


# Wagyu Feeder Check: A genomic-based tool to identify performance differences of Australian Wagyu and Wagyu crossed cattle

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## ABSTRACT

**Context.** Wagyu Feeder Check is a genomic-based tool designed to provide genomic estimated breeding values (GEBV) for five feedlot growth and carcass traits. At present, Wagyu Feeder Check is based on a reference population of 8316 genotyped and phenotyped Australian fullblood (FB;  $N = 2120$ ) Wagyu and Wagyu-crossed (XB;  $N = 6196$ ) cattle, principally Wagyu  $\times$  Angus F1 animals. **Aims.** We provide technical details behind the development of the Wagyu Feeder Check and validate the ability of its GEBV to predict differences in performance of Wagyu cattle in daily weight gain at feedlot, carcass weight, carcass eye muscle area, carcass marbling score and carcass rump fat at the P8 site. **Methods.** Data supplied from eight commercial supply chains across Australia was used to generate GEBV using mixed-model equations that incorporated a genomic relationship matrix build with 82504 autosomal markers. The bias, dispersion, and accuracy of the GEBV were evaluated using a four-way cross-validation scheme where, in each turn, the phenotypes from a random 1549 (or 25%) XB cattle were set as missing. **Key results.** The genomic estimate of the Wagyu content in the FB and XB population averaged 99.12% and 59.55%, respectively, and with most of the non-Wagyu content associated with Angus. The estimates of heritability ( $\pm$  s.e.) were  $0.497 \pm 0.016$ ,  $0.474 \pm 0.004$ ,  $0.347 \pm 0.014$ ,  $0.429 \pm 0.003$  and  $0.422 \pm 0.003$  for daily weight gain at feedlot, carcass weight, eye muscle area, marbling and rump fat, respectively. Averaged across the four XB validation populations, the accuracy of GEBV was 0.624, 0.634, 0.385, 0.620, and 0.526 for the same set of traits. **Conclusions.** Genomic predictions generated by Wagyu Feeder Check can predict differences in feedlot and carcass performance of Australian Wagyu cattle. Given the large content of Angus in the XB population, further research is required to determine the predictive ability of GEBV in Wagyu  $\times$  *Bos indicus* and Wagyu  $\times$  dairy animals. **Implications.** Commercial feedlot operators finishing animals with a strong Wagyu breed component will benefit from using Wagyu Feeder Check for decision making.

**Keywords:** accuracy, beef cattle, bias, carcass, feedlot, genomic predictions, heritability, marbling.

## Introduction

Building on a long line of research mapping phenotypes to genotypes, genomic technologies have changed and may continue to change animal breeding (Johnsson 2023). Nowadays, genomic-based technologies are allowing commercial beef producers to predict the genetic merit of individual animals in their herds of unknown pedigree for the first time (Reverter *et al.* 2016; Hine *et al.* 2021; Alexandre *et al.* 2022).

Specifically for the Australian beef cattle industry, recent examples of such genomic tools include the Angus HeiferSELECT (Alexandre *et al.* 2022) and the Angus SteerSELECT (Hine *et al.* 2021). The former has been validated using historical data from 153978 registered Angus animals; the latter has been validated using a population of 522 short-fed (100 days) or long-fed (270 days) Angus steers finished in commercial feedlots. Also, for SteerSELECT

the potential benefit of incorporating commercial data in the reference population has been evaluated (Reverter *et al.* 2023).

Expanding on the premises of that prior work, Wagyu Feeder Check is a genomic-based tool designed with the express purpose of providing genomic estimated breeding values (GEBV) for five traits related to feedlot growth and carcass characteristics. The Wagyu Feeder Check tool was launched in April 2023 during the WagyuEdge23 Conference. Practical aspects and details about how producers can benefit from using Wagyu Feeder Check can be found online from the Australian Wagyu Association website: <https://www.wagyu.org.au/for-members/wagyu-feeder-check>. At present, Wagyu Feeder Check is based on a reference population of 8316 genotyped and phenotyped Australian Wagyu fullblood and Wagyu-crossed cattle, principally Wagyu × Angus F1 animals.

A recent study by Takeda *et al.* (2021) with a Japanese Black cattle population showed that, for carcass traits, a total of 7000–11 000 animals is a sufficient reference population size for genomic prediction. In this sense, previous studies have explored the benefits of expanding the reference population, for instance, incorporating multiple breeds in the context of crossbreeding programs and for the selection of purebreds for optimal crossbred performance (Porto-Neto *et al.* 2015; van Grevenhof and van der Werf 2015; Karaman *et al.* 2021).

Therefore, in addition to providing the technical details behind the development of the Wagyu Feeder Check genomic tool, our aim for this study is to undertake a comprehensive internal cross-validation to ascertain the quality of Wagyu Feeder Check GEBV in the crossbred population.

## Materials and methods

### Wagyu fullblood (FB) and crossbred (XB) population details

The Wagyu Feeder Check is based on a reference population of 8316 genotyped and phenotyped Australian fullblood Wagyu (FB,  $N = 2120$ ) and Wagyu-crossed (XB,  $N = 6196$ ) cattle, principally Wagyu × Angus F1 animals. Feedlot and carcass records were supplied by independent commercial supply chains from eight populations including three FB populations (POP1,  $N = 1455$ ; POP2,  $N = 477$ ; and POP3,  $N = 188$ ) and five XB populations (POP4,  $N = 1049$ ; POP5,  $N = 1285$ ; POP6,  $N = 2456$ ; POP7,  $N = 654$ ; and POP8,  $N = 752$ ). Animals were slaughtered from 2013 to 2022, with XB animals slaughtered only in 2021 ( $N = 2098$ ) and 2022 ( $N = 4098$ ). Phenotypes included daily gain at feedlot finishing (FADG), carcass weight (CWT), carcass eye muscle area (CEMA), carcass AUS-MEAT marbling score (MARB) and carcass rump fat at the P8 site (CP8). To accommodate high marbling content, MARB was measured using a modified

AUS-MEAT scoring system (AUS-MEAT 2005), which ranges from 1 (nil) to 12 (abundant) in increments of 1.

For the analysis of phenotypes, a contemporary group (CG) was defined as a combination of population of origin (eight levels combining feedlot and abattoir), sex (two levels), and kill date. There were 71 and 13 kill dates for the FB and XB populations, respectively. For the FB populations all months were represented, whereas for the XB population all months were represented except for December and January. Initial edits aimed at removing animals without genotypes or from CG with less than three individuals. For the FB population, there were 82 CG with an average of 25.8 cattle and ranging from 3 to 145. For the XB population, there were 29 CG with an average of 213.6 cattle and ranging from 8 to 576.

