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Beef trait genetic parameters based on old and recent data and its implications for genomic predictions in Italian Simmental cattle

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Abstract

This study aimed to evaluate the changes in variance components over time to identify a subset of data from the Italian Simmental (**IS**) population that would yield the most appropriate estimates of genetic parameters and breeding values for beef traits to select young bulls. Data from bulls raised between 1986 and 2017 were used to estimate genetic parameters and breeding values for four beef traits (average daily gain [**ADG**], body size [**BS**], muscularity [**MUS**], and feet and legs [**FL**]). The phenotypic mean increased during the years of the study for ADG, but it decreased for BS, MUS, and FL. The complete dataset (**ALL**) was divided into four generational subsets (**Gen1**, **Gen2**, **Gen3**, and **Gen4**). Additionally, ALL was divided into two larger subsets: the first one (**OLD**) combined data from Gen1 and Gen2 to represent the starting population, and the second one (**CUR**) combined data from Gen3 and Gen4 to represent a subpopulation with stronger ties to the current population. Genetic parameters were estimated with a four-trait genomic animal model using a single-step genomic average information restricted maximum likelihood algorithm. Heritability estimates from ALL were 0.26 ± 0.03 for ADG, 0.33 ± 0.04 for BS, 0.55 ± 0.03 for MUS, and 0.23 ± 0.03 for FL. Higher heritability estimates were obtained with OLD and ALL than with CUR. Considerable changes in heritability existed between Gen1 and Gen4 due to fluctuations in both additive genetic and residual variances. Genetic correlations also changed over time, with some values moving from positive to negative or even to zero. Genetic correlations from OLD were stronger than those from CUR. Changes in genetic parameters over time indicated that they should be updated regularly to avoid biases in genomic estimated breeding values (**GEBV**) and low selection accuracies. GEBV estimated using CUR variance components were less biased and more consistent than those estimated with OLD and ALL variance components. Validation results indicated that data from recent generations produced genetic parameters that more appropriately represent the structure of the current population, yielding accurate GEBV to select young animals and increasing the likelihood of higher genetic gains.

Key words: cattle, genetic correlation, genomic, single-step approach, variance components

Abbreviations

ADG	average daily gain
AIREML	average information restricted maximum likelihood
ALL	complete dataset
ANAPRI	Italian Simmental Breeders Association
BS	body size
FL	feet and legs
GEBV	genomic estimated breeding values
GEBVp	GEBV in the partial dataset
GEBVw	GEBV in the complete dataset
IS	Italian Simmental
LD	linkage disequilibrium
MUS	muscularity
PT	performance test
PTI	performance test beef index
ssG_AIREML	single-step genomic AIREML

Introduction

Italian Simmental (**IS**) is a dual-purpose cattle breed raised mainly in small herds (~11 cows) located in the mountainous areas of Northern Italy (60% of the farms). This breed is well-known for its ability to adapt to suboptimal farming and breeding conditions. Originally, it was a triple-purpose breed developed for work, milk, and meat production, emerging in the second half of the 1800s in Northeastern Italy. Currently, the breeding program for Simmental is well-established in Italy, but foreign bulls from countries such as Germany and Austria have been heavily used. The strength of IS lies in the fact that its breeding program has a selection index aimed at increasing both milk (44%) and meat (24%) production as well as morphology (19.5%) and fitness (12.5%). It is crucial for IS breeders to consider meat production as a breeding goal because of the value that animals have in the marketplace. Although milk and beef traits have a negative genetic correlation, it is possible to improve one set of traits without compromising the other.

Because of their economic relevance, it is clear that having accurate estimates of genetic parameters for beef traits is important for the breeding program of the Italian Simmental Breeders Association (**ANAPRI**). However, changes in selection goals over time and utilization of sires from several countries may have changed the genetic base of the IS population and affected its allele frequencies. Thus, it is important to understand how variance components may have changed from the beginning of the IS breeding program until now.

Estimation of variance components using data collected over a long period of time is challenging because the estimates of variance components may be influenced by a variety of factors. In particular, selection could have a strong effect on estimates of variance components over time. Under selection, variance components, heritabilities, and genetic correlations are subject to change, with the amount of change depending on the initial value of the genetic variance and selection intensity (Falconer and Mackay, 1996; Walsh and Lynch, 2018). Additionally, directional selection creates negative linkage disequilibrium (**LD**) introducing a negative correlation between pairs of loci, which decreases genetic variance, heritability, and selection response. The directional selection leads to an increase in the frequency of favorable alleles and to a decrease of unfavorable ones. With that, the frequency of heterozygous genotypes may also increase. As those heterozygous genotypes have both favorable and unfavorable alleles, the increase in their frequency is associated to a negative covariance (i.e., negative LD) and to a reduction in the genetic variance (Silvela et al., 1999). Therefore, the intermediate genotypes (heterozygous) may be more abundant than the extreme ones (homozygous). Conversely, disruptive selection generates positive LD, introducing a positive correlation between pairs of loci (Bulmer, 1971; Walsh and Lynch, 2018).

