

# Genetic and phenotypic associations of feed efficiency with growth and carcass traits in Australian Angus cattle<sup>1</sup>

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**ABSTRACT:** Genetic and phenotypic parameters for feed efficiency, growth, and carcass traits for Australian Angus beef cattle were estimated. Growth traits included birth weight (**BWT**), 200-d weight (200dWT), 400-d weight (400dWT), and 600-d weight (600dWT). Traits associated with feed efficiency were average daily weight gain (**ADG**), metabolic midweight, average of daily feed intake (**FI**), feed conversion ratio (**FCR**), residual feed intake (**RFI**), and residual gain (**RG**). Carcass traits involved were carcass eye muscle area (**CEMA**), carcass intramuscular fat (**IMF**), subcutaneous fat depths at the 12th/13th rib (**CRIB**), rump P8 fat depth (**P8FAT**), and carcass weight (**CWT**). For growth traits, heritability estimates ranged from  $0.14 \pm 0.03$  for 200dWT to  $0.48 \pm 0.06$  for 600dWT. For feed efficiency traits, direct heritability estimates for FI, FCR, RFI, and RG were  $0.55 \pm 0.08$ ,  $0.20 \pm 0.06$ ,  $0.40 \pm 0.07$ , and  $0.19 \pm 0.06$ , respectively. High heritability

estimates were observed for CEMA, IMF, P8FAT, and CWT of  $0.52 \pm 0.09$ ,  $0.61 \pm 0.09$ ,  $0.55 \pm 0.09$ , and  $0.66 \pm 0.09$ , respectively. Strong positive genetic correlations were found for FI with 200dWT, 400dWT, and 600dWT of  $0.68 \pm 0.09$ ,  $0.42 \pm 0.11$ , and  $0.61 \pm 0.07$ , respectively. Weak genetic correlations were observed between RFI and growth traits. For carcass traits, genetic correlations between RFI and CEMA, IMF, CRIB, P8FAT, CWT were  $-0.19 \pm 0.14$ ,  $0.31 \pm 0.14$ ,  $0.18 \pm 0.16$ ,  $0.24 \pm 0.13$ , and  $0.40 \pm 0.12$ , respectively. There was a tendency for low to moderate unfavorable genetic associations between feed efficiency traits, evaluated as RFI and RG, with growth and carcass traits. This implies that selection for RFI would have slight negative impacts on growth and reduce carcass quality. To avoid this, it would be necessary to build selection indices to select feed efficient animals without compromising growth and meat quality.

**Key words:** beef cattle, carcass traits, feed efficiency, genetic correlation, growth traits, heritability

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## INTRODUCTION

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The cost of feed is a major expense in beef cattle production systems (Archer et al., 1999). Due to this cost, the efficiency of converting feed into useable animal products, commonly referred to as feed efficiency, has become a common objective in many beef cattle breeding programs (Arthur and Herd, 2008; Berry and Crowley, 2013). Feed efficiency in beef cattle breeding programs has been commonly targeted using residual feed intake (**RFI**), which is defined as the difference between actual and predicted intake based on its live weight

and growth rate over a given period (Koch et al., 1963). In Australia, the interest in feed efficiency has received much attention over the last 2 decades, with many studies designed to better understand the genetic relationships between feed efficiency and other traits in the breeding objective.

Previous studies have documented genetic variation between RFI and its component traits, as well as genetic associations between RFI with growth and carcass traits in growing cattle destined for markets that utilize short-grain feeding periods (Archer et al., 1999; Berry and Crowley, 2013). These studies were often constrained by the number of animals tested for all traits due to the high cost of recording such data. Despite the attention that RFI has received, there is not a general consensus relative to the genetic relationship among growth, carcass, and feed efficiency traits (Archer et al., 1999; Hill, 2012; Berry and Crowley, 2013). These genetic correlations strongly affect the ability to select for improved feed efficiency alongside improvement of growth and carcass quality. Consequently, the objective of this study was to estimate genetic and phenotypic parameters for feed efficiency traits with growth and carcass traits under a long-grain finishing feedlot regime for an Australian Angus cattle population.