### Genotypes and genomic relationships

Genotypes for 82 504 autosomal single nucleotide polymorphisms (SNP) were available for all 8316 animals included in this study and used to compute the genomic relationship matrix (GRM) following Method 1 of VanRaden (2008) with the modification of Karoui *et al.* (2012) to make it invertible:

$$\text{GRM} = 0.95 \cdot \frac{\mathbf{S}\mathbf{S}^T}{2 \sum p_i(1 - p_i)} + 0.05 \cdot \mathbf{I},$$

where  $\mathbf{S}$  is the centred matrix relating SNP genotypes (recoded as 0, 1 or 2) in columns with animals in rows, and  $p_i$  is the frequency of the second allele of the  $i$ -th SNP, and  $\mathbf{I}$  is an identity matrix included to make GRM invertible by enlarging the diagonal elements.

To obtain a measure of the genomic similarity between the two populations, FB and XB, we explored the SNP allele frequencies, the values of the GRM and performed a principal components analysis (PCA) based on a singular value decomposition of the GRM (Misztal and Legarra 2017). Additionally, using a smaller panel of 27 883 SNPs and numerical approaches outlined in Reverter *et al.* (2020) we estimated the genomic breed composition of FB and XB cattle across 10 breeds including: Wagyu, Angus, Brahman, Charolais, Hereford, Holstein, Limousin, Santa Gertrudis, Shorthorn and Simmental.

Finally, the genomic relationships among all individuals were processed following the network-based Pedigromics pipeline (Reverter *et al.* 2019) by establishing network connections after considering genomic relationships  $\geq 0.125$  corresponding to the equivalent of a great-grandparent to great-grand offspring relationship.

### Genomic predictions and cross-validation accuracy

Variance components, heritability ( $h^2$ ), genetic ( $r_g$ ) and residual ( $r_e$ ) correlations were estimated based on GBLUP

methodology (genomic best linear unbiased prediction) using the Qxpk5 software (Pérez-Enciso and Misztal 2011). For the genomic prediction models, we carried out GBLUP analyses including one pentivariate analysis with the entire dataset to produce the most accurate genomic predictions to use as reference; and a series of 20 univariate analyses from the cross-validation datasets (with 20 from five traits by four validation groups). In all cases, the GBLUP models contained the fixed effects of CG and the linear regression covariates of slaughter age (in days), and the first three principal components of the GRM. Fitting the principal components aims at accounting for hidden population structures, likely with FB and XB populations, that could have been missed if only fitting CG. Additionally, the random additive polygenic and residual effects were fitted in the GBLUP models with assumed distributions  $N(\mathbf{0}, \mathbf{G} \otimes \mathbf{V})$  and  $N(\mathbf{0}, \mathbf{I} \otimes \mathbf{R})$ , respectively, where  $\mathbf{G}$  represents the GRM described earlier,  $\mathbf{V}$  is the genetic covariance matrix,  $\mathbf{I}$  is an identity matrix,  $\mathbf{R}$  is the residual variance–covariance matrix and  $\otimes$  represents the Kronecker product.

Firstly, the resulting GEBV from the pentivariate analysis were termed  $\hat{\mathbf{u}}_w$  to indicate that they are based on the *whole* dataset. Secondly, for the cross-validation of genomic predictions, we created four cross-validation datasets each with the phenotypes from a random 1549 (or 25%) XB cattle set as missing. In each cross-validation schema, the resulting GEBV were termed  $\hat{\mathbf{u}}_p$  to indicate that they are based on *partial* data.

Finally, traditional (Bolormaa *et al.* 2013) and LR method (Legarra and Reverter 2018) approaches were used to estimate accuracy, bias, and dispersion of GEBV. The following four metrics were employed:

1. *Traditional Accuracy* ( $ACC_T$ ): In the context of cross-validation, the accuracy of a GEBV is traditionally computed from the Pearson correlation between a GEBV and the adjusted phenotype ( $y^*$ ; phenotype  $y$  adjusted for fixed effects) for individuals in the validation population, and divided by the square root of heritability:

$$ACC_T = \frac{r(\hat{\mathbf{u}}_p, y^*)}{\sqrt{h^2}}$$

2. *Method LR Accuracy* ( $ACC_{LR}$ ): For individuals in the validation population, Method LR accuracy was computed as follows:

$$ACC_{LR} = \sqrt{\frac{\text{cov}(\hat{\mathbf{u}}_w, \hat{\mathbf{u}}_p)}{(1 + \bar{F} - 2\bar{f})\sigma_{g,\infty}^2}},$$

where  $\bar{F}$  is the average inbreeding coefficient obtained by subtracting one from the diagonal elements of  $\mathbf{G}$ ,  $2\bar{f}$  is the average relationship between individuals obtained from the off-diagonal elements of  $\mathbf{G}$ , and  $\sigma_{g,\infty}^2$  is the genetic variance at equilibrium in a population under selection.

Assuming the individuals in the validation population are not under selection,  $\sigma_{g,\infty}^2$  can be approximated by the additive genetic variance estimated from the partial dataset.

3. *Method LR Bias* ( $Bias_{LR}$ ): This is the difference between the average GEBV of individuals in the validation population using the partial data minus that using the whole data:

$$Bias_{LR} = \bar{\hat{\mathbf{u}}}_p - \bar{\hat{\mathbf{u}}}_w$$

In the absence of bias, the expected value of  $Bias_{LR}$  is 0; positive and negative values indicate respectively overestimation and underestimation of GEBV for validation animals when their own observation was not included.

4. *Method LR Dispersion* ( $Disp_{LR}$ ): For individuals in the validation population, dispersion was measured from the slope of the regression of  $\hat{\mathbf{u}}_w$  on  $\hat{\mathbf{u}}_p$ :

$$Disp_{LR} = 1 - \frac{\text{cov}(\hat{\mathbf{u}}_w, \hat{\mathbf{u}}_p)}{\text{var}(\hat{\mathbf{u}}_p)}$$

In the absence of bias, the expected value of  $Disp_{LR}$  is 0. Values less than 0 indicate under-dispersion (or deflation) of  $\hat{\mathbf{u}}_p$  into  $\hat{\mathbf{u}}_w$  as phenotypes become available. Values greater than 1 indicate over-dispersion (or inflation) of  $\hat{\mathbf{u}}_p$  into  $\hat{\mathbf{u}}_w$ .

For bias and dispersion, we constructed 95% confidence intervals based on  $\pm 1.96$  s.e. around the observed means across the 20 scenarios, i.e. 5 traits  $\times$  4 validation datasets.

