

On the value of adding commercial data into the reference population of the Angus SteerSELECT genomic tool

Antonio Reverter^{A,*} , Laercio Porto-Neto^A, Brad C. Hine^B , Pamela A. Alexandre^A,
Malshani Samaraweera^C, Andrew I. Byrne^C, Aaron B. Ingham^A and Christian J. Duff^C 

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

Antonio Reverter
CSIRO Agriculture and Food, Queensland
Bioscience Precinct, 306 Carmody Road,
St Lucia, Brisbane, Qld 4067, Australia
Email: toni.reverter-gomez@csiro.au

Handling Editor:

Sue Hatcher

Received: 13 December 2022

Accepted: 20 February 2023

Published: 14 March 2023

Cite this:

Reverter A *et al.* (2023)
Animal Production Science, **63**(10–11),
947–956.
doi:[10.1071/AN22452](https://doi.org/10.1071/AN22452)

© 2023 The Author(s) (or their employer(s)). Published by CSIRO Publishing.
This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License ([CC BY-NC-ND](https://creativecommons.org/licenses/by-nc-nd/4.0/)).

OPEN ACCESS

ABSTRACT

Context. Angus SteerSELECT is a genomic tool designed to provide genomic estimated breeding values (GEBV) for nine traits related to growth, feedlot performance, carcass characteristics and immune competence. At present, GEBV for carcass characteristics are based on a reference population of 3766 Australian Angus steers. **Aims.** We aimed to investigate the potential benefit of incorporating commercial data into the existing reference population of the Angus SteerSELECT. To this aim, we employ a population of 2124 genotyped commercial Angus steers with carcass performance data from four commercial feedlot operators. **Methods.** The benefit of incorporating the commercial data (COMM) into the reference (REFE) population was assessed in terms of quality and integrity of the COMM data and meta-data to model the phenotypes adequately. We computed bias, dispersion, and accuracy of GEBV for carcass weight (CWT) and marbling (MARB) before and after including the COMM data, in whole or in partial, into the REFE population. **Key results.** The genomic estimate of the Angus content in the COMM population averaged 96.9% and ranged from 32.87% to 100%. For CWT, the estimates of heritability were 0.419 ± 0.026 and 0.368 ± 0.038 for the REFE and COMM populations respectively, and with a genetic correlation of 0.756 ± 0.068 . For MARB, the same three parameter estimates were 0.357 ± 0.027 , 0.340 ± 0.038 and 0.879 ± 0.073 respectively. The ACC of CWT GEBV increased significantly ($P < 0.0001$) from 0.475 when the COMM population was not part of the REFE to 0.546 (or 15%) when a random 50% of the COMM population was included in the REFE. Similarly significant increases in ACC were observed for MARB GEBV (0.470–0.521 or 11%). **Conclusions.** The strong genomic relationship between the REFE and the COMM populations, coupled with the significant increases in GEBV accuracies, demonstrated the potential benefits of including the COMM population into the reference population of a future improved version of the Angus SteerSELECT genomic tool. **Implications.** Commercial feedlot operators finishing animals with a strong Angus breed component will benefit from having their data represented in the reference population of the Angus SteerSELECT genomic tool.

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

Introduction

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). Angus SteerSELECT is a genomic-based tool that aims to predict the performance of Australian Angus steers during feedlot finishing, especially in commercial Australian feedlots. It provides genomic predictions for a range of traits including growth, feed intake, carcass and immune competence. The ability of Angus SteerSELECT to predict differences in performance, in terms of carcass weight, marbling score, ossification score and carcass value, has been previously validated by Hine *et al.* (2021) by using a population of 522 short-fed (100 days) or long-fed (270 days) Angus steers finished in commercial feedlots.

Over the past decade, a great deal of effort has been devoted towards finding and understanding the factors influencing genomic prediction accuracy. These include the size of the reference population (Daetwyler *et al.* 2008; Goddard 2009; Habier *et al.* 2010), heritability of the trait (Goddard 2009; Daetwyler *et al.* 2010), relatedness between reference and validation population (de Roos *et al.* 2009; Wientjes *et al.* 2013), linkage disequilibrium (LD) between single-nucleotide polymorphism (SNP) markers and quantitative trait loci (QTL; Habier *et al.* 2007; Wientjes *et al.* 2013), marker density (Meuwissen and Goddard 2010; Clark *et al.* 2011), number of QTL (Daetwyler *et al.* 2010; Clark *et al.* 2011), and minor allele frequencies of causative mutations and the SNP markers used in the predictions (Druet *et al.* 2014; Wientjes *et al.* 2015).

De los Campos *et al.* (2013) argued that the critical factor driving accuracy is the extent to which marker-based relationships properly describe the unobserved genetic relationships at trait loci. Hence, if the training and test data sets have related individuals, the markers can be good predictors even if the LD between markers and trait genes is weak (see also Wray *et al.* 2013).

From these findings, here we have focussed primarily on improving our understanding of the effect of the size of the reference population and its genomic relationship with the validation population, specifically as it relates to the Angus SteerSELECT genomic tool. These factors are of interest as they are operational (as opposed to biological) and can be manipulated during the development and application of a genomic selection program.

A recent study by Takeda *et al.* (2021) with 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, such as, 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).

In the present study, we explore the potential benefits of incorporating data from commercial un-pedigreed and un-registered cattle into the existing reference population of the Angus SteerSELECT genomic tool.