## MATERIALS AND METHODS

### *Animal Care*

Animal records for feedlot based traits were collected with animal ethics approval AEC12-082. Data for growth and carcass traits for the animals used in this study were provided by the Angus Society of Australia (ASA) which were collected as part of routine commercial animal management and, therefore, were not subject to animal care and animal ethics committee approval.

### *Data*

All phenotypic data were collected on a group of Angus steers and heifers from the Angus Sire Benchmarking Program (ASBP, also known as the Angus Beef Information Nucleus). This structured dataset represented a progeny test of registered Angus sires from herds located in New South Wales and Victoria, Australia (Banks, 2011). Growth data included records for 6,371 animals, born between 2011 and 2016, for birth weight (BWT), 200-d weight (200dWT), 400-d weight (400dWT), and 600-d weight (600dWT).

Feed efficiency data were collected on 2,220 Angus steers of the ASBP, from 2013 to 2017 at Tullimba research feedlot (30°20'S, 151°10'E, altitude 560 m) near Kingstown, NSW, Australia. Initially, animals' age ranged from 500 to 600 d and animals weighed an average of 578 kg. Upon entry to the feedlot, animals were fed with a conditioned diet for 21-d period and they were subsequently measured for body weight (BW, kg; fortnightly) and daily feed intake (FI) over an additional 70-d (approximately) test period. During the test period, animals had *ad libitum* access to a full mixed ration composed of 74.8% tempered barley, 4.6% cotton hulls, 6% cottonseed, 5% mill run, 4.6% chopped hay, and 5% liquid mineral supplement. Daily individual FI (kg/d) was measured using the GrowSafe automatic feeding system installed at Tullimba, Kingstown, NSW, Australia (GrowSafe Systems Ltd., Airdrie, Alberta, Canada). The automatic feeding system was described and validated by Basarab et al. (2002, 2003). During the test period, average daily weight gain (ADG; kg/d) was calculated as the regression of weight on time (d), whereas metabolic weight at the midpoint of the test period (MMWT) was obtained as the midpoint BW raised to the 0.73 power ( $BW^{0.73}$ ) (Arthur et al., 2001b; Berry and Crowley, 2013). Feed conversion ratio (FCR) was obtained as the average daily FI divided by the ADG. RFI (kg/d) was estimated as the residual of regressing FI on ADG and MMWT with contemporary group (CG) included in the model, where the CG effect was defined as the concatenation of herd, year of birth, birth type (single or twin), breeder-defined management group, observation date, and age. Similarly, residual gain (RG; kg/d) was estimated as the residual of regressing ADG on FI and MMWT in the model that included the CG effect as defined previously (Arthur and Herd, 2008; Berry and Crowley, 2012; Berry and Crowley, 2013).

On completion of FI testing, the steers were feed for a further ~180 d to give a total grain finishing period of ~270 d as described by Duff et al. (2018). At the completion of the long-grain finishing period, carcass traits were recorded. Measured traits included carcass eye muscle area (CEMA), intramuscular fat (IMF), subcutaneous fat depth at the 12th/13th rib (CRIB), rump P8 fat depth (P8FAT), and carcass weight (CWT), with an average age at slaughter of 793 d for all traits. CGs for each trait were formed according to the BREEDPLAN format, which in this case included herd, year of birth, sex, birth type (single or twin),

breeder-defined management group, trial, day of measurement, and age, with animals subdivided by age in slices of 45 d (Graser et al., 2005).

Duplicated records and CG of less than 5 animals or with incomplete information were eliminated. The final number of CG for each trait was 138 for BWT and 200dWT; 85 for 400dWT; 108 for 600dWT; 80 for ADG, MMWT, FI, FCR, RFI, and RG; and 51 for CEMA, IMF, CRIB, P8FAT, and CWT. Descriptive statistics of the data after editing are in Table 1. Ranges of age for 200dWT, 400dWT, and 600dWT were 97 to 290, 291 to 492, and 493 to 820 d, respectively, with averages of 188, 404, and 552 d, respectively. The final pedigree file included ancestors over 14 generations with a total of 14,662 animals involving 1,454 sires and 7,835 dams; with 232 sires and 4,341 dams having progeny with phenotypic records.