Breeding programs rely on accurate variance components estimates that should reflect the current state of the population, especially when the objective is to accurately identify young candidates for selection. Selection accuracy is crucial to realize predicted genetic gains and ignoring the reduction in genetic variance under directional selection leads to an overestimation of selection accuracy (Bijma, 2012; Gorjanc et al., 2015). With the worldwide adoption of genomic selection, the generation interval in livestock populations has decreased considerably, which, in turn, has increased the rate of change of genetic parameters. Lower genetic standard deviations were observed for variance components estimated using genotypes in single-step genomic average information restricted maximum likelihood (**ssG_AIREML**) compared with other approaches (Forni et al., 2011; Veerkamp et al., 2011). Cesarani et al. (2020) found similar results between average information restricted maximum likelihood (AIREML) and ssG_AIREML, with lower standard deviations in the latter, when estimating variance components for two dairy functional traits in IS. Hidalgo et al. (2020) indicated that a strong selection reduced heritabilities and emphasized the antagonistic genetic relationships between fitness and growth traits in a pig population under genomic selection. A reduction in inflation of dairy type trais genomic estimated breeding values (**GEBV**) for young bulls was observed when heritability was halved, likely because the original variance components used for evaluation differed from the parameters in the most recent population (Tsuruta et al., 2019).

Variance components and genetic parameters for beef traits that appropriately represent the current structure of the IS population are required to achieve a high degree of accuracy of selection. Thus, the aim of this study was to investigate the changes in variance components and genetic parameters for beef traits over time to identify a subset of data from the IS population that would yield the most appropriate estimates of genetic parameters and breeding values to select young bulls.

Materials and Methods

Animal Care and Use Committee approval was not needed as data were obtained from preexisting databases.

IS data

Approximately 200 steer progeny from the best sires and dams in the IS population are chosen every year, based on a traditional pedigree selection index, for a performance test (**PT**) operated by ANAPRI in its control herd (Fiume Veneto, PN, Italy). Steers selected for the PT must come from herds that follow animal health rules defined by ANAPRI, such as absence of brucellosis. Prior to PT, animals must be quarantined in a specific barn far away from the test center and tested for various diseases (e.g., bovine rhino-tracheitis, bovine rhino-tracheitis; viral diarrhea, viral diarrhea). Steers are raised in pens of four to six animals until weaning at about 4 mo of age. The PT begins after an adaptation period of about 30 d, when animals are 5 mo old, and it ends when the animals reach 12 mo of age. During the test, steers are raised in multiple pens (six individuals each), and they are weighted every 6 wk to assess average daily gains (**ADG**). During the last weighting stage, height at withers and sacrum, depth and circumference of the chest, length of back, width of back, circumference of the anterior tibia, and skin thickness are also recorded. A performance test beef index (**PTI**) is calculated by using multiple-trait genetic predictions for ADG, body size (**BS**), muscularity (**MUS**), and feet and legs (**FL**). The PTI is standardized with mean 100 and standard deviation 12, and each trait has a different weight: ADG (40%), BS (10%), MUS (40%), and FL (10%). The ADG is expressed in kg/d, whereas the other three traits (i.e., BS, MUS, and FL) are assessed using scores from 1 to 9 (with high values indicating better morphology) given by three expert technicians from ANAPRI. The three values received by each animal are then averaged, and the average values are transformed into a more user-friendly scale, which goes from 68 to 93, before the analyses. Therefore, the scale from 68 to 93 was used in this study for the variance components and for GEBV estimation. After each PT, animals are ranked based on the PTI, and the top 15% (20 to 30 bulls per year) are used for artificial insemination, the top 16% to 25% are used for natural service, and the remaining 60% are harvested.

This study used information from PT conducted between 1986 and 2017. The complete dataset (**ALL**) was divided into four nonoverlapping generation intervals (**Gen1**, 1986 to 1993; **Gen2**, 1994 to 2001; **Gen3**, 2002 to 2009; and **Gen4**, 2010 to 2017) based on an assumed generation interval of 7 yr. The data subsets of the last two generations (Gen3 and Gen4) were merged to consider only animals actively contributing to the current population and is referred to as current data (**CUR**, 2002 to 2017). Similarly, the data subsets of the first two generations (Gen1 and Gen2) were combined into a starting population and it was referred to as old data (**OLD**, 1986 to 2001). Table 1 shows the number of records, pedigree animals, and genotypes used in each data subset and the complete dataset.