Materials and methods

Reference and commercial population details

For carcass traits, the reference (REFE) population underpinning the Angus SteerSELECT tools currently comprises phenotypes and genotypes for 3766 Angus steers that were progeny of the Australian Angus Sire Benchmarking Program (ASBP), representing Years 1–8 of the program (described as

Cohorts 1–8 with 360, 514, 570, 273, 547, 559, 520 and 423 steers respectively). The ASBP is a major initiative of Angus Australia, with support from Meat & Livestock Australia (MLA) and industry partners, that aims to generate progeny test data on contemporary Angus bulls, particularly for hard-to-measure traits such as feed efficiency, carcass measurements, meat-quality attributes and female reproduction (<https://www.angusaustralia.com.au/sire-benchmarking>).

The contemporary group (CG) for steers in the REFE population (CG_R) was defined as a combination of cohort, property of origin, month of birth, management group and date of phenotype measurement. Management group accounted for some steers being short-fed (~100 days) and others long-fed (~270 days) during the feedlot period. In total, there were 105 CG_R with an average of 35.9 steers per CG and ranging from 5 to 213 steers per CG.

After initial edits aimed at removing steers without genotypes or from CG with fewer than five individuals, the commercial (COMM) population comprised 2124 Angus-based steers from four commercial feedlots identified herein as Flot_1 (*N* = 453), Flot_2 (*N* = 720), Flot_3 (*N* = 495 steers) and Flot_4 (*N* = 456). The CG for the COMM population (CG_C) was defined as a combination of feedlot, supplier (*N* = 19), abattoir and kill date. Steers were slaughtered in 23 kill groups from 18 January 2021 to 2 June 2022. There were 46 CG_C, with an average of 46.2 steers per CG and ranging from 5 to 271 steers per CG.

For the present study, phenotypes for the REFE population included hot carcass weight (CWT) and Meat Standards Australia marbling score (MSA-MARB) measured in scores ranging from 100 to 1100 in increments of 10, with higher scores indicating greater marbling (McGilchrist *et al.* 2019). For the COMM population, phenotypes included CWT and AUSMEAT marbling score using the AUSMEAT scoring system, which ranges from 0 (nil) to 9 (abundant) in increments of 1 (AUS-MEAT 2005).

Genotypes for 45 364 autosomal SNPs were available for all the animals included in this study (i.e. 3766 REFE + 2124 COMM = 5890 total) and were used to compute the genomic relationship matrix (**G**) following Method 1 of VanRaden (2008), with the modification of Karoui *et al.* (2012) to make it invertible, as follows:

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

where **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 **I** is an identity matrix included to make the genomic relationship matrix (GRM) invertible by enlarging the diagonal elements.

To obtain a measure of the genomic similarity between the two populations, we explored the SNP allele frequencies, the values of the GRM and performed a principal-component

analysis (PCA) on the basis of a singular value decomposition of the GRM (Misztal and Legarra 2017).

Genomic predictions and cross-validation models

Variance components, heritability (h^2), genetic (r_g) and residual (r_e) correlations were estimated on the basis of GBLUP methodology using the Qxpak5 software (Pérez-Enciso and Misztal 2011). For the genomic prediction models, we performed GBLUP analyses by using a series of uni- and bi-variate analyses and three cross-validation schemes. In all cases, for the REFE population, the GBLUP models for the analysis of CWT and MSA-MARB contained the fixed effects of CG_R and age of dam in years (AOD, six levels, 2–7+ years) and the linear regression covariates of age at measurement (AGE) in days, and the first three principal components of the GRM. Similarly, for the COMM population, the GBLUP models for the analysis of CWT and AUS-MARB contained the fixed effect of CG_C and the linear regression covariates of days on feed (DOF), and the first three principal components of the GRM.

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 genomic relationship matrix described earlier, \mathbf{V} is the genetic co-variance matrix, \mathbf{I} is an identity matrix, \mathbf{R} is the residual variance–covariance matrix and \otimes represents the Kronecker product.

First, to obtain a measure of the genetic similarity, based on h^2 and r_g for a given trait in the two populations, we fitted two bi-variate GBLUP models. The first bi-variate model treated CWT as a different trait in the two populations. The second bi-variate model contained MSA-MARB and AUS-MARB for REFE and COMM respectively. The intent was to confirm that each trait had similar h^2 in both populations and, equally importantly, a strong positive r_g .

Second, the genotypes and phenotypes from both populations were merged into a single dataset and, for each trait CWT and MARB, the resulting genomic estimated breeding values (GEBV) from the analysis using this merged dataset are termed $\hat{\mathbf{u}}_w$ to indicate that they are based on the *whole* dataset. Before merging them, phenotypes were adjusted for fixed effects and covariates, and, within population, standardised using the z-score transformation (i.e. dividing by the within-population standard deviation). This was particularly important for marbling traits as they were measured on different scales in the two populations.

Third, for the cross-validation of genomic predictions, we employed three validation scenarios (VAL1, VAL2 and VAL3) depending on how many COMM phenotypes were included in the reference population, as follows:

1. VAL1 – all-out: no commercial phenotypes were included in the reference population. So, the reference population comprised the original REFE of 3766 steers with genotypes and phenotypes.