## Results and discussion

### Phenotypes

Table 1 provides summary statistics for all raw and unadjusted phenotypes, and the slaughter age covariate used in the analyses. Based on the fixed effects model used to adjust phenotypes, the CG effects and covariates combined accounted for 33.5%, 37.1%, 30.7%, 30.8% and 45.2% of the variation in FADG, CWT, CEMA, MARB and CP8, respectively, and with all effects being highly significant ( $P < 0.001$ ) for all traits, except for slaughter age ( $P > 0.1$ ) for CEMA, which was likely captured by the effect of CG. On average and compared to FB, XB cattle were 15 days older, with 6.5% heavier carcasses and 27% less marble, but 46% more subcutaneous fat. For the XB cattle, the values in Table 1 are very similar to those reported by Connolly *et al.* (2019) with a Wagyu crossbred population with a Wagyu content estimated at  $73.0 \pm 0.7\%$ . In that work, and after 163 days on feed and an average age at slaughter of 1147 days, the authors reported means  $\pm$  s.e. for CWT, CEMA, MARB and CP8 of  $434 \pm 5.2$  kg,  $41.4 \pm 0.85$  cm<sup>2</sup>,  $5.9 \pm 0.52$  scores and  $23.7 \pm 1.01$  mm, respectively.

With respect to FADG, our averages of 0.83 kg/day for FB and of 0.92 kg/day for XB are comparable to those from

**Table 1.** Summary statistics including mean, standard deviation (s.d.), minimum and maximum for the raw and unadjusted feedlot and carcass traits and slaughter age covariates in the fullblood (FB) and crossbred (XB) populations.

Population	Trait	N	Mean	s.d.	Min.	Max.
FB	AGE (day)	2120	874.27	125.49	614.00	1746.00
	FADG (kg/day)	2120	0.83	0.11	0.38	1.16
	CWT (kg)	2120	408.60	41.37	213.00	563.50
	CEMA (cm <sup>2</sup> )	1738	90.88	11.82	42.00	139.00
	MARB (score)	2119	7.52	1.87	2.00	12.00
	CP8 (mm)	2095	16.49	6.46	4.00	50.00
	XB	AGE (day)	6196	890.46	98.83	750.00
FADG (kg/day)		4880	0.92	0.16	0.26	1.51
CWT (kg)		6155	435.03	45.03	239.40	628.00
CEMA (cm <sup>2</sup> )		4551	89.35	8.51	17.00	140.00
MARB (score)		6155	5.91	1.48	2.00	9.00
CP8 (mm)		4877	24.06	8.46	7.00	62.00

FB, fullblood population; XB, crossbred population; AGE, slaughter age; FADG, average daily gain during feedlot finishing; CWT, hot carcass weight; CEMA, carcass eye muscle area; MARB, AUS-MEAT marbling score; CP8, carcass subcutaneous fat depth at the rump or P8 site.

Vázquez-Mosquera et al. (2022), who reported daily weight gains of 0.916 kg/day for Wagyu purebred steers ( $N = 262$ ) and 1.046 kg/day for Wagyu × Angus crossbred steers ( $N = 103$ ) during the weaning to growing period, and 0.628 kg/day for purebred and 0.640 kg/day for crossbred during the growing to fattening phase. Similarly, the study of Alexandre et al. (2021) with 3408 Australian Angus steers slaughtered at an average of 734.53 days reported means ± s.d. for FADG, CWT, and CEMA of  $1.59 \pm 0.33$  kg/day,  $432.99 \pm 65.60$  kg and  $90.06 \pm 10.86$  cm<sup>2</sup>, respectively. More recently, Reverter et al. (2023) with a population of 2120 Angus-based steers from four commercial feedlots feed for an average of 222.46 day, reported means ± s.d. for CWT and MARB of  $425.45 \pm 43.94$  kg and  $3.64 \pm 1.33$ , respectively.

## Genotypes and genomic relationships

On average, the estimated percentage of genomic Wagyu content in the FB and XB cattle was 99.12% and 59.55%, respectively. Also on average, the sum of Wagyu and Angus content in the XB cattle was 94.12% and with the remaining 5.88% estimated to originate from mostly Holstein, Santa Gertrudis, and Shorthorn with more than 1% (Table 2). Given the large content of Angus in the XB population, caution will be needed when exploring the applicability of the Wagyu Feeder Check tool in Wagyu × *Bos indicus* crossbred animals. In particular, among the XB cattle, there were 129 (or 2.1%) for which the summed Wagyu and Angus content was <50%. For these animals, the average Wagyu and

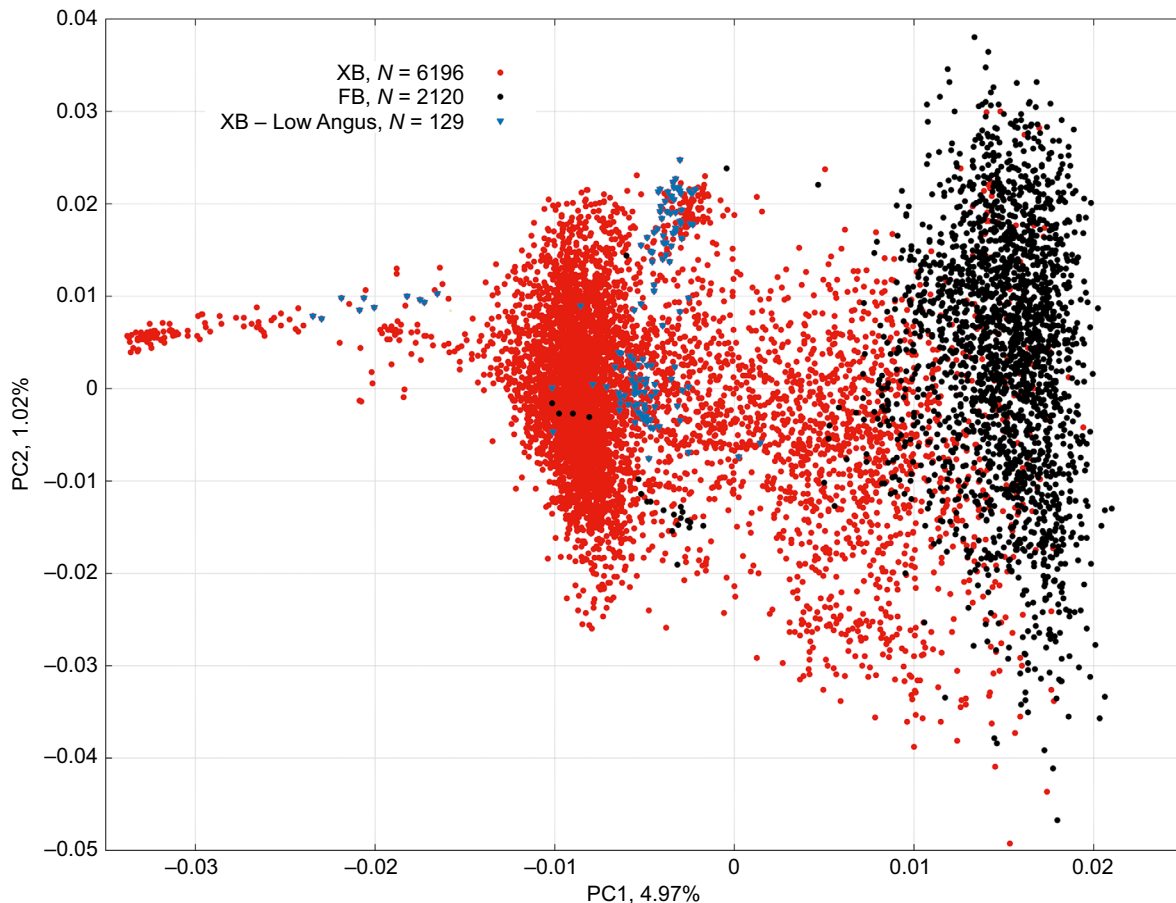
**Table 2.** Genomic breed composition of the crossbred population: summary statistics including mean, standard deviation (s.d.), minimum and maximum for the estimated percentage of genomic breed content of Wagyu, Angus, Holstein, Santa Gertrudis, Shorthorn, Hereford, Charolais and Brahman in the 6196 crossbred populations.