Model and analyses

Variance components were estimated using a four-trait animal model as follows:

$$\begin{bmatrix} y_{ADG} \\ y_{BS} \\ y_{MUS} \\ y_{FL} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{ADG} & 0 & 0 & 0 \\ 0 & \mathbf{X}_{BS} & 0 & 0 \\ 0 & 0 & \mathbf{X}_{MUS} & 0 \\ 0 & 0 & 0 & \mathbf{X}_{FL} \end{bmatrix} \begin{bmatrix} b_{ADG} \\ b_{BS} \\ b_{MUS} \\ b_{FL} \end{bmatrix} + \begin{bmatrix} Z_{ADG} & 0 & 0 & 0 \\ 0 & Z_{BS} & 0 & 0 \\ 0 & 0 & Z_{MUS} & 0 \\ 0 & 0 & 0 & Z_{FL} \end{bmatrix} \begin{bmatrix} u_{ADG} \\ u_{BS} \\ u_{MUS} \\ u_{FL} \end{bmatrix} + \begin{bmatrix} e_{ADG} \\ e_{BS} \\ e_{MUS} \\ e_{FL} \end{bmatrix}$$

where ADG, BS, MUS, and FL stand for ADG, body size, muscularity, and feet and legs, respectively; ***y*** is the vector of observations; ***b*** is a vector of contemporary group (year and month of birth and pen), age at recording (mo), litter size (1 or 2), and parity fixed effects; ***u*** is the vector of additive direct genetic animal effects; **X** and **Z** are incidence matrices relating elements of ***y*** to elements of ***b*** and ***u***, respectively; and ***e*** is a vector of random residuals. The single-step approach (Aguilar et al., 2010) was used to solve the mixed model equations. The covariance matrix for vector *u* is $\mathbf{H} \otimes \mathrm{V_a}$, where **H** is a matrix that accounts for pedigree and genomic relationships among animals in vector *u*; $\mathrm{V_a}$ is a 4 × 4 matrix of additive direct genetic variances and covariances among ADG, BS, MUS, and FL; and $\otimes$ is the Kronecker product. Aguilar et al. (2010) showed that the inverse of **H** ($\mathbf{H}^{-1}$) needed to construct the mixed model equations has the following form:

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}$$

where $\mathbf{A}^{-1}$ is the inverse of the pedigree relationship matrix, $\mathbf{A}_{22}^{-1}$ is the inverse of the pedigree relationship matrix among genotyped animals, and $\mathbf{G}^{-1}$ is the inverse of the genomic relationship matrix. VanRaden (2008) suggested computing $\mathbf{G}^{-1}$ as follows:

$$\mathbf{G} = 0.95 \frac{\mathbf{MM}'}{2\sum p_j(1-p_j)} + 0.05 \quad \mathrm{A}_{22}$$

where **M** is a matrix of gene contents, and p_j is the allele frequency of SNP *j*. The blending of 95% of $\frac{\mathbf{MM}'}{2\sum p_j(1-p_j)}$ with 5% of A_{22} was used to avoid singularity problems.

The covariance matrix for vector ***e*** is equal to $\mathrm{I} \otimes \mathrm{V_e}$, where I is an identity matrix, and $\mathrm{V_e}$ is a 4 × 4 matrix of variances and covariances among residuals for ADG, BS, MUS, and FL.

Variance components and GEBV were computed using the AIREML algorithm implemented in AIREMLF90 (BLUPF90 family of programs; Misztal et al., 2014), which uses the YAMS package (Masuda et al., 2015) for more efficient computations of sparse operations in multi-trait models utilizing genomic information. Program AIREMLF90 was also used to compute heritabilities, genetic correlations, and their corresponding standard errors. Standard errors of heritabilities and genetic correlations were obtained using the repeated sampling procedure (Meyer and Houle, 2013) implemented in AIREMLF90. Lastly, correlations between GEBV for all pairwise trait combinations were also computed.

Validation

Two statistics based on the Linear Regression (**LR**) method (Legarra and Reverter, 2018) were used for validation, namely the correlation coefficient (*r*) and the regression coefficient (b_1). In the LR method, GEBV computed using the complete dataset (**GEBVw**) were compared with GEBV computed with a partial

Table 1. Number of records, pedigree animals, and genotypes for all datasets

Dataset[1]	Records	Pedigree[2]	Genotypes
Gen1	1,310	6,321	184
Gen2	1,545	7,414	440
Gen3	1,821	8,503	801
Gen4	1,805	7,700	2,831
OLD	2,855	11,327	517
CUR	3,626	13,228	3,091
ALL	6,481	21,344	3,201

[1] Gen1, 1986 to 1993; Gen2, 1994 to 2001; Gen3, 2002 to 2009; Gen4, 2010 to 2017; OLD, 1986 to 2001; CUR, 2002 to 2017; ALL, 1986 to 2017.

[2] Pedigree included animals with phenotypes and/or genotypes and ancestors from five generations.

dataset that excluded phenotypes of selection candidates and their contemporaries (**GEBVp**). The complete dataset comprised phenotypes from 1986 to 2017, whereas the partial dataset contained phenotypes from 1986 to 2016. The correlation between GEBVw and GEBVp and the regression coefficient of GEBVw on GEBVp were obtained using 196 validation animals that had phenotypes in the complete dataset but not in the partial dataset. The validation was performed for scenarios where variance components were estimated using OLD, CUR, and ALL datasets. A greater correlation between GEBVw and GEBVp indicates a higher predictive ability of the partial dataset. The regression coefficient of GEBVw on GEBVp was used as a measure of bias for genomic predictions because a value lower than 1 means inflation of GEBV, whereas a value greater than 1 indicates deflation of GEBV.