2. VAL2 – leave-one-feedlot-out: phenotypes from a given feedlot were excluded from the reference, while those from the remaining three feedlots were included. This approach was repeated four times, excluding phenotypes from one of the four feedlots each time.
3. VAL3 – leave-half-out: a random 50% of the COMM phenotypes across all feedlots were included in the reference, with the remainder being excluded from the reference but included in the validation.

In each cross-validation schema, the resulting GEBV from the analyses that treated as missing values records from a given commercial feedlot are termed $\hat{\mathbf{u}}_p$ to indicate that they are based on *partial* data.

Finally, traditional (Bolormaa *et al.* 2013) and linear regression (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, as follows:

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

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, $2\bar{f}$ is the average relationship between individuals, 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* ($Bias_{LR}$): difference among the average GEBVs of individuals in the validation population by using the partial data minus that using the whole data, as follows:

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

In the absence of bias, the expected value of $Bias_{LR}$ is zero, while positive and negative values indicate respectively, over-estimation and under-estimation 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{u}_w on \hat{u}_p , as follows:

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

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

For bias and dispersion, we constructed 95% confidence intervals based on ± 1.96 s.e. around the observed means across the 24 scenarios, i.e. 2 traits \times 4 feedlots \times 3 validation schemes.

Results and discussion

Phenotypes, fixed effects and covariates

Table 1 provides summary statistics for all phenotypes and covariates used in the analyses. For the REFE population, two steers had missing CWT and four had missing MSA-MARB. For the COMM population, the number of records with AUS-MARB scores of 1–9 was 36, 323, 817, 419, 337, 130, 44, 14, and 4 respectively.

For the REFE population, the fixed effects and covariates accounted for 77.9% and 38.6% of the variation in CWT and MSA-MARB respectively, and with all effects being highly significant ($P < 0.001$), except for slaughter age ($P > 0.1$), which was likely to have been captured by the effect of CG_R . In comparison, for the COMM population, the fixed effects and covariates accounted for 62.9% and 42.1% of the variation in CWT and AUS-MARB respectively, and with all effects being highly significant ($P < 0.001$), except for DOF ($P > 0.1$), which was likely to have been captured by the effect of Feedlot and CG_C . The average DOF (\pm standard deviation, s.d.) for Flot_1, Flot_2, Flot_3 and Flot_4 was 230.49 ± 8.03 , 182.10 ± 8.77 , 224.67 ± 47.18 , and 275.81 ± 0.98 . The longest DOF, with

the smallest variation, was observed for Flot_4 due to steers being either 275 DOF ($N = 271$ steers) or 277 DOF ($N = 185$ steers). Table 2 presents the least-square means for CWT and AUS-MARB, across the four feedlots. Steers from Flot_4 had heavier CWT ($P < 0.01$) than those from the other three feedlots (reflecting additional DOF), which were not different from each other ($P > 0.10$). However, the ranking in CWT was not matched by the ranking in AUS-MARB, for which $\text{Flot}_2 < \text{Flot}_4 = \text{Flot}_3 < \text{Flot}_1$.

Fig. 1 shows the violin plots of the distribution of CWT observation in the REFE population and from each of the four feedlots represented in the COMM population. The apparent bimodality of the CWT records from the REFE population was attributed to some steers being short-fed (~ 100 days) and others being long-fed (~ 270 days) during the feedlot period.

Genotypes, genomic relationships and genetic parameters

Across the 45 364 SNPs, the correlation between the frequency of the first allele in the REFE and in the COMM population was very high at 0.996. In agreement with theoretical expectations, the 5890 diagonal elements of the genomic relationship matrix \mathbf{G} created with the combined population averaged 1.001, with a standard deviation (s.d.) of 0.031, and ranged from 0.914 to 1.337. Meanwhile, the 17 343 105 off-diagonal elements of \mathbf{G} averaged -0.000 , with a s.d. of 0.025, and ranged from -0.112 to 0.657. These values are very similar to the ones reported by Reverter et al. (2021a) using a population of 3715 Angus steers and heifers that were progeny of ASBP sires. Also, the similarity in the variance of diagonal and off-diagonal elements indicates that both a sufficiently large number of SNPs was used to estimate relationships and the presence of a single-breed population (Simeone et al. 2011). Finally, the PCA of \mathbf{G} did not show any clusters in the combined population, with the first three PCs accounting for only 0.79%, 0.52% and 0.43% of genomic diversity respectively. These results further confirmed the high Angus content of the steers in the COMM population.

Table 1. Summary statistics, including mean, standard deviation (s.d.), minimum and maximum for the carcass traits and covariates in the two studied populations.

Population	Variable	N	Mean	s.d.	Min.	Max.
REFE	AGE (days)	3766	726.89	98.71	505.00	990.00
	CWT (kg)	3764	427.09	66.85	211.30	607.00
	MARB (score)	3762	492.26	125.88	160.00	1030.00
COMM	DOF (days)	2124	222.46	41.67	159.00	277.00
	CWT (kg)	2124	425.45	43.94	292.40	575.00
	MARB (score)	2124	3.64	1.33	1.00	9.00

REFE, reference population; COMM, commercial population; AGE, slaughter age; CWT, hot carcass weight; MARB, marbling score (MSA and AUSMEAT score for REFE and COMM respectively); DOF, days on feed.

Table 2. Number of records (*N*) and least-square means (\pm standard error, s.e.) for carcass traits for each feedlot in the commercial population of 2124 steers.