Breed	Mean	s.d.	Min.	Max.
Wagyu	59.55	17.18	0.00	100.00
Angus	34.57	19.24	0.00	100.00
Holstein	1.17	6.79	0.00	62.19
Santa Gertrudis	1.10	4.38	0.00	50.44
Shorthorn	0.89	4.44	0.00	43.53
Hereford	0.84	3.86	0.00	50.58
Charolais	0.81	2.84	0.00	33.13
Brahman	0.77	3.73	0.00	50.03

Angus content was 42.63% and 2.33%, respectively. Therefore, these 129 XB cattle could be considered F1 Wagyu × non-Angus. Other significant breed percentages represented among these 129 XB cattle were Shorthorn (17.80%), Santa Gertrudis (12.90%), Charolais (7.07%), Holstein (6.21%) and Hereford (5.46%).

The percentage of variation in genomic relationships accounted for the first three principal components was 4.97%, 1.02% and 0.90%, respectively. Fig. 1 displays the scatter plot of the PCA for the first two principal components (PC1 and PC2) with the two populations (FB and XB) distinctly highlighted. Also highlighted in Fig. 1 are the 129 XB cattle with low Angus content. Explaining 4.97% of the variation in genomic relationships, PC1 shows a clear separation between FB and XB. On closer examination, we found a very strong Pearson correlation coefficient ( $r$ ) between the genomic estimate of Wagyu content and PC1 ( $r = 0.976 \pm 0.002$ ). This correlation remained strong when examined within the FB ( $r = 0.687 \pm 0.016$ ) and within the XB ( $r = 0.959 \pm 0.004$ ) populations. In multibreed beef populations, it is not uncommon for PC1 to distinguish between *Bos taurus* and *Bos indicus* cattle. For recent examples, see for instance Yonesaka et al. (2016) and Porto-Neto et al. (2023). The work by Yonesaka et al. (2016) is of particular relevance because although their PC1 explained 17.6% of the variation, indeed separating *Bos taurus* from *Bos indicus* population, PC2 explained 4.5% (very close to our 4.96%) and distinguished Japanese Black cattle in one extreme and Angus on the other.

Fig. 2a shows the structure of the Wagyu Feeder Check population using the Pedigromics network approach (Reverter et al. 2019). The centre of the network is dominated by the three FB populations whereas the five XB populations, with smaller node sizes, are scattered around the periphery. To better illustrate the interconnectivity within and across populations, the insert in Fig. 2b shows a subset of the whole Pedigromics network where only the 10 most



**Fig. 1.** Scatter plot of the first two principal component, PC1 and PC2, of the genomic relationship among individuals in the Wagyu fullblood (FB; black dots), Wagyu crossbreds (XB; red dots) populations, and in the 129 XB cattle with low Angus content (blue inverted triangles).

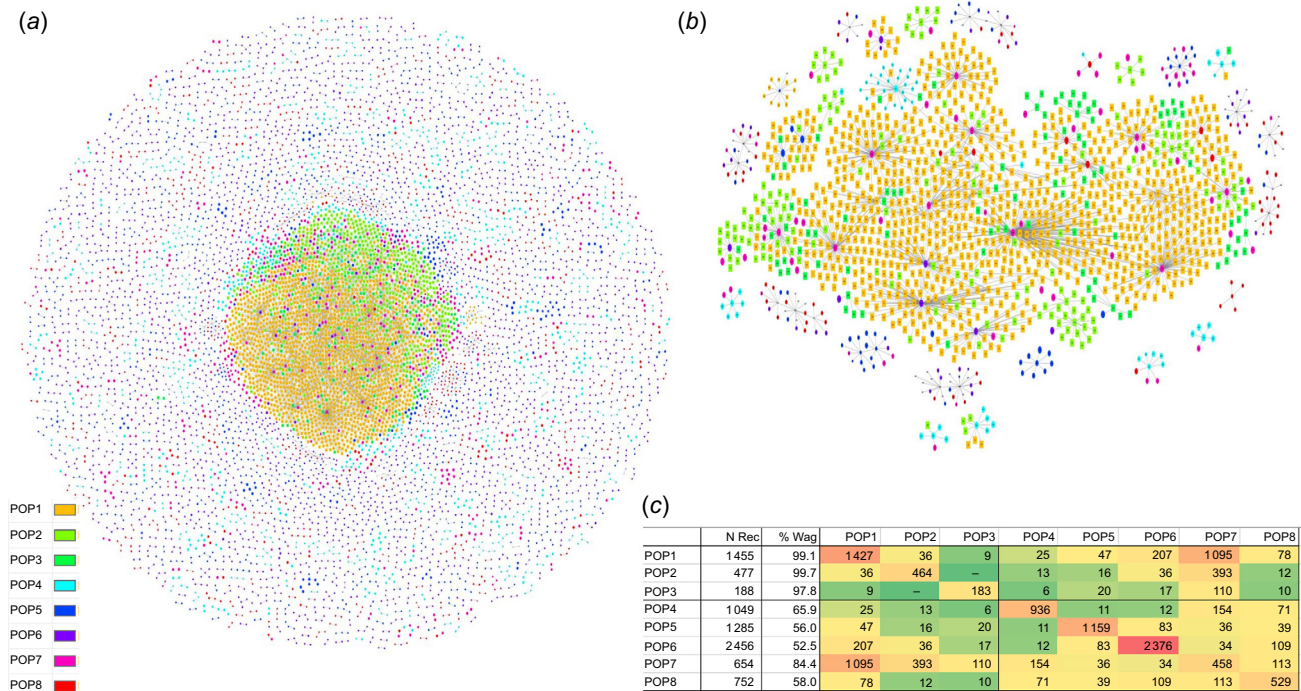
connected animals within each of the eight populations are displayed. As expected, due to the larger size of POP1 among the FB, most of the connectivity from XB to FB happens through POP1. This interconnectivity within and across populations is further exemplified in Fig. 2c where a heatmap of genomic relationships  $>12.5\%$  is tabled. The diagonals are showing the connectivity within a population and populations are more highly correlated within themselves than across populations. Although there's little connectivity among the three FB populations (POP1, POP2 and POP3) including no connectivity between POP2 and POP3, all five XB populations (POP4 to POP8) have connections with the FB populations. Also, the XB population with the highest Wagyu content (POP7 and 84.4% Wagyu) has the highest connectivity with the three FB populations. Importantly, the Wagyu content was not estimated based on connections to the FB populations.