Results and Discussion

Phenotypic means, standard deviations, maximum, and minimum values for Gen1, Gen2, Gen3, and Gen4 data subsets are shown in Table 2. Mean ADG changed from 1.29 ± 0.06 kg/d in Gen1 to 1.5 ± 0.09 kg/d in Gen4, with a net gain of about 0.21 kg/d. Lower values for ADG (0.98 ± 0.16 kg/d) were reported for Mongolian Simmental cattle born between 2008 and 2013 (Zhang et al., 2016), whereas higher values were reported for Simmental bulls (1.8 ± 0.3 kg/d) and similar for heifers (1.2 ± 0.4 kg/d) in Ireland (McKenna et al., 2018). From Gen1 to Gen4, FL and MUS decreased to 0.8, whereas BS decreased to 0.6. During this period, bulls selected by ANAPRI became slightly smaller but had higher ADG. This increase in ADG indicated that farmers breeding efforts were aimed at having animals with higher daily gains. However, the BS of animals decreased during this time. All traits showed the largest standard deviation in the last generation, possibly a consequence of genetic selection. Animals with higher genetic merit expressed better performance, whereas the lower merit ones showed worse performance, which increased the distance between these two groups. It is worth noting that the top 40% of animals based their EBV for PT traits are selected to be breeders (artificial insemination and natural service), and the bottom 60% of animals are harvested.

Additive genetic and residual variances, as well as heritabilities estimated with subsets of data over time (Gen1, Gen2, Gen3, Gen4, OLD, and CUR) and with ALL, are shown in Table 3. Heritabilities ± SE for the four traits computed using the complete dataset (1986 to 2017) were 0.26 ± 0.03 (ADG), 0.33 ± 0.04 (BS), 0.55 ± 0.03 (MUS), and 0.23 ± 0.03 (FL). The same estimate of heritability for ADG (0.26) was reported by Rolfe et al. (2011) for mixed-breed steers. Greater values (0.47) were found by Bonfatti et al. (2013) for daily body weight gain (g/d) in Piedmontese cattle. In our study, heritability estimates were not stable over time. The heritability for ADG and BS decreased by 0.21 and 0.27, respectively, between Gen1 and Gen4. Conversely, an increase was observed for MUS (+0.18) and FL (+0.01) during this period. Heritabilities for BS progressively decreased from Gen1 to Gen4, whereas heritabilities for ADG decreased from Gen1 to Gen3, and slightly increased in Gen4. Heritabilities for MUS and FL oscillated across generations because of the changes in additive genetic and residual variances over time. Additive genetic variances decreased for ADG (5.33 to 3.91 [kg/d]^2) and BS (6.36 to 1.96 [units]^2), but they increased for MUS (3.72 to 5.73 [units]^2) and FL (0.89 to 0.93 [units]^2) from Gen1 to Gen4. Conversely, residual variance increased for ADG (7.42 to 14.22 [kg/d]^2) and BS (7.00 to

Table 2. Phenotypic means, standard deviations, maximum, and minimum values for the Gen1, Gen2, Gen3, and Gen4 datasets

Dataset[1]	Trait2	Mean	SD	Min.	Max.
Gen1	ADG	1.29	0.06	1.20	1.40
	BS	5.93	0.17	5.61	6.21
	MUS	5.95	0.14	5.77	6.15
	FL	5.45	0.08	5.34	5.59
Gen2	ADG	1.32	0.04	1.25	1.37
	BS	5.85	0.25	5.54	6.27
	MUS	5.64	0.24	5.29	5.96
	FL	5.11	0.16	4.76	5.52
Gen3	ADG	1.32	0.06	1.26	1.42
	BS	5.76	0.30	5.24	6.03
	MUS	5.58	0.29	5.01	6.15
	FL	5.07	0.22	4.75	5.25
Gen4	ADG	1.50	0.09	1.27	1.59
	BS	5.34	0.37	4.75	5.89
	MUS	5.13	0.40	4.71	5.42
	FL	4.64	0.33	3.98	4.94

[1]Gen1, 1986 to 1993; Gen2, 1994 to 2001; Gen3, 2002 to 2009; Gen4, 2010 to 2017.
[2]ADG expressed in kg/d; and BS, MUS, and FL expressed in units. The three subjective traits (BS, MUS, and FL) were scored on a numeric scale, with units from 1= very bad to 9 = excellent, and transformed into a more user-friendly scale (68 to 93).