Feedlot	<i>N</i>	CWT (kg)	MARB (score)
Flot_1	453	407.43a \pm 2.13	4.81a \pm 0.08
Flot_2	720	413.43a \pm 7.23	2.87b \pm 0.27
Flot_3	495	408.25a \pm 4.52	3.70c \pm 0.17
Flot_4	456	466.41b \pm 10.60	3.07c \pm 0.40

CWT, hot carcass weight; MARB, AUSMEAT marbling score.

Within a trait, values with different letters indicate significant difference (at $P = 0.01$).

On the basis of previously described approaches to estimate genomic breed composition (Reverter *et al.* 2020), using the 45 364 SNPs, the genomic estimate of the Angus content in the COMM population averaged 96.9% and ranged from 32.87% to 100%. Of the 2124 steers, 1703 (or 80.2%) were estimated to be 100% Angus, while a further 229 steers (10.8%) being estimated to have an Angus content <100% but $\geq 87.5\%$ (or 7/8).

After fitting the bi-variate GBLUP model that treated the same trait (CWT or MARB) as a different trait in the two populations (REFE and COMM), the estimates (mean \pm s.e.) of heritability (h^2) for CWT were 0.419 ± 0.026 and 0.368 ± 0.038 for the REFE and COMM population respectively, and with a genetic correlation (r_g) of 0.756 ± 0.068 . For MARB, the same three parameter estimates were 0.357 ± 0.027 , 0.340 ± 0.038 and 0.879 ± 0.073 respectively. Again, the similar h^2 estimates for a given trait in the two populations coupled with the strong r_g point

towards the convenience of merging both populations into a single larger reference population.

Very similar to the h^2 estimates reported here, the review of Ríos Utrera and Van Vleck (2004) reported average h^2 estimates for CWT and MARB score of 0.40 and 0.37 respectively. However, using a subset of the Australian Angus cattle employed here, higher h^2 estimates for CWT and MARB have been published, including the 0.75 ± 0.06 and 0.53 ± 0.05 respectively, of Duff *et al.* (2021), and the 0.63 ± 0.11 and 0.61 ± 0.09 respectively, of Reverter *et al.* (2021b).

There is a body of literature describing the strong relationship between different measures of marbling (for a recent account, see, for instance, Liu *et al.* (2021) and Martín *et al.* (2022)). Liu *et al.* (2021) reported a phenotypic correlation of 0.91 ($P < 0.001$) between AUS-MARB and MSA-MARB. Mateescu *et al.* (2015) reported a r_g estimate of 1.00 ± 0.01 between marbling score and intramuscular fat content.

Genomic predictions and cross-validation results

The genomic prediction accuracies for both traits across four commercial feedlots are shown in Fig. 2. Averaged across all feedlots and based on both accuracy metrics (ACC_T and ACC_{LR}), genomic prediction accuracy for CWT increased from VAL1 ($ACC_T = 0.356$; $ACC_{LR} = 0.475$) to VAL2 ($ACC_T = 0.420$; $ACC_{LR} = 0.524$) to VAL3 ($ACC_T = 0.485$; $ACC_{LR} = 0.546$).

Similar to our previous findings (Reverter *et al.* 2021b), in the present study we observed a strong correlation between ACC_T and ACC_{LR} across the 24 measures ($r = 0.603 \pm 0.170$), and, on average, the ACC_{LR} accuracies were 15% higher than ACC_T accuracies (0.511 vs 0.444) and less variable (s.d. = 0.038 vs 0.106).

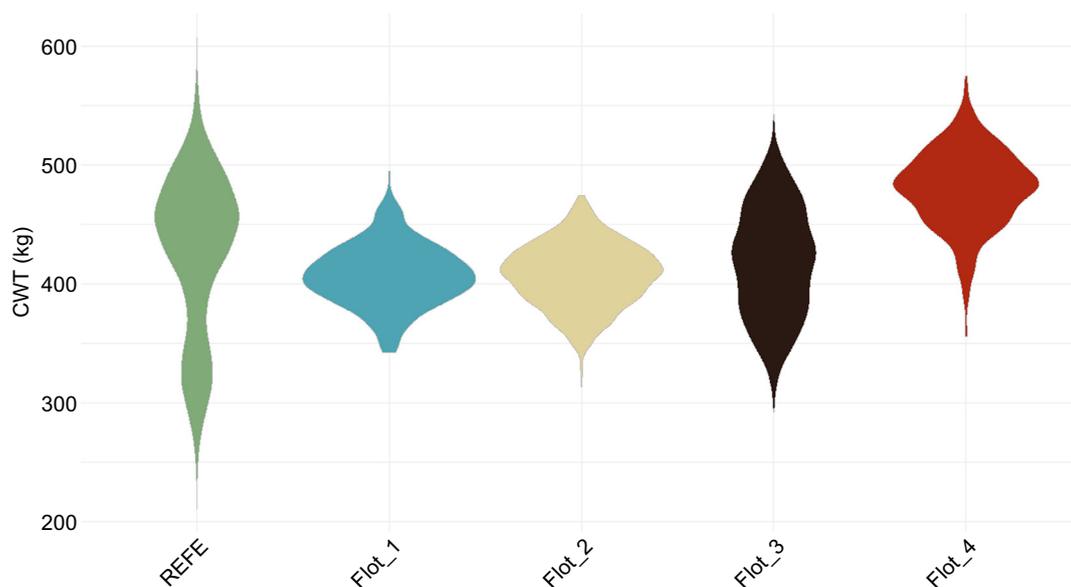


Fig. 1. Violin plot of the distribution of carcass weight (CWT) in the reference population (REFE) and from each of the four feedlots of the commercial population.