Upon closer inspection of the GRM, the proportion of genomic relationships  $>25\%$  (indicating potential half-sibs) was 5.30%, 11.82%, 6.79%, 1.30%, 0.73%, 0.64%, 0.61%, and 0.27% for POP1 to POP8, respectively. Therefore, the

proportion of half-sibs within each XB population (POP4 to POP8) does not seem to be higher than that observed within the FB populations (POP1 to POP3).

### Genetic parameter estimates

Table 3 shows the estimates of heritability ( $h^2$ ,  $\pm$  standard error (s.e.)), genetic ( $r_g$ ) and residual correlation ( $r_e$ ) obtained from the pentivariate GBLUP model with the entire dataset. Heritability estimates were generally moderate to high, ranging from  $0.347 \pm 0.021$  for CEMA to  $0.526 \pm 0.018$  for FADG. Our  $h^2$  estimates are very similar to those recently reported by Rostamzadeh Mahdabi *et al.* (2023) using a population of 9850 Wagyu steers and heifers. In that work, the authors reported  $h^2$  estimates of  $0.510 \pm 0.014$  for CWT,  $0.430 \pm 0.015$  for CEMA,  $0.473 \pm 0.015$  for CP8 and  $0.486 \pm 0.014$  for MARB. In Japanese Black cattle, Onogi *et al.* (2014) reported  $h^2$  for CWT (0.56), CEMA (0.43) and MARB (0.66), which are higher than those from our study. Similarly,  $h^2$  estimates for carcass traits in Korean Hanwoo cattle have been reported recently. Estimates from Mehrban *et al.* (2019)



**Fig. 2.** (a) Structure of the Wagyu Feeder Check population using the Pedigromics network approach (Reverter et al. 2019), where animals from the eight populations (POP1 to POP8) are nodes, genomic relationships >12.5% are edges and the percent Wagyu content is mapped to the size of each node. (b) A subset of the whole Pedigromics network where only the 10 most connected animals within each of the eight populations are displayed. (c) Interconnectivity within and across the eight populations (POP1 to POP8) including number of records (N Rec), percentage of Wagyu content (% Wag) and based on genomic relationships >12.5%.

**Table 3.** Estimates ( $\pm$ s.e.) of heritabilities (bold, diagonal), genetic correlations (above diagonal) and residual correlations (below diagonal) for the feedlot and carcass traits.

	FADG	CWT	CEMA	MARB	CP8
FADG	<b>0.526 <math>\pm</math> 0.018</b>	0.832 $\pm$ 0.012	0.307 $\pm$ 0.047	-0.083 $\pm$ 0.04	0.131 $\pm$ 0.040
CWT	0.742 $\pm$ 0.009	<b>0.475 <math>\pm</math> 0.017</b>	0.391 $\pm$ 0.045	0.026 $\pm$ 0.037	0.139 $\pm$ 0.039
CEMA	0.199 $\pm$ 0.020	0.275 $\pm$ 0.018	<b>0.347 <math>\pm</math> 0.021</b>	0.333 $\pm$ 0.048	-0.124 $\pm$ 0.05
MARB	0.036 $\pm$ 0.019	0.081 $\pm$ 0.018	0.209 $\pm$ 0.018	<b>0.437 <math>\pm</math> 0.018</b>	-0.085 $\pm$ 0.04
CP8	0.097 $\pm$ 0.022	0.148 $\pm$ 0.020	0.016 $\pm$ 0.020	0.017 $\pm$ 0.019	<b>0.428 <math>\pm</math> 0.021</b>

FADG, average daily gain during feedlot finishing; CWT, hot carcass weight; CEMA, carcass eye muscle area; MARB, AUS-MEAT marbling score; CP8, carcass subcutaneous fat depth at the rump or P8 site.

include CWT (0.39), CEMA (0.45), MARB (0.64) and CP8 (0.51); and estimates from Naserkheil et al. (2021) were 0.42, 0.50, 0.59, and 0.56 for CWT, CEMA, MARB and CP8, respectively.

The review of Ríos Utrera and Van Vleck (2004) reported average  $h^2$  estimates for CWT, CP8, CEMA and MARB of 0.40, 0.36, 0.40, and 0.37, respectively. Therefore, at  $0.347 \pm 0.021$  our  $h^2$  estimate for CEMA is somewhat lower than what has been generally reported. On the other extreme, at  $0.526 \pm 0.018$  our  $h^2$  estimate for FADG is higher than published values including the 0.33 of Torres-Vázquez et al. (2018) and the 0.30 of Alexandre et al. (2021) both with

Angus cattle, and the 0.31 of Somavilla et al. (2017) with Nellore cattle.

Estimates of  $r_g$  were strong and positive between FADG and CWT ( $0.832 \pm 0.012$ ), and moderate and positive between CWT and CEMA ( $0.391 \pm 0.045$ ) and between CEMA and MARB ( $0.333 \pm 0.048$ ). For the same three pairs of traits, the study of Alexandre et al. (2021) with Angus cattle reported  $r_g$  estimates of 0.65, 0.37 and 0.14, respectively; with Hanwoo cattle, Naserkheil et al. (2021) estimated  $r_g$  of 0.56 between CWT and CEMA and 0.35 between CEMA and MARB. In general, all other  $r_g$  estimates were within two s.e. and likely not significantly different from zero. Also, in general, the

estimates of  $r_e$  were lower and closer in magnitude to zero than the  $r_g$  estimates.

Heritabilities, genetic and residual correlations are trait- and population-specific parameters; therefore, a diversity of estimates can be observed in different studies even with the same breed and trait. Factors such as breed, environment, age at measurement, accuracy of measurement and data source (i.e. pedigree or genomic), as well as the analytical methodology may affect the estimates. Because of this diversity, it is always worthwhile to explore the quality of the resulting genomic predictions in terms of their accuracy, bias, and dispersion. This is particularly the case when, as in the current study, the main objective is to develop a genomic tool to be deployed at scale in commercial scenarios.