### Statistical Analyses

For each trait, an optimal model was derived by testing the significance of fixed effects. The fixed effects tested were CG for each trait as well as linear and quadratic covariates of age (except BWT) and dam age; for carcass traits (other than CWT), linear and quadratic covariates of CWT were also tested. Analyses of the fixed effects were done with JMP version 14 software package (SAS Institute Inc., Cary, NC).

Variance components and heritabilities were estimated with univariate animal models. Models for the analysis included the significant fixed effects shown in Table 2. For all traits, a direct additive

genetic effect was included as a random effect; and for BWT and 200dWT, a maternal genetic effect was also included as a random effect. Genetic and phenotypic correlations were estimated using bivariate models with similar fixed (Table 2) and random effects as the univariate models. Univariate and bivariate models were analyzed using ASReml software (Gilmour et al., 2009).

In matrix notation, univariate animal models for 400dWT, 600dWT, feed efficiency, and carcass traits can be represented as follows:

$$y = Xb + Z_1u + e \quad (1)$$

For BWT and 200dWT, the univariate maternal effect models can be represented as follows:

$$y = Xb + Z_1u + Z_2m + e \quad (2)$$

where  $y$  is the vector of the phenotypes for the traits;  $b$  is the vector of fixed effects for the analyzed traits;  $u$  is the vector which contains animal random effects;  $m$  is the vector of random maternal genetic effects of the dams (model 2);  $X$  and  $Z_1$  are the incidence matrices relating observations to fixed and animal effects, respectively;  $Z_2$  is the incidence matrix relating observations to maternal effects (model 2); and  $e$  is the vector of residual effects for the analyzed traits. Model 2 assumed that direct and maternal genetic effects were uncorrelated, i.e.,  $\sigma_{AM} = 0$ .

For model 1, the expectations and variance matrices for random vectors are described as follows:

**Table 1.** Descriptive statistics for feed efficiency, growth, and carcass traits

Trait	<i>n</i>	Mean	Min <sup>1</sup>	Max <sup>2</sup>	SD	CV, %
Birth weight, kg	5,920	38.04	18.00	61.00	5.23	13.75
200-d weight, kg	5,764	229.37	88.00	394.00	44.49	19.40
400-d weight, kg	3,204	371.27	206.00	548.00	59.90	16.13
600-d weight, kg	3,513	511.81	289.00	882.00	106.83	20.87
Average daily gain, kg d	1,998	1.59	0.44	3.07	0.35	22.03
Metabolic midweight, kg	1,998	103.78	87.45	121.73	6.18	5.96
Feed intake, kg d	1,998	14.90	9.24	20.76	1.88	12.59
Feed conversion ratio	1,998	9.78	4.82	33.78	2.24	22.87
Residual feed intake, kg d	1,998	0.00	-5.62	4.08	1.11	-
Residual gain, kg d	1,998	0.00	-0.97	1.11	0.24	-
Carcass eye muscle area, mm <sup>2</sup>	1,634	90.23	66.00	124.00	9.31	10.32
Carcass intramuscular fat, %	1,382	10.02	3.20	25.10	3.25	32.38
Fat depths at the 12th/13th rib, mm	1,612	18.89	7.00	40.00	5.44	28.78
Rump P8 fat depth, mm	1,636	22.81	9.00	43.00	6.14	26.92
Carcass weight, kg	1,640	458.08	338.10	568.60	36.53	7.97

<sup>1</sup>Min is the minimum value.

<sup>2</sup>Max is the maximum value.

**Table 2.** Significant fixed effects for growth, feed efficiency, and carcass quality traits

Trait	Fix effect <sup>1</sup>						
	CG	Age	Age <sup>2</sup>	Dam	Dam <sup>2</sup>	CWT	CWT <sup>2</sup>
Birth weight, kg	<0.001***			<0.001***	<0.001***		
200-d weight, kg	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***		
400-d weight, kg	<0.001***	<0.001***	0.022*	0.012*	0.011*		
600-d weight, kg	<0.001***	<0.001***		<0.001***	<0.001***		
Average daily gain, kg d	<0.001***						
Metabolic midweight, kg	<0.001***						
Feed intake, kg d	<0.001***						
Feed conversion ratio	<0.001***						
Residual feed intake, kg d	<0.001***						
Residual gain, kg d	<0.001***						
Carcass eye muscle area, mm <sup>2</sup>	<0.001***	0.018*				0.007**	
Carcass intramuscular fat, %	<0.001***			0.044*			
Fat depths at the 12th/13th rib, mm	<0.001***	0.004**				0.002**	0.006**
Rump P8 fat depth, mm	<0.001***	0.003**					
Carcass weight, kg	<0.001***						

