holsteins, the rate of change in the difference between F_{ROH} and F_{PED} increased between 12.5 and 14.5 CGE (Figure 1). This indicated that a large number of distant ancestors common to both parental lineages of the target population entered the pedigree between 12.5 and 14.5 CGE.
With sufficient pedigree depth, F_{PED} should be an unbiased estimator of the actual inbreeding coefficient, however, F_{ROH} may still be more precise because it can account for variation due to Mendelian sampling. In this study, the average absolute difference in F_{ROH} between full-siblings was between 1.1% (Limousin) and 2.0% (Holstein). This variation due to Mendelian sampling may reflect the upper limit of per-animal precision attainable by F_{PED}.
The results of this study may be of particular relevance to national evaluations which only use partial pedigree data to calculate inbreeding coefficients (Cole, 2024). From a breeding perspective, using F_{PED} calculated from a reduced pedigree to advise against mating closely related animals may limit the formation of long ROH and the erosion of genetic diversity. However, more accurate inbreeding estimates may improve the accuracy genomic evaluations and estimates of inbreeding depression, which under an additive model is proportional to the inbreeding coefficient (Falconer and Mackay, 1996).

Conclusion

In most breeds, F_{ROH} increased year-on-year, particularly in the Holsteins which had an effective population size of only 66 based on F_{ROH} trends over the past 30 years. In all breeds, F_{ROH} was consistently underestimated by F_{PED}, with considerable variability in the difference between F_{ROH} and F_{PED} even at similar levels of pedigree completeness across breeds. Notably, F_{PED} did not converge to F_{ROH} even with up to 17 CGE. When genomic data are available, the expected F_{ROH} of progeny should be considered when making breeding decisions; otherwise, all available pedigree data should be used to estimate co-ancestry between prospective parents to limit unintended accumulation of inbreeding. This is particularly important in breeds with low effective population sizes which are the most vulnerable to erosion of genetic diversity.

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