### Genomic predictions and cross-validation results

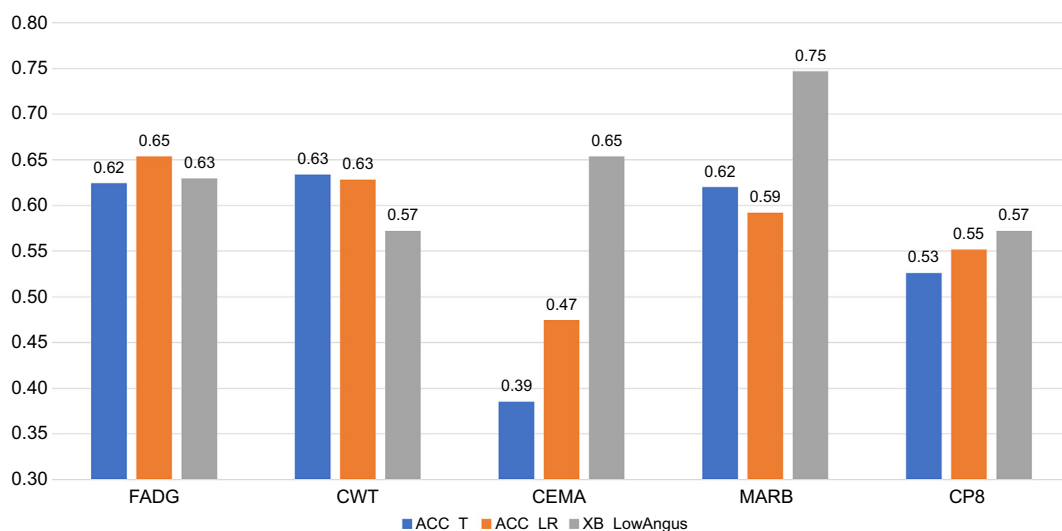
Shown in Fig. 3 are the genomic prediction accuracies for all traits averaged across the four cross-validation samples and based on both accuracy metrics,  $ACC_T$  and  $ACC_{LR}$ . Also in Fig. 3 are the  $ACC_T$  for the 129 XB cattle with low Angus content. Across the 20 accuracy estimates obtained from five traits and four validation datasets, the correlation between  $ACC_T$  and  $ACC_{LR}$  was 0.922, an estimate higher than the 0.73 reported by Alexandre *et al.* (2021) across 49 estimates, and the 0.831 reported by Reverter *et al.* (2021) across 15 estimates and both studies with feedlot and carcass traits in Angus cattle.

Accuracies were in the range of 55–65% for all traits except for CEMA, which were in the 40–50% range. This lower accuracy for CEMA was attributed to its lower  $h^2$  of  $\sim 0.35$  compared to  $h^2 > 0.45$  for the other traits (Table 3). Our

GEV accuracies are consistent with the theoretical expectation of  $\sim 55\%$  and  $\sim 65\%$  respectively for traits of 0.3 and 0.5 heritability and a reference population of  $\sim 7000$  individuals (Goddard and Hayes 2009), which is the equivalent of 8316 total animals in our case minus the  $\sim 1500$  XB animals set aside for each validation. If a whole sub-population of XB had their phenotypes set to missing the expectation is that the ACC would be diminished, particularly if that sub-population is poorly connected. However, all XB populations have connections among themselves and among all three FB populations (Fig. 2c). In addition, because most sub-populations of XB have less than 1549 animals or 25% of XB cattle (the exception being POP6 with 2456 cattle), setting their phenotypes to missing would imply that the remaining ‘reference’ is larger which might result in higher genomic prediction ACC. This phenomenon has been recently reported by Reverter *et al.* (2023) where data from four commercial feedlots were removed one feedlot at a time and compared to removing 50% of all the commercial data.

The study of Onogi *et al.* (2014) with Japanese Black cattle reported a predicted ability (correlation between the GEV and the adjusted phenotypes) of 0.44, 0.42 and 0.39 for CWT, CEMA and MARB, respectively. Meanwhile, the study of Mehrban *et al.* (2019) with Hanwoo cattle estimated GEV accuracies of 0.56, 0.44, 0.36 and 0.33 for CWT, CEMA, MARB and CP8, respectively.

For the 129 XB cattle with low Angus content GEV accuracies were not markedly affected for FADG and CP8, whereas they were somewhat lower for CWT, and higher for CEMA and MARB. This rather unexpected result was attributed to the low number of animals affecting the precision of the ACC



**Fig. 3.** Genomic prediction accuracy based on traditional accuracy ( $ACC_T$ ) and LR method accuracy ( $ACC_{LR}$ ) across the entire population and  $ACC_T$  in 129 XB cattle with low Angus content for average daily gain during feedlot finishing (FADG), hot carcass weight (CWT), carcass eye muscle area (CEMA), AUS-MEAT marbling score (MARB), and carcass subcutaneous fat depth at the rump or P8 site (CP8).

estimates, and to the large proportion of Wagyu content in these cattle (average 42.6%, range = 0–49.9%). Nevertheless, we maintain that caution will be needed when exploring the applicability of the Wagyu Feeder Check tool in Wagyu × non-Angus, particularly Wagyu × *Bos indicus* crossbred animals.

Averaged across all validation datasets, and indicating no bias, the 95% confidence interval for GEBV bias contained zero in all traits (Table 4, upper part). Similarly, the 95% confidence intervals for the dispersion in GEBV contained zero for all traits except FADG for which the 95% confidence interval showed a tendency for under-dispersion (or deflation) of GEBV (Table 4, lower part). Nevertheless, this under-dispersion vanished at 99% confidence interval.

Unlike the recent work of Reverter et al. (2023) with 3766 purebred Angus steers plus 2124 Angus-based commercial steers, in the present study we did not observe a tendency for over-dispersion (or inflation) of GEBV for CWT or MARB. Similarly, the recent work by Koo et al. (2023) exploring the quality of the genomic evaluation of Korean Hanwoo cattle based on a large number of genotyped cows, steers and young animals applied the LR method to confirm a slight negative bias (GEBV overestimation) for all traits and animal groups, but a slight positive bias (GEBV underestimation) for CEMA and MARB in steers. However, their estimates of bias did not deviate significantly from zero. Similarly, their LR estimate of dispersion did not deviate markedly from the expected value of 1 suggesting that GEBV were neither inflated nor deflated.

Like the case for genetic parameters, estimates of GEBV quality metrics (i.e. bias, dispersion, and accuracy) can be affected by a myriad of reasons including the size of the reference population, heritability of the trait, relatedness

**Table 4.** Mean ( $\pm$ s.e.) and lower (LB) and upper (UB) bounds for the 95% confidence interval for bias and dispersion of genomic predictions for the feedlot and carcass traits.