Table 3. Additive genetic variances, residual variances, and heritabilities and SE for all datasets

Dataset[1]	Trait	Additive genetic variance[2]	Residual variance[2]	Heritability
Gen1	ADG	5.33 ± 1.37	7.42 ± 1.10	0.42 ± 0.10
	BS	6.36 ± 1.63	7.00 ± 1.27	0.47 ± 0.11
	MUS	3.72 ± 1.06	6.93 ± 0.89	0.35 ± 0.09
	FL	0.89 ± 0.44	6.39 ± 0.46	0.12 ± 0.06
Gen2	ADG	2.88 ± 0.93	7.49 ± 0.78	0.28 ± 0.08
	BS	4.27 ± 1.27	8.23 ± 1.02	0.34 ± 0.09
	MUS	6.52 ± 1.11	2.71 ± 0.79	0.70 ± 0.09
	FL	2.68 ± 0.68	4.34 ± 0.54	0.38 ± 0.09
Gen3	ADG	2.60 ± 0.92	11.22 ± 0.87	0.19 ± 0.06
	BS	4.45 ± 1.31	11.32 ± 1.13	0.28 ± 0.08
	MUS	6.67 ± 1.19	5.22 ± 0.89	0.56 ± 0.08
	FL	1.87 ± 0.65	7.40 ± 0.61	0.20 ± 0.06
Gen4	ADG	3.91 ± 1.21	14.22 ± 1.14	0.21 ± 0.06
	BS	1.96 ± 0.67	7.79 ± 0.64	0.20 ± 0.07
	MUS	5.73 ± 0.89	5.07 ± 0.65	0.53 ± 0.07
	FL	0.93 ± 0.44	6.07 ± 0.45	0.13 ± 0.06
OLD	ADG	4.16 ± 0.77	7.36 ± 0.62	0.36 ± 0.06
	BS	4.93 ± 0.96	8.00 ± 0.75	0.38 ± 0.06
	MUS	5.69 ± 0.78	4.24 ± 0.57	0.57 ± 0.07
	FL	1.84 ± 0.38	1.42 ± 0.33	0.28 ± 0.06
CUR	ADG	3.21 ± 0.71	12.64 ± 0.66	0.20 ± 0.04
	BS	3.21 ± 0.67	9.68 ± 0.58	0.25 ± 0.05
	MUS	5.96 ± 0.68	5.22 ± 0.49	0.53 ± 0.05
	FL	1.81 ± 0.40	6.48 ± 0.36	0.22 ± 0.04
ALL	ADG	3.48 ± 0.50	10.27 ± 0.43	0.26 ± 0.03
	BS	4.30 ± 0.57	8.65 ± 0.45	0.33 ± 0.04
	MUS	5.84 ± 0.49	4.72 ± 0.35	0.55 ± 0.03
	FL	1.77 ± 0.26	5.91 ± 0.23	0.23 ± 0.03

[1]Gen1, 1986 to 1993; Gen2, 1994 to 2001; Gen3, 2002 to 2009; Gen4, 2010 to 2017; OLD, 1986 to 2001; CUR, 2002 to 2017; ALL, 1986 to 2017.
[2]Additive genetic and residual variances expressed in (kg/d)^2 for ADG and in (units)^2 for BS, MUS, and FL.

7.79 [units]^2) and decreased for MUS (6.93 to 5.07 [units]^2) and FL (6.39 to 6.07 [units]^2) from Gen1 to Gen4. Fluctuations in genetic variances could be explained by selection pressure on favorable, but rare alleles. The frequency of these alleles would increase with selection causing an increase in genetic variance during this time (Walsh and Lynch, 2018). Positive assortative mating could also increase additive genetic variance by increasing homozygosity in loci related to similarities among individuals (Falconer and Mackay, 1996; Johnston et al., 2019).

When data from Gen1 and Gen2 (OLD) were used to estimate genetic parameters, which mimics a situation where variance components were estimated a long time ago but are still used in the evaluation system, heritabilities were higher than heritabilities computed with data from Gen3 and Gen4 (CUR) for all traits. On average, heritabilities in CUR were 33% lower than in OLD, with the largest differences for ADG (0.16) and BS (0.13). These differences could be due to the smaller amounts of data in OLD than in CUR, which resulted in greater SE and, consequently, lower accuracies of estimation of variance components and heritabilities. Additionally, the old data may not appropriately reflect the selection that occurred recently in the population. Estimates of heritability from ALL were also higher (on average 3%) than heritability estimates from CUR for all traits. Residual variances from ALL were lower than residual variances from CUR for all traits, whereas additive genetic variances from ALL were higher than those from CUR for all traits except MUS.

Heritability estimates from either ALL or CUR were slightly lower than those from Gen4 for ADG, BS, and FL, but higher for MUS. As expected, heritability estimates from ALL and CUR yielded the smallest standard errors because they had the largest amounts of data.