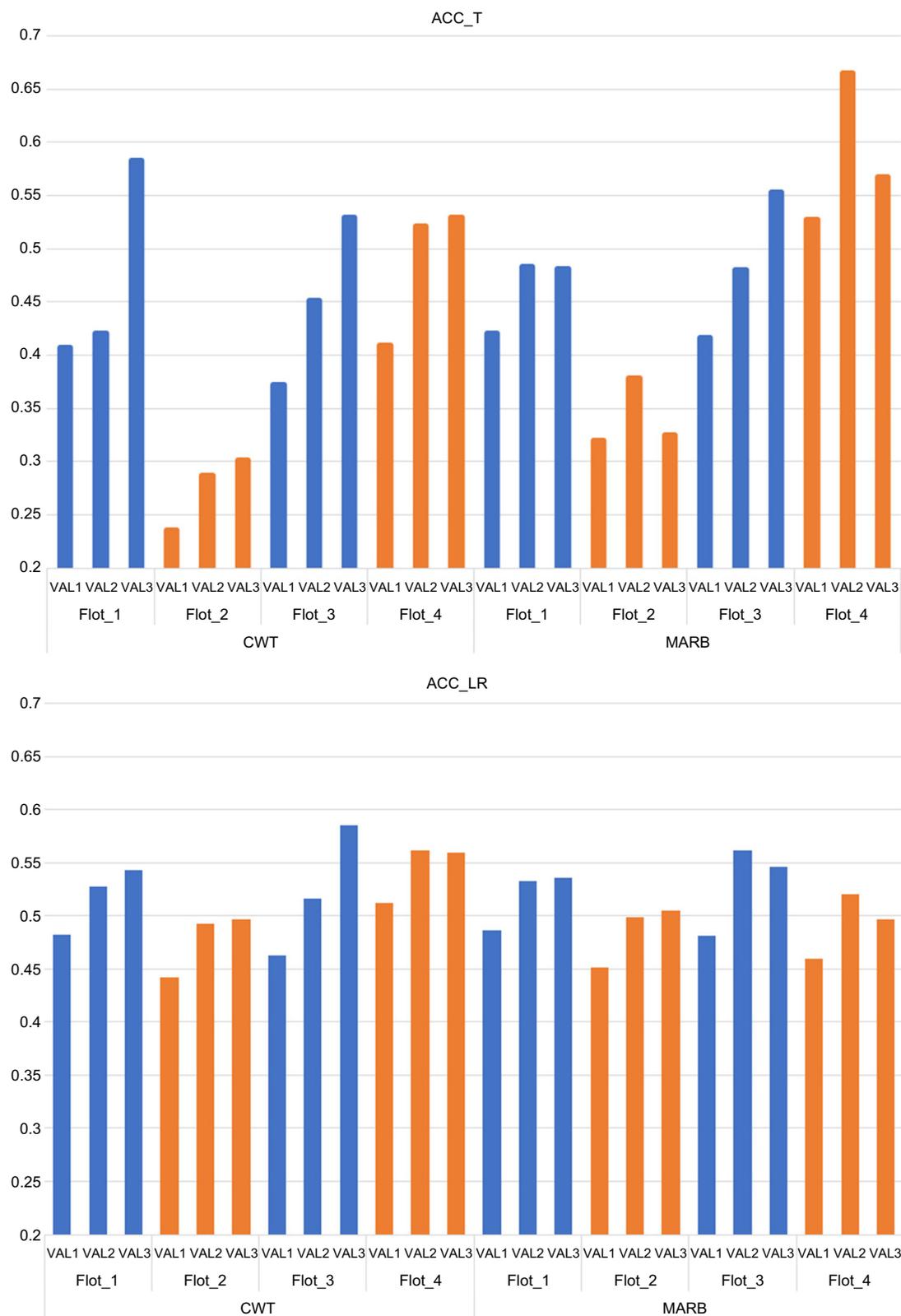


Fig. 2. Genomic prediction accuracy based on traditional accuracy, ACC_T (top panel), and LR method accuracy, ACC_LR (bottom panel), for CWT and MARB in the four feedlots (Flot_1, Flot_2, Flot_3 and Flot_4) and for the three validation schemes (VAL1, VAL2 and VAL3).

The increase in prediction accuracy from VAL1 to VAL2 can be attributed in part to relationships between the steers from the feedlot being validated and the steers from the other feedlots, but also to an increase in the size of the new reference population, i.e. the original REFE population of 3766 steers plus all the steers from the other feedlots. However, the increase in accuracy from VAL2 to VAL3 can be mostly attributed to relationships between steers from the same feedlot to the one being validated. It is worth noting that the reference population for VAL3 comprised 4796 steers (the original 3766 steers from REFE plus a random 1030 steers from COMM), which is less than the number of steers in the reference populations for VAL2 (the original 3766 steers from REFE plus all the steers from COMM except those from the feedlot being validated). As commercial feedlot operators tend to source their steers from ‘preferred’ suppliers, the increase in accuracy observed in VAL3 relative to VAL2, and even with a smaller reference in VAL3, highlights the importance of having their own cattle represented in the reference population.