<sup>1</sup>CG = contemporary group effect; Age = age in days when the trait was measured; Age<sup>2</sup> = age of the measurement squared; Dam = age of the dam in days; Dam<sup>2</sup> = age of the dam squared; CWT = carcass weight, kg; CWT<sup>2</sup> = carcass weight squared, kg<sup>2</sup>.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

$$\mathbf{E} \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \end{bmatrix}; \mathbf{V} \begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix}$$

The expectations and variance matrices for random vectors in model 2 are described as follows:

$$\mathbf{E} \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \\ 0 \end{bmatrix}; \mathbf{V} \begin{bmatrix} \mathbf{u} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix}$$

The bivariate animal models involving feed efficiency and carcass traits can be represented as follows:

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{e} \quad (3)$$

Bivariate models involving BWT and 200dWT can be represented as follows:

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{m} + \mathbf{e} \quad (4)$$

where  $\mathbf{Y}$  is the vector of records for the traits;  $\mathbf{b}$  is the vector of fixed effects for the analyzed traits;  $\mathbf{u}$  is the vector which contains animal random effects;  $\mathbf{m}$  is the vector of random maternal genetic effects of the dams (model 4);  $\mathbf{X}$  and  $\mathbf{Z}_1$  are the incidence matrices relating observations to fixed and animal effects, respectively;  $\mathbf{Z}_2$  is the incidence matrix relating observations to maternal effects (model 4); and

$\mathbf{e}$  is the vector of residual effects for the analyzed traits. Model 4 assumed that direct and maternal genetic effects were uncorrelated, i.e.,  $\sigma_{AM} = 0$ .

For model 3, the expectations and variance matrices for random vectors are described as follows:

$$\mathbf{E} \begin{bmatrix} \mathbf{Y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \end{bmatrix};$$

$$\mathbf{V} \begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \\ \mathbf{R} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_u & 0 \\ 0 & \mathbf{I}_0 \otimes \mathbf{R} \end{bmatrix}$$

For model 4, the expectations and variance matrices for random vectors are described as follows:

$$\mathbf{E} \begin{bmatrix} \mathbf{Y} \\ \mathbf{u} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \\ 0 \end{bmatrix};$$

$$\mathbf{V} \begin{bmatrix} \mathbf{u} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_u & 0 & 0 \\ 0 & \mathbf{G}_m & 0 \\ 0 & 0 & \mathbf{R} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_u & 0 & 0 \\ 0 & \mathbf{A} \otimes \mathbf{G}_m & 0 \\ 0 & 0 & \mathbf{I}_0 \otimes \mathbf{R} \end{bmatrix}$$

where  $\mathbf{G}_u$ ,  $\mathbf{G}_m$ , and  $\mathbf{R}$  denote  $2 \times 2$  matrices containing additive genetic, maternal genetic (model 4),

and residual (co) variance components, respectively;  $\mathbf{A}$  is the numerator relationship matrix;  $\mathbf{I}_0$  is an identity matrix for the total number of observations; and  $\otimes$  is the Kronecker product.

## RESULTS AND DISCUSSION

Descriptive statistics for the studied traits are summarized in Table 1. Variance components and heritability estimates are presented in Table 3. In this study, high estimates of heritability were observed for carcass traits (from 0.34 to 0.66) compared with growth (from 0.14 to 0.48) and feed efficiency traits (from 0.19 to 0.55).