Holm et al. (2004) reported identical heritability estimates for the number of piglets born alive in the first and second parities (0.10 ± 0.01) in a pig population under selection. van Pelt et al. (2016) reported that genetic and residual variances and heritability for survival in dairy cattle decreased over time; however, the mean survival increased. In another study, the heritabilities for a productive life in dairy cattle (Tsuruta et al., 2004) remained unchanged over time, likely because of the lack of directional selection for this trait, as evidenced by genetic trends. Haile-Mariam and Pryce (2015) reported a reduction in heritabilities for survival from 0.07 (1993–1994) to 0.03 (2007–2008) and for calving interval from 0.06 (1993–1994) to 0.03 (2007–2008). These authors stated that the decrease in heritability for calving interval was related to a reduction in the genetic variance and an increase in the residual variance. A similar pattern existed for ADG in our study. Hidalgo et al. (2020) found a reduction in heritabilities for a trait related to litter survival from 0.11 (2009 to 2011) to 0.8 (2015 to 2018) and for a growth trait from 0.36 (2009 to 2011) to 0.17 (2015 to 2018) in a swine genomic selection study. These lower heritabilities were associated with decreases in additive genetic variances and increases in residual variances. Hidalgo et al. (2020) also reported stable heritabilities over time for a trait related to prolificacy and for a second trait related to piglet survival. Under the infinitesimal model and assuming an infinite population size, Bulmer (1971) showed that with repeated cycles of selection, an equilibrium is eventually achieved where the genetic variance lost by selection is regenerated by recombination. Yang and Su (2016) reported that, given a fixed number of generations in the pedigree, estimated additive genetic variances increased as the number of generations with phenotypic data increased. They also indicated that the impact of the number of generations was smaller for the trait with lower selection pressure.

The body traits considered in this study (BS, MUS, and FL) are subjective. Although ANAPRI used scores from three different experts and took the average value of the three scores, a certain degree of bias could still have affected these traits. Additionally, the experts evaluating the selection candidates from 1986 to 2017 were not always the same, which could be responsible for extra fluctuations in the phenotypic and genetic trends (not shown). Changes in means for BS, MUS, and FL over time could also be caused by changes in the breed composition of the IS population. Until 1996, the IS population was mainly derived from a Bavarian (German) lineage, which is known for slower growth. From 1996 to 2011, there was a great contribution of Montbéliarde dairy bulls to the IS population, which generated smaller, lighter animals. Starting in 2012, the contribution of Montbéliarde bulls was markedly reduced and IS animals started to show higher ADG.

Tsuruta et al. (2005) studied the effect of changing the definition of productive life on genetic correlations in the U.S. Holstein. Productive life was defined as the total number of days in milk up to 84 mo of age with a restriction of 305, 500, or 999 d per lactation. As the maximum recordable productive life increased from 305 to 999 d per lactation, the genetic correlation with milk production increased from −0.11 to +0.14 and from −0.62 to −0.27 with days open. Their results show that management changes and trait definitions could play an important role in the estimation of variance components and genetic correlations.

Genetic correlations ± SE and correlations between GEBV using four-trait genomic models for all datasets are shown in Table 4. Genetic correlations tended to decrease from Gen1 to Gen4. However, their SE were very high, sometimes even higher than the genetic correlation estimate. This may have been largely due to the small number of observations in each generation dataset. The genetic correlations between BS and MUS and between BS and FL changed from positive to negative across generational datasets, but their high SE indicated that these estimates may not be different from 0. Smaller SE were found for genetic correlations in the larger OLD and CUR datasets, perhaps due to higher numbers of observations. Overall, genetic correlations decreased when moving from OLD to CUR datasets. In particular, the correlation between ADG and BS decreased by 0.36 from OLD to CUR, which corresponds to a reduction of 54%, whereas the corresponding reduction in additive genetic variance was 23% for ADG and 35% for BS. The main causes of genetic correlation are pleiotropy and LD. Even when two traits are not controlled by the same genes, LD can create covariances through co-inheritance of alleles (Walsh and Lynch, 2018). According to Walsh and Lynch (2018), pleiotropy can be complementary when traits change in the same direction or antagonistic when traits change in the opposite direction. Under selection, the frequency of alleles with antagonistic effects increase, which decreases genetic covariances. In this way, changes in covariances are less predictable than changes in variances.

Genetic correlations based on ALL were greater than with CUR. Thus, if the objective is to have more reliable predictions for young selection candidates, using variance components from ALL to compute GEBV may overestimate selection indexes and create false expectations about genetic gains. With a few exceptions, correlations between GEBV were greater than genetic correlations, which was expected because breeding values were scaled up by relationships. Under assortative mating, the resemblance between individuals in the same family increases (Falconer and Mackay, 1996), which results in a more similar GEBV. This higher degree of genetic resemblance among individuals impacts genetic correlations to a lesser extent than correlations among GEBV. Increases in additive genetic variances under assortative mating are, however, outweighed by reductions in additive genetic variances (Bulmer effect) and covariances (antagonistic pleiotropy) in populations under artificial selection (Falconer and Mackay, 1996; Walsh and Lynch, 2018).