The 95% confidence interval for GEBV bias contained zero in 22 of the 24 scenarios considered (Fig. 3). The two anomalous scenarios correspond to CWT GEBV for Flot_2 steers being over-estimated. While further research is needed to ascertain the reason for this over-estimation, one possibility points towards the difficulty in modelling data from Flot_2 as it represents the largest sample size (720 steers compared with <500 for the other feedlots) across the largest number of suppliers (10 compared with the second-largest 6 for Flot_4). Nevertheless, this over-estimation vanishes at 99% confidence interval.

The 95% confidence intervals for the dispersion in GEBV showed a tendency for over-dispersion (or inflation), particularly for Flot_2 steers across both traits, and for Flot_3 steers in CWT and for Flot_1 steers in MARB. Again, while further research is needed to ascertain the reason for this inflation, a plausible reason is the use of an incorrect heritability, in this case higher for inflation, or the existence of a hidden trend in the data (Macedo *et al.* 2020). Similarly, this over-dispersion was observed in our previous study (Reverter *et al.* 2022) and attributed to higher h^2 estimates

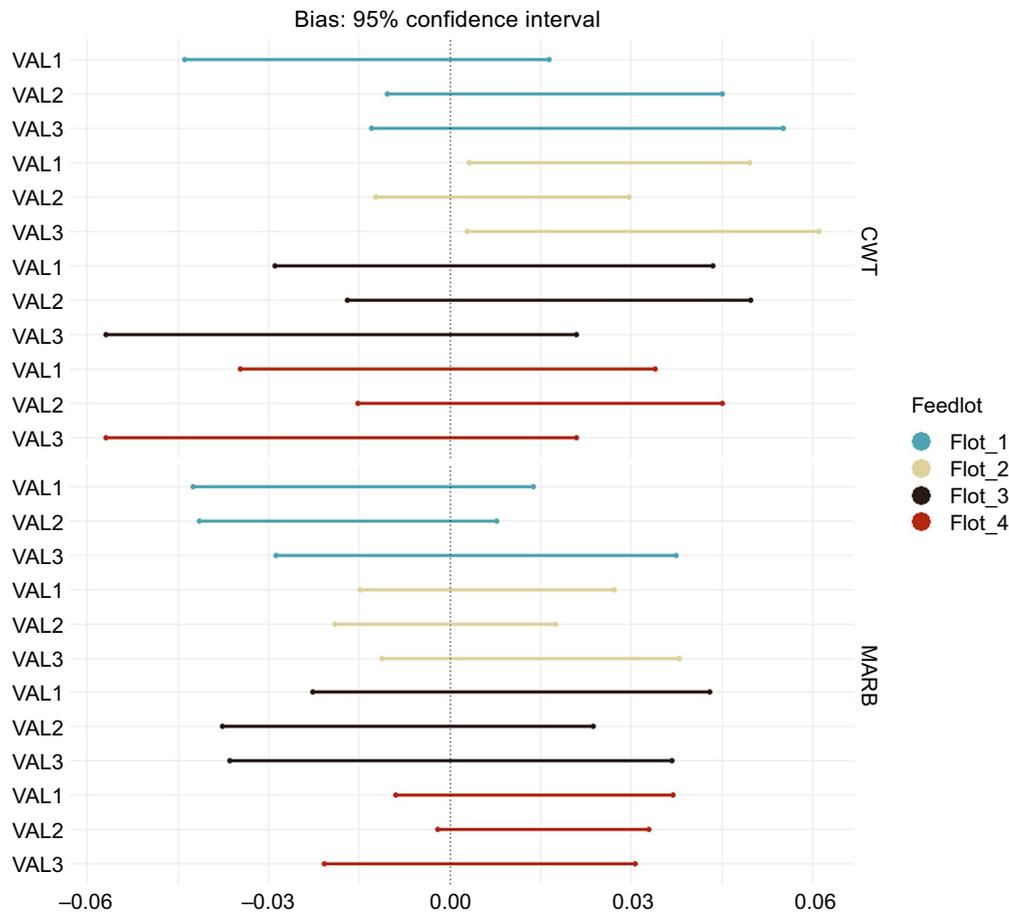


Fig. 3. Prediction bias 95% confidence interval across the 24 scenarios: two traits (CWT and MARB) by four feedlots (Flot_1, Flot_2, Flot_3 and Flot_4) and for the three validation schemes (VAL1, VAL2 and VAL3).