Trait	Mean	95% LB	95% UP
Bias			
FADG (kg/day)	$-0.000 \pm 0.001$	-0.003	0.002
CWT (kg)	$0.063 \pm 0.318$	-0.559	0.683
CEMA (cm <sup>2</sup> )	$0.022 \pm 0.067$	-0.110	0.154
MARB (score)	$0.001 \pm 0.011$	-0.019	0.022
CP8 (mm)	$0.031 \pm 0.061$	-0.090	0.151
Dispersion			
FADG (kg/day)	$-0.056 \pm 0.025$	-0.106	-0.007
CWT (kg)	$-0.034 \pm 0.021$	-0.074	0.007
CEMA (cm <sup>2</sup> )	$-0.001 \pm 0.031$	-0.062	0.060
MARB (score)	$0.005 \pm 0.019$	-0.032	0.042
CP8 (mm)	$-0.010 \pm 0.027$	-0.062	0.042

FADG, average daily gain during feedlot finishing; CWT, hot carcass weight; CEMA, carcass eye muscle area; MARB, AUS-MEAT marbling score; CP8, carcass subcutaneous fat depth at the rump or P8 site.

**Table 5.** Mean measured trait values for validation Wagyu crossbreed animals assigned to quartiles on the basis of genomic estimated breeding values and difference (Q1mQ4) between top (Q1) and bottom (Q4) quartile.

Trait	Q1	Q2	Q3	Q4	Q1mQ4
FADG (kg/day)	0.076	0.019	-0.016	-0.078	0.154
CWT (kg)	20.701	5.496	-5.835	-20.220	40.92
CEMA (cm <sup>2</sup> )	2.044	0.287	0.002	-2.324	4.368
MARB (score)	0.736	0.178	-0.226	-0.683	1.419
CP8 (mm)	3.043	0.709	-0.916	-2.282	5.325

FADG, average daily gain during feedlot finishing; CWT, hot carcass weight; CEMA, carcass eye muscle area; MARB, AUS-MEAT marbling score; CP8, carcass subcutaneous fat depth at the rump or P8 site.

between reference and validation population, and marker density. Again, because of this diversity, it is always worthwhile to explore the quality of the resulting GEBV in terms of their ability to reflect phenotypic differences in the highest and lowest GEBV quartile.

Table 5 presents phenotypic values for validation XB animals assigned to quartiles on the basis of GEBV and the difference (Q1mQ4) between the top (Q1) and the bottom (Q4) quartile. In agreement with the theoretical expectation of a linear relationship between ACC and phenotypic differences in predefined percentiles (Reverter et al. 2022), we observed a Q1mQ4 difference of 0.154 kg/day in FADG, 40.92 kg of CWT, 4.368 cm<sup>2</sup> of CEMA, 1.419 scores of MARB and 5.325 mm of CP8.

## Conclusions

The present study highlights the potential of genomic predictions generated by Wagyu Feeder Check regarding differences in feedlot and carcass performance of Australian Wagyu cattle. Given the large content of Angus in the XB population, further research is required to determine the predictive ability of GEBV in Wagyu × *Bos indicus* and Wagyu × dairy animals. Our preliminary results indicate that commercial feedlot operators finishing animals with a strong Wagyu breed component will benefit from using Wagyu Feeder Check. Benefits will come from identifying and discarding low genetic merit animals from long-fed programs, as well as from minimising days on feed required to achieve a high marbling product. Future research will focus on the expansion of the database constituting the reference population and on the recalibration of the genomic predictions.

## References

Alexandre PA, Li Y, Hine BC, Duff CJ, Ingham AB, Porto-Neto LR, Reverter A (2021) Bias, dispersion, and accuracy of genomic predictions for feedlot and carcass traits in Australian Angus steers. *Genetics Selection Evolution* 53, 77. doi:10.1186/s12711-021-00673-8