Heritability estimates for growth traits ranged from 0.14 for 200dWT to 0.48 for 600dWT. For BWT, both direct ( $0.33 \pm 0.04$ ) and maternal genetic ( $0.12 \pm 0.02$ ) were similar to the ranges of 0.34 to 0.52, and 0.07 to 0.13, respectively, published by Meyer (1992) in Australian Angus cattle. However, the direct heritability estimate for 200dWT ( $0.14 \pm 0.03$ ) was lower than the range (of 0.19 to 0.44) documented by Meyer (1992). The maternal heritability estimate for 200dWT in this study ( $0.25 \pm 0.02$ ) was higher than recent estimates in beef cattle (Torres-Vázquez and Spangler, 2016). A possible reason for the high maternal heritability estimate could be the amount of information available for dams in this dataset. There was a

lack of pedigree information on the dams and dams rarely had more than one progeny which made it difficult to separate maternal genetic and environmental components. Despite the problems with the structure of the data, some other authors have published similar maternal heritabilities in beef cattle consistent with the finding of this study (Trus and Wilton, 1988; Hetzel et al., 1990). The estimate of direct heritability for 400dWT ( $0.26 \pm 0.05$ ) was in the range of 0.21 to 0.31 published for several authors and summarized by Meyer (1992) in different beef cattle populations; however, our estimate for 600dWT ( $0.48 \pm 0.06$ ) was high when compared with the range summarized (0.26 to 0.43) for this trait. The higher heritability estimate for 600dWT observed in this study was more in line with papers by Meyer (2005) and Jeyaruban et al. (2009) (of 0.44 and 0.40, respectively), which illustrate that estimates of variance components can substantially change over time and therefore need to be reestimated as the population changes.

The heritability estimated for ADG ( $0.33 \pm 0.07$ ), FCR ( $0.20 \pm 0.06$ ), and RFI ( $0.40 \pm 0.07$ ) (Table 3) was similar to the pooled heritability estimates published by Berry and Crowley (2013), using a meta-analysis of 39 scientific publications on feed efficiency traits in growing animals. Furthermore, the heritability estimate for MMWT (of  $0.46 \pm 0.07$ ) in this study was similar

**Table 3.** Variance component and heritability estimates (SE) using univariate models for growth, feed efficiency, and carcass traits in Angus cattle

Trait <sup>2</sup>	Parameter <sup>1</sup>					
	$\sigma_a^2$	$\sigma_m^2$	$\sigma_e^2$	$\sigma_p^2$	$h_a^2$	$h_m^2$
BWT	6.25 ± 0.90	2.37 ± 0.47	10.38 ± 0.63	19.00 ± 0.40	0.33 ± 0.04	0.12 ± 0.02
200dWT	63.48 ± 12.81	111.95 ± 11.37	276.18 ± 12.57	451.61 ± 9.01	0.14 ± 0.03	0.25 ± 0.02
400dWT	219.70 ± 42.25	–	622.74 ± 38.58	842.44 ± 22.36	0.26 ± 0.05	–
600dWT	603.63 ± 81.59	–	655.99 ± 65.58	1,259.60 ± 34.78	0.48 ± 0.06	–
ADG	0.03 ± 0.01	–	0.05 ± 0.01	0.08 ± 0.00	0.33 ± 0.07	–
MMWT	10.28 ± 1.81	–	11.83 ± 1.53	22.11 ± 0.77	0.46 ± 0.07	–
FI	1.14 ± 0.18	–	0.94 ± 0.15	2.07 ± 0.07	0.55 ± 0.08	–
FCR	0.71 ± 0.22	–	2.83 ± 0.22	3.54 ± 0.12	0.20 ± 0.06	–
RFI	0.52 ± 0.10	–	0.78 ± 0.09	1.30 ± 0.04	0.40 ± 0.07	–
RG	0.01 ± 0.00	–	0.05 ± 0.00	0.06 ± 0.00	0.19 ± 0.06	–
CEMA	31.34 ± 5.87	–	28.63 ± 4.85	59.97 ± 2.36	0.52 ± 0.09	–
IMF	5.60 ± 0.99	–	3.56 ± 0.80	9.16 ± 0.40	0.61 ± 0.09	–
CRIB	8.83 ± 2.22	–	16.87 ± 1.97	25.69 ± 0.98	0.34 ± 0.08	–
P8FAT	16.62 ± 3.01	–	13.63 ± 2.46	30.25 ± 1.20	0.55 ± 0.09	–
CWT	740.85 ± 122	–	384.22 ± 96.93	1,125.10 ± 46.15	0.66 ± 0.09	–

<sup>1</sup> $\sigma_a^2$  = additive genetic variance;  $\sigma_m^2$  = maternal genetic variance;  $\sigma_e^2$  = residual variance;  $\sigma_p^2$  = phenotypic variance;  $h_a^2$  = additive heritability;  $h_m^2$  = maternal heritability.