The changes in heritability and genetic correlation estimates across generational datasets indicated that the IS population was changing over time in response to artificial selection and changes in breed composition. This suggests that the current population (Gen4), from which the selection candidates are born and chosen from, is genetically different from the initial population (Gen1). Keeping old data when estimating variance components may result in genetic parameters that more closely resemble those from the base population than genetic parameters from the current population. Thus, including all available data when estimating variance components could lead to biases in GEBV for young selection candidates.

Validation of GEBV for ADG, BS, MUS, and FL using the r and b_1 statistics and variance components estimated with the OLD, CUR, and ALL datasets is presented in Table 5. Correlations between GEBVw and GEBVp and regressions of GEBVw on GEBVp utilized 196 validation animals. Correlations between GEBVw and GEBVp were stronger when variance components were from the CUR dataset. This indicated that the CUR dataset had the best predictive ability of the three datasets. In fact, correlations between GEBVw and GEBVp with CUR variance components were 8% and 3% greater than with OLD and ALL variance components, respectively. Overall, the least biased predictions were those computed with CUR variance components. In particular, BS had a b_1 of 0.92 with CUR variance components but a b_1 of 0.76 with OLD and ALL variance

Table 4. Genetic correlations ± SE and correlations between GEBV for all datasets using four-trait genomic models

		Genetic correlation			Correlation between GEBV		
Dataset[1]	Trait	BS	MUS	FL	BS	MUS	FL
Gen1	ADG	0.62 ± 0.13	0.65 ± 0.15	0.58 ± 0.33	0.67	0.69	0.69
	BS		0.27 ± 0.20	0.32 ± 0.38		0.23	0.33
	MUS			0.74 ± 0.35			0.87
	FL						
Gen2	ADG	0.60 ± 0.18	0.52 ± 0.15	0.58 ± 0.16	0.56	0.62	0.72
	BS		0.04 ± 0.17	0.35 ± 0.19		−0.05	0.27
	MUS			0.61 ± 0.11			0.77
	FL						
Gen3	ADG	0.33 ± 0.23	0.32 ± 0.18	0.33 ± 0.28	0.31	0.33	0.38
	BS		0.04 ± 0.17	−0.15±0.25		−0.04	−0.25
	MUS			0.59 ± 0.20			0.84
	FL						
Gen4	ADG	0.33 ± 0.27	0.45 ± 0.14	0.04 ± 0.39	0.07	0.60	0.20
	BS		−0.07 ± 0.20	−0.09 ± 0.54		−0.31	−0.30
	MUS			0.40 ± 0.29			0.61
	FL						
OLD	ADG	0.67 ± 0.08	0.55 ± 0.08	0.50 ± 0.10	0.72	0.57	0.60
	BS		0.23 ± 0.11	0.34 ± 0.13		0.19	0.33
	MUS			0.65 ± 0.08			0.82
	FL						
CUR	ADG	0.31 ± 0.13	0.38 ± 0.10	0.16 ± 0.13	0.22	0.46	0.28
	BS		−0.09 ± 0.10	−0.13 ± 0.16		−0.20	−0.31
	MUS			0.46 ± 0.10			0.69
	FL						
ALL	ADG	0.46 ± 0.08	0.45 ± 0.06	0.31 ± 0.10	0.46	0.48	0.45
	BS		−0.02 ± 0.07	0.09 ± 0.10		−0.07	0.04
	MUS			0.51 ± 0.06			0.70
	FL						

[1] Gen1, 1986 to 1993; Gen2, 1994 to 2001; Gen3, 2002 to 2009; Gen4, 2010 to 2017; OLD, 1986 to 2001; CUR, 2002 to 2017; ALL, 1986 to 2017.

Table 5. Validation of genomic EBV with two statistics and variance components estimated with OLD, CUR, and ALL datasets[1]

	OLD				CUR				ALL			
Statistic[2]	ADG	BS	MUS	FL	ADG	BS	MUS	FL	ADG	BS	MUS	FL
r	0.67	0.56	0.82	0.74	0.77	0.67	0.83	0.76	0.74	0.62	0.83	0.75
b_1	1.02	0.76	1.04	1.04	1.03	0.92	1.01	1.03	1.13	0.76	1.02	1.05

[1] OLD, 1986 to 2001; CUR, 2002 to 2017; ALL, 1986 to 2017.

[2] r, correlation coefficient between GEBV estimated with the complete dataset (1986 to 2017) and GEBV estimated with the partial dataset (1986 to 2016); b_1, regression coefficient of GEBV estimated with the complete dataset (1986 to 2017) on GEBV estimated with the partial dataset (1986 to 2016).

components. According to VanRaden et al. (2014), heritabilities for milk yield traits were reduced from about 0.3 to 0.2 in the U.S. Holstein, Jersey, and Brown Swiss to decrease biases in genomic evaluations. Misztal et al. (2017) also showed a reduction in bias when heritability for type traits decreased by 50%. When b_1 deviates from 1, the ability to correctly shrink GEBV for young animals is compromised, and, therefore, undesirable animals may be chosen as breeders. Having appropriate genetic parameters will result in more accurate GEBV as well as more appropriate selection decisions. Thus, to better identify young selection candidates in the IS population, current data should be used to estimate variance components.