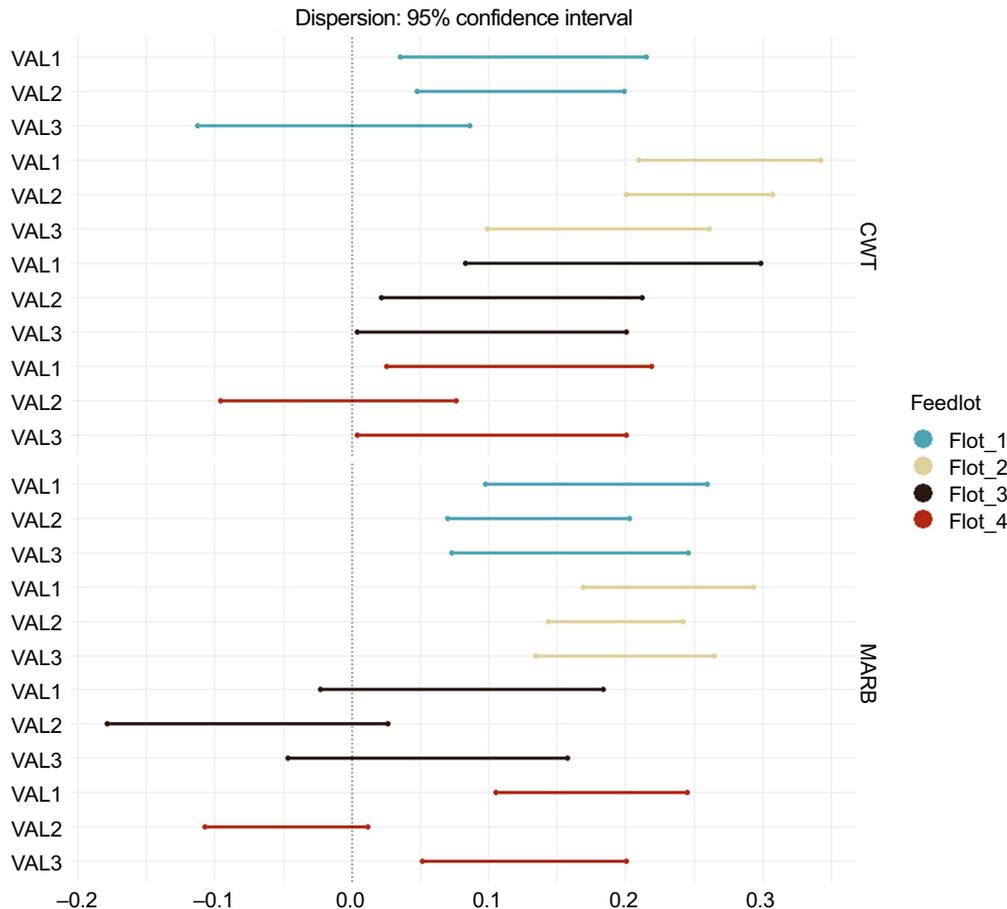


Fig. 4. Prediction dispersion 95% confidence interval across the 24 scenarios: two traits (CWT and MARB) by four feedlots (Flot_1, Flot_2, Flot_3 and Flot_4) and for the three validation schemes (VAL1, VAL2 and VAL3).

when phenotypes of the validation cohort were treated as missing values compared with h^2 estimates, using the whole dataset (Fig. 4).

Conclusions

Notwithstanding the importance of and difficulty in accurately modelling phenotypes from commercial operations, where data recording practices could be less stringent than in seedstock operations and research herds, the present study has highlighted the potential benefits of incorporating commercial data from Angus-based beef supply chain, which are independent of the ASBP and the Angus Australia reference population, into the existing reference population of Angus SteerSELECT genomic tool. In addition, the results have helped demonstrate to commercial beef producers the opportunity to apply genomic tools within commercial populations as part of routine management, since higher accuracies translate into an improved ability to predict performance,

reducing the risk of steers not performing to expectation during short- or long-feeding regimes.

References

- 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, 3–8 July 2022, Rotterdam, The Netherlands'. (Wageningen Academic Publishers)
- AUS-MEAT (2005) 'Handbook of Australian meat international red meat manual.' 7th edn. (AUS-MEAT: Sydney, NSW, 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
- Clark SA, Hickey JM, van der Werf JHJ (2011) Different models of genetic variation and their effect on genomic evaluation. *Genetics Selection Evolution* **43**, 18. doi:10.1186/1297-9686-43-18
- Daetwyler HD, Villanueva B, Woolliams JA (2008) Accuracy of predicting the genetic risk of disease using a genome-wide approach. *PLoS ONE* **3**, e3395. doi:10.1371/journal.pone.0003395