<sup>2</sup>BWT = birth weight; 200dWT = 200-d weight; 400dWT = 400-d weight; 600dWT = 600-d weight; ADG = average daily gain; MMWT = metabolic midweight; FI = feed intake; FCR = feed conversion ratio; RFI = residual feed intake; RG = residual gain; CEMA = carcass eye muscle area; IMF = carcass intramuscular fat; CRIB = subcutaneous fat depths at the 12th/13th rib; P8FAT = rump P8 fat depth; CWT = carcass weight.

to the estimate of  $0.40 \pm 0.02$  provided by Arthur et al. (2001b) for Australian Angus cattle. Our estimate for FI ( $0.55 \pm 0.08$ ) was higher than previously estimated by Arthur et al. (2001a) of 0.39 in Australian Angus cattle and more recently by Mao et al. (2013) of 0.39 in a Canadian Angus population. In our study, FI was more heritable than RFI which is in contrast to previous studies (Arthur et al., 2001b; Mao et al., 2013). Interestingly, the heritability estimates for RG ( $0.19 \pm 0.06$ ) was lower than the mean heritability estimate of  $0.28 \pm 0.03$  published by Berry and Crowley (2013) in growing cattle. A possible explanation for the differences observed between the current study and those previously mentioned is animals in this study that were substantially older ( $\sim 520$  d) than those utilized by Arthur et al. (2001b) ( $\sim 268$  d) and Mao et al. (2013) ( $\sim 330$  d) and those summarized by Berry and Crowley (2013). The differences in heritability estimates confirm that feed efficiency traits can change over an animal's lifetime (i.e., feed efficiency traits measured at postweaning are different from late stage feedlot and cow feed efficiency) as suggested by Arthur et al. (2004). Furthermore, maternal and permanent environmental variance components for feed efficiency traits were not evident for this study because animals were measured at a later age than most previous studies. In the current study, estimates of both maternal genetic and maternal permanent environmental components for feed efficiency traits were zero, which is in agreement with the results from several other authors suggesting that the maternal components for feed efficiency traits are low (Hoque et al., 2007; Crowley et al., 2010).

Carcass traits in the present work were moderately to highly heritable, which is in agreement with previous work in beef cattle (Meyer et al., 2004; Rios-Utrera and Van Vleck, 2004). In general, heritability estimates for carcass traits were higher than those estimated for growth and feed efficiency traits. Our heritability estimates for CEMA ( $0.52 \pm 0.09$ ) and CRIB ( $0.34 \pm 0.08$ ) were close to the estimate of  $0.49 \pm 0.14$  and  $0.35 \pm 0.12$ , respectively, published by Mao et al. (2013) in Angus and Charolais steers. Furthermore, the estimates for CEMA were similar to the estimates reported by Meyer et al. (2004) in Australian Hereford cattle (0.59 to 0.67). The heritability estimate for CRIB ( $0.34 \pm 0.08$ ) was close to the estimate published by Reverter et al. (2003), of 0.41, in tropically adapted beef breeds in Australia, and Meyer et al. (2004), from 0.25 to 0.31, in Australian Hereford bulls. This illustrates that for traits such as CEMA- and

CRIB-estimated heritabilities seem to be relatively similar across breed types, the sex of the animal, and age of measurement. The heritability estimate for P8FAT ( $0.55 \pm 0.09$ ) was above the range of 0.20 to 0.30 Meyer et al. (2004), and Reverter et al. (2003) in temperate (0.36) and tropically adapted breeds (0.30), respectively. The estimate for IMF ( $0.61 \pm 0.09$ ) was higher than what was recently estimated in Angus animals by Mao et al. (2013) ( $0.37 \pm 0.11$ ) and also higher than those estimated by several authors in different beef cattle populations (Reverter et al., 2003; Meyer et al., 2004; Mateescu et al., 2015). Beef cattle in Australia are produced in 3 major finishing systems: 1) grass fed beef production with no grain feeding; 2) short period of grain finishing ( $<150$  d on feed); and 3) long periods of grain finishing ( $>200$  d on feed). This last period of grain finishing is generally associated with high-value markets that require a premium meat quality and large carcasses. Carcass traits in this study were measured after a long feeding period (250 to 270 d) with heavy animals at slaughter (458 kg) and perhaps animals could express more genetic variation compared with those fed for a short period (for 140 d) or pasture-based trials as observed in previous studies.