- Alexandre PA, Porto-Neto LR, Hine B, Ingham A, Duff C, Samaraweera M, Reverter A (2022) Validation of HeiferSELECT genomic product using historical data. In 'Proceedings of the 12th World Congress on Genetics Applied to Livestock Production, Rotterdam, The Netherlands, 3–8 July 2022'. (Wageningen Academic Publishers)
- AUS-MEAT (2005) 'Handbook of Australian meat. International red meat manual.' 7th edn. (AUS-MEAT: Sydney, Australia)
- Bolormaa S, Pryce JE, Kemper K, Savin K, Hayes BJ, Barendse W, Zhang Y, Reich CM, Mason BA, Bunch RJ, Harrison BE, Reverter A, Herd RM, Tier B, Graser H-U, Goddard ME (2013) Accuracy of prediction of genomic breeding values for residual feed intake and carcass and meat quality traits in *Bos taurus*, *Bos indicus*, and composite beef cattle. *Journal of Animal Science* **91**, 3088–3104. doi:10.2527/jas.2012-5827
- Connolly S, Dona A, Wilkinson-White L, Hamblin D, D'Occhio M, González LA (2019) Relationship of the blood metabolome to subsequent carcass traits at slaughter in feedlot Wagyu crossbred steers. *Scientific Reports* **9**, 15139. doi:10.1038/s41598-019-51655-2
- Goddard ME, Hayes BJ (2009) Mapping genes for complex traits in domestic animals and their use in breeding programmes. *Nature Reviews Genetics* **10**, 381–391. doi:10.1038/nrg2575
- Hine BC, Duff CJ, Byrne A, Parnell P, Porto-Neto L, Li Y, Ingham AB, Reverter A (2021) Development of Angus SteerSELECT: a genomic-based tool to identify performance differences of Australian Angus steers during feedlot finishing: Phase 1 validation. *Animal Production Science* **61**, 1884–1892. doi:10.1071/AN21051
- Johansson M (2023) Genomics in animal breeding from the perspectives of matrices and molecules. *Hereditas* **160**, 20. doi:10.1186/s41065-023-00285-w
- Karaman E, Su G, Croue I, Lund MS (2021) Genomic prediction using a reference population of multiple pure breeds and admixed individuals. *Genetic Selection Evolution* **53**, 46. doi:10.1186/s12711-021-00637-y
- Karoui S, Carabano MJ, Diaz C, Legarra A (2012) Joint genomic evaluation of French dairy cattle breeds using multiple-trait models. *Genetics Selection Evolution* **44**, 39. doi:10.1186/1297-9686-44-39
- Koo Y, Alkholder H, Choi T-J, Liu Z, Reents R (2023) Genomic evaluation of carcass traits of Korean beef cattle Hanwoo using a single-step marker effect model. *Journal of Animal Science* **101**, skad104. doi:10.1093/jas/skad104
- Legarra A, Reverter A (2018) Semi-parametric estimates of population accuracy and bias of predictions of breeding values and future phenotypes using the LR method. *Genetics Selection Evolution* **50**, 53. doi:10.1186/s12711-018-0426-6
- Mehrban H, Lee DH, Naserkheil M, Moradi MH, Ibáñez-Escriche N (2019) Comparison of conventional BLUP and single-step genomic BLUP evaluations for yearling weight and carcass traits in Hanwoo beef cattle using single trait and multi-trait models. *PLoS ONE* **14**, e0223352. doi:10.1371/journal.pone.0223352
- Misztal I, Legarra A (2017) Invited review: efficient computation strategies in genomic selection. *Animal* **11**, 731–736. doi:10.1017/S1751731116002366
- Naserkheil M, Lee D-H, Kong H-S, Seong J, Mehrban H (2021) Estimation of genetic parameters and correlation between yearling ultrasound measurements and carcass traits in Hanwoo cattle. *Animals* **11**, 1425. doi:10.3390/ani11051425
- Onogi A, Ogino A, Komatsu T, Shoji N, Simizu K, Kurogi K, Yasumori T, Togashi K, Iwata H (2014) Genomic prediction in Japanese Black cattle: application of a single-step approach to beef cattle. *Journal of Animal Science* **92**, 1931–1938. doi:10.2527/jas.2014-7168
- Pérez-Enciso M, Misztal I (2011) Qxpak.5: old mixed model solutions for new genomics problems. *BMC Bioinformatics* **12**, 202. doi:10.1186/1471-2105-12-202
- Porto-Neto LR, Barendse W, Henshall JM, McWilliam SM, Lehnert SA, Reverter A (2015) Genomic correlation: harnessing the benefit of combining two unrelated populations for genomic selection. *Genetic Selection Evolution* **47**, 84. doi:10.1186/s12711-015-0162-0
- Porto-Neto LR, Alexandre PA, Hudson NJ, Bertram J, McWilliam SM, Tan AWL, Fortes MRS, McGowan MR, Hayes BJ, Reverter A (2023) Multi-Breed genomic predictions and functional variants for fertility of tropical bulls. *PLoS One* **18**, e0279398. doi:10.1371/journal.pone.0279398
- Reverter A, Porto-Neto LR, Fortes MRS, McCulloch R, Lyons RE, Moore S, Nicol D, Henshall J, Lehnert SA (2016) Genomic analyses of tropical beef cattle fertility based on genotyping pools of Brahman cows with unknown pedigree. *Journal of Animal Science* **94**, 4096–4108. doi:10.2527/jas.2016-0675
- Reverter A, Dominik S, Ferraz JBS, Corrigan L, Porto-Neto LR (2019) Pedigromics: a network-inspired approach to visualise and analyse pedigree structures. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **23**, 540–543. Available at <https://www.cabdirect.org/cabdirect/abstract/20203356360>
- Reverter A, Hudson NJ, McWilliam S, Alexandre PA, Li Y, Barlow R, Welti N, Daetwyler H, Porto-Neto LR, Dominik S (2020) A low-density SNP genotyping panel for the accurate prediction of cattle breeds. *Journal of Animal Science* **98**, skaa337. doi:10.1093/jas/skaa337
- Reverter A, Hine BC, Porto-Neto L, Alexandre PA, Li Y, Duff CJ, Dominik S, Ingham AB (2021) ImmuneDEX: updated genomic estimates of genetic parameters and breeding values for Australian Angus cattle. *Animal Production Science* **61**, 1919–1924. doi:10.1071/AN21054
- Reverter A, Alexandre PA, Li Y, Hine BC, Duff CJ, Ingham AB, Porto-Neto LR (2022) Genomic prediction accuracy: how low can we go? In 'Proceedings of the 12th World Congress on Genetics Applied to Livestock Production, Rotterdam, The Netherlands, 3–8 July 2022'. (Wageningen Academic Publishers)
- Reverter A, Porto-Neto L, Hine BC, Alexandre PA, Samaraweera M, Byrne AI, Ingham AB, Duff CF (2023) On the value of adding commercial data into the reference population of the Angus SteerSELECT genomic tool. *Animal Production Science* **63**, 947–956. doi:10.1071/AN22452
- Rostamzadeh Mahdabi E, Tian R, Li Y, Wang X, Zhao M, Li H, Yang D, Zhang H, Li SF, Esmailzadeh A (2023) Genomic heritability and correlation between carcass traits in Japanese Black cattle evaluated under different ceilings of relatedness among individuals. *Frontiers in Genetics* **14**, 1053291. doi:10.3389/fgene.2023.1053291
- Ríos Utrera A, Van Vleck LD (2004) Heritability estimates for carcass traits of cattle: a review. *Genetics and Molecular Research* **30**, 380–394.
- Somavilla AL, Regitano LCA, Rosa GJM, Mokry FB, Mudadu MA, Tizioto PC, Oliveira PSN, Souza MM, Coutinho LL, Munari DP (2017) Genome-enabled prediction of breeding values for feedlot average daily weight gain in Nelore cattle. *G3 Genes|Genomes|Genetics* **7**, 1855–1859. doi:10.1534/g3.117.041442
- Takeda M, Inoue K, Oyama H, Uchiyama K, Yoshinari K, Sasago N, Kojima T, Kashima M, Suzuki H, Kamata T, Kumagai M, Takasugi W, Aonuma T, Soma Y, Konno S, Saito T, Ishida M, Muraki E, Inoue Y, Takayama M, Nariai S, Hideshima R, Nakamura R, Nishikawa S, Kobayashi H, Shibata E, Yamamoto K, Yoshimura K, Matsuda H, Inoue T, Fujita A, Terayama S, Inoue K, Morita S, Nakashima R, Suezawa R, Hanamura T, Zoda A, Uemoto Y (2021) Exploring the size of reference population for expected accuracy of genomic prediction using simulated and real data in Japanese Black cattle. *BMC Genomics* **22**, 799. doi:10.1186/s12864-021-08121-z
- Torres-Vázquez JA, van der Werf JHJ, Clark SA (2018) Genetic and phenotypic associations of feed efficiency with growth and carcass traits in Australian Angus cattle. *Journal of Animal Science* **96**, 4521–4531. doi:10.1093/jas/sky325
- van Grevenhof IEM, van der Werf JHJ (2015) Design of reference populations for genomic selection in crossbreeding programs. *Genetic Selection Evolution* **47**, 14. doi:10.1186/s12711-015-0104-x
- VanRaden PM (2008) Efficient methods to compute genomic predictions. *Journal of Dairy Science* **91**, 4414–4423. doi:10.3168/jds.2007-0980
- Vázquez-Mosquera JM, de Mercado E, Fernández-Novo A, Gardón JC, Pesántez-Pacheco JL, Pérez-Solana ML, Revilla-Ruiz Á, Martínez D, Villagrà A, Sebastián F, Pérez-Garnelo SS, Astiz S (2022) Comparison of pure and crossbred Japanese black steers in growth performance and metabolic features from birth to slaughter at a Spanish fattening farm. *Animals* **12**, 1671. doi:10.3390/ani12131671
- Yonesaka R, Sasazaki S, Yasue H, Niwata S, Inayoshi Y, Mukai F, Mannen H (2016) Genetic structure and relationships of 16 Asian and European cattle populations using DigiTag2 assay. *Animal Science Journal* **87**, 190–196. doi:10.1111/asj.12416

**Data availability.** The data that support this study may be shared upon reasonable request to the corresponding author.

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