- Daetwyler HD, Pong-Wong R, Villanueva B, Woolliams JA (2010) The impact of genetic architecture on genome-wide evaluation methods. *Genetics* **185**, 1021–1031. doi:10.1534/genetics.110.116855
- de los Campos G, Vazquez AI, Fernando R, Klimentidis YC, Sorensen D (2013) Prediction of complex human traits using the genomic best linear unbiased predictor. *PLoS Genetics* **9**, e1003608. doi:10.1371/journal.pgen.1003608
- de Roos APW, Hayes BJ, Goddard ME (2009) Reliability of genomic predictions across multiple populations. *Genetics* **183**, 1545–1553. doi:10.1534/genetics.109.104935
- Druet T, Macleod IM, Hayes BJ (2014) Toward genomic prediction from whole-genome sequence data: impact of sequencing design on genotype imputation and accuracy of predictions. *Heredity* **112**, 39–47. doi:10.1038/hdy.2013.13
- Duff CJ, van der Werf JHJ, Parnell PF, Clark SA (2021) Redefining residual feed intake to account for marbling fat in beef breeding programs. *Animal Production Science* **61**, 1837–1844. doi:10.1071/AN21107
- Goddard M (2009) Genomic selection: prediction of accuracy and maximisation of long term response. *Genetica* **136**, 245–257. doi:10.1007/s10709-008-9308-0
- Habier D, Fernando RL, Dekkers JCM (2007) The impact of genetic relationship information on genome-assisted breeding values. *Genetics* **177**, 2389–2397. doi:10.1534/genetics.107.081190
- Habier D, Tetens J, Seefried F-R, Lichtner P, Thaller G (2010) The impact of genetic relationship information on genomic breeding values in German Holstein cattle. *Genetics Selection Evolution* **42**, 5. doi:10.1186/1297-9686-42-5
- 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
- Karaman E, Su G, Croue I, Lund MS (2021) Genomic prediction using a reference population of multiple pure breeds and admixed individuals. *Genetics 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
- 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
- Liu J, Pogorzelski G, Neveu A, Legrand I, Pethick D, Ellies-Oury M-P, Hocquette J-F (2021) Are marbling and the prediction of beef eating quality affected by different grading sites? *Frontiers in Veterinary Science* **8**, 611153. doi:10.3389/fvets.2021.611153
- Macedo FL, Reverter A, Legarra A (2020) Behavior of the linear regression method to estimate bias and accuracies with correct and incorrect genetic evaluation models. *Journal of Dairy Science* **103**, 529–544. doi:10.3168/jds.2019-16603
- Martín NP, Schreurs NM, Morris ST, López-Villalobos N, McDade J, Hickson RE (2022) Meat quality of beef-cross-dairy cattle from Angus or Hereford sires: a case study in a pasture-based system in New Zealand. *Meat Science* **190**, 108840. doi:10.1016/j.meatsci.2022.108840
- Mateescu RG, Garrick DJ, Garmyn AJ, VanOverbeke DL, Mafi GG, Reecy JM (2015) Genetic parameters for sensory traits in longissimus muscle and their associations with tenderness, marbling score, and intramuscular fat in Angus cattle. *Journal of Animal Science* **93**, 21–27. doi:10.2527/jas.2014-8405
- McGilchrist P, Polkinghorne RJ, Ball AJ, Thompson JM (2019) The meat standards Australia index indicates beef carcass quality. *Animal* **13**, 1750–1757. doi:10.1017/S1751731118003713
- Meuwissen T, Goddard M (2010) Accurate prediction of genetic values for complex traits by whole-genome resequencing. *Genetics* **185**, 623–631. doi:10.1534/genetics.110.116590
- Misztal I, Legarra A (2017) Invited review: efficient computation strategies in genomic selection. *Animal* **11**, 731–736. doi:10.1017/S1751731116002366
- Pérez-Enciso M, Misztal I (2011) Qxpk.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. *Genetics Selection Evolution* **47**, 84. doi:10.1186/s12711-015-0162-0
- 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, 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 (2021a) 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, Hine BC, Porto-Neto L, Li Y, Duff CJ, Dominik S, Ingham AB (2021b) ImmuneDEX: a strategy for the genetic improvement of immune competence in Australian Angus cattle. *Journal of Animal Science* **99**, skaa384. doi:10.1093/jas/skaa384
- 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, 3–8 July 2022, Rotterdam, The Netherlands'. (Wageningen Academic Publishers)
- Ríos Utrera A, Van Vleck LD (2004) Heritability estimates for carcass traits of cattle: a review. *Genetics and Molecular Research* **30**, 380–394.
- Simeone R, Misztal I, Aguilar I, Legarra A (2011) Evaluation of the utility of diagonal elements of the genomic relationship matrix as a diagnostic tool to detect mislabelled genotyped animals in a broiler chicken population. *Journal of Animal Breeding and Genetics* **128**, 386–393. doi:10.1111/j.1439-0388.2011.00926.x
- 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
- van Grevenhof IEM, van der Werf JHJ (2015) Design of reference populations for genomic selection in crossbreeding programs. *Genetics 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
- Wientjes YCJ, Veerkamp RF, Calus MPL (2013) The effect of linkage disequilibrium and family relationships on the reliability of genomic prediction. *Genetics* **193**, 621–631. doi:10.1534/genetics.112.146290
- Wientjes YCJ, Calus MPL, Goddard ME, Hayes BJ (2015) Impact of QTL properties on the accuracy of multi-breed genomic prediction. *Genetics Selection Evolution* **47**, 42. doi:10.1186/s12711-015-0124-6
- Wray NR, Yang J, Hayes BJ, Price AL, Goddard ME, Visscher PM (2013) Pitfalls of predicting complex traits from SNPs. *Nature Reviews Genetics* **14**, 507–515. doi:10.1038/nrg3457

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

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. This research did not receive any specific funding.

Acknowledgements. The authors acknowledge the vital in-kind support (steer access, data, personnel) provided by the participating feedlots of Bective (Whyalla Beef-NH Foods), Rangers Valley (Marubeni Corporation), Kerwee (Stockyard Beef) and Killara (Elders Rural Services). The technical assistance from Adrián López-Catalina and Fernanda Raidan is truthfully appreciated.

Author affiliations

^ACSIRO Agriculture and Food, Queensland Bioscience Precinct, 306 Carmody Road, St Lucia, Brisbane, Qld 4067, Australia.

^BCSIRO Agriculture and Food, F.D. McMaster Laboratory, Chiswick, New England Highway, Armidale, NSW 2350, Australia.

^CAngus Australia, 86 Glen Innes Road, Armidale, NSW 2350, Australia.