To further investigate the impact of variance components on the estimation of breeding values, GEBV of animals with phenotypes in the OLD and CUR datasets were correlated with those in the ALL dataset (Table 6). The mean of the correlations between GEBV from OLD and ALL for the ADG, BS, MUS, and FL was 0.95 ± 0.02, whereas the corresponding mean of the correlation between GEBV from CUR and ALL was 0.97 ± 0.02. Correlations between GEBV from OLD and ALL and correlations between GEBV from CUR and ALL were similar for all traits. However, lower correlations between GEBV from smaller datasets (Gen1, Gen2, Gen3, and Gen4) and GEBV from ALL were obtained (data not shown). This probably occurred because variance components estimated within generations were less accurate (larger SE), which could cause some GEBV to be biased. The GEBV correlations indicate that the variance components estimated using the complete dataset may not be ideal to predict younger (Gen4) or older (Gen1) animals (results not shown). However, GEBV biases can be reduced by considering multiple generations together such as OLD and CUR in this study. If the final goal is to estimate accurate GEBV for young candidates, our results suggest that it is better to use all available phenotype and pedigree data (complete population) and variance components estimated in the population where young candidates come from (current population).

The study of genetic parameters over time is challenging because of changes in trait definitions, selection intensities, genetic bases, selection indexes, and types of mating. In particular, unaccounted changes in genetic parameters can lead to biased selection indexes that will negatively impact genetic gains (McMillan et al., 1995). Moreover, as observed in our study, changes in genetic covariances occur faster than those in the genetic variances (McMillan et al., 1995), which leads to strong changes in genetic correlations. Thus, GEBV from multiple-trait models will likely be more affected than GEBV from single-trait models when genetic variances and covariances change over time. The effects of single and/or multiple trait selection on the genetic correlation have been investigated in many studies. Villanueva and Kennedy (1990) reported that the absolute value of the genetic correlation between directly and indirectly selected traits always decreases. On the other hand, the absolute value of the genetic correlation between two traits not under direct selection can either increase or decrease according to the sign and magnitude of the genetic correlation and the heritabilities of the two traits. Strandén et al. (1993) analyzing a simulated dataset under directional selection reported that the absolute value of the genetic correlation tended to decrease with single-trait selection. However, when the starting genetic correlation was low and the associated residual correlation had a concordant sign, the genetic correlation tended to increase. When both traits were selected, the change in the genetic correlation was always negative, and, therefore, the selection made the traits less positively correlated.

Hidalgo et al. (2020) reported that negative genetic correlations among fitness and growth traits became more negative over time in swine undergoing genomic selection for these traits. The genetic correlations changed from −0.32 (2009 to 2011) to −0.50 (2015 to 2018) between a fitness trait related to prolificacy and a growth trait, and from −0.28 (2009 to 2011) to −0.45 (2015 to 2018) between a fitness trait related to litter survival and a growth trait. The correlation between a second trait related to litter survival and a growth trait which initially was positive and low remained stable over time changing from 0.14 (2009 to 2011) to 0.18 (2015 to 2018). These authors indicated that LD between these two traits could be the reason for the stability of their genetic correlation over time. In our study, the genetic correlation between BS and FL changed from positive to negative, or zero considering the high SE, when moving from old to current data. The same trend was observed by Tsuruta et al. (2004) when computing genetic correlations between productive life and fat yield in the U.S. Holstein over several years; correlations dropped from 0.21 in 1983 to −0.08 in 1993. These authors concluded that if the changes in the genetic correlation are gradual, they can be estimated using a random regression model.

Table 6. Correlations between genomic EBV from OLD and ALL and from CUR and ALL datasets

Trait	OLD and ALL[1]	CUR and ALL
n^2	2,855	3,626
ADG	0.94	0.95
BS	0.93	0.96
MUS	0.97	0.99
FL	0.96	0.97
Mean ± SD	0.95 ± 0.02	0.97 ± 0.02

[1] OLD, 1986 to 2001; CUR, 2002 to 2017; ALL, 1986 to 2017.
[2] *n*, number of animals in common.

Conclusions

This study reinforces the importance of accounting for changes in genetic parameters over time and the need to regularly update the estimates of variance components to avoid biases in genetic correlations and, consequently, in breeding values from multi-trait models. This is supported by the fact that covariances are more sensitive to selection than variances. Less than optimal variance components and breeding values could lead to inaccurate selection indexes and incorrect expectations of genetic gains. When the objective is to accurately estimate breeding values for young selection candidates, keeping data from old generations to estimate variance components should be avoided. Validation results indicated that data from the last 10 to 15 yr in the IS population would produce genetic parameters that more appropriately represent the structure of the current population, yielding accurate GEBV to select young animals and increasing the likelihood of higher genetic gains.

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Conflict of interest statement

The authors declare no conflicts of interest.

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