Genetic and phenotypic correlations estimated between growth traits are shown in Table 4. In the present work, the genetic correlations between BWT with the other growth traits were moderated with a range from 0.50 to 0.53, and between the other growth traits these correlations were higher (from 0.92 to 0.96). Genetic correlations, between growth traits, abound in the scientific literature and tend to be from moderate to high for different beef cattle populations, suggesting that the expression of these growth traits would be determined for the same group of genes (Meyer, 1992; Davis, 1993; Koots et al., 1994).

Genetic and phenotypic correlations among measures of feed efficiency and growth traits are summarized in Tables 5 and 6, respectively. As

**Table 4.** Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations with their standard errors between growth traits

Trait <sup>1</sup>	BWT	200dWT	400dWT	600dWT
BWT		$0.50 \pm 0.10$	$0.53 \pm 0.08$	$0.53 \pm 0.07$
200dWT	$0.37 \pm 0.01$		$0.96 \pm 0.03$	$0.92 \pm 0.03$
400dWT	$0.36 \pm 0.02$	$0.70 \pm 0.01$		$0.92 \pm 0.03$
600dWT	$0.39 \pm 0.02$	$0.64 \pm 0.01$	$0.77 \pm 0.01$	

<sup>1</sup>BWT = birth weight; 200dWT = 200-d weight; 400dWT = 400-d weight; 600dWT = 600-d weight.

**Table 5.** Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations with their standard errors between feed efficiency traits

Trait <sup>1</sup>	ADG	MMWT	FI	FCR	RFI	RG
ADG		0.63 ± 0.10	0.72 ± 0.08	-0.69 ± 0.09	0.34 ± 0.14	0.81 ± 0.06
MMWT	0.33 ± 0.02		0.67 ± 0.07	-0.21 ± 0.17	0.18 ± 0.13	0.21 ± 0.17
FI	0.45 ± 0.02	0.54 ± 0.02		-0.12 ± 0.16	0.83 ± 0.04	0.19 ± 0.16
FCR	-0.78 ± 0.01	-0.02 ± 0.02	0.05 ± 0.02		0.20 ± 0.16	-0.92 ± 0.04
RFI	0.01 ± 0.02	0.00 ± 0.02	0.80 ± 0.01	0.37 ± 0.02		-0.13 ± 0.17
RG	0.89 ± 0.01	0.00 ± 0.02	0.00 ± 0.02	-0.90 ± 0.00	-0.34 ± 0.02	

<sup>1</sup>ADG = average daily gain; MMWT = metabolic midweight; FI = feed intake; FCR = feed conversion ratio; RFI = residual feed intake; RG = residual gain.

**Table 6.** Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations with their standard errors between carcass traits

Trait <sup>1</sup>	CEMA	IMF	CRIB	P8FAT	CWT
CEMA		0.06 ± 0.13	-0.08 ± 0.15	-0.22 ± 0.13	0.03 ± 0.13
IMF	0.03 ± 0.03		-0.11 ± 0.15	-0.07 ± 0.13	0.21 ± 0.12
CRIB	-0.14 ± 0.03	0.04 ± 0.03		0.50 ± 0.12	0.14 ± 0.15
P8FAT	-0.16 ± 0.03	0.01 ± 0.03	0.33 ± 0.02		0.27 ± 0.11
CWT	0.01 ± 0.04	0.09 ± 0.03	0.02 ± 0.04	0.24 ± 0.03	

<sup>1</sup>CEMA = carcass eye muscle area; IMF = carcass intramuscular fat; CRIB = subcutaneous fat depths at the 12th/13th rib; P8FAT = rump P8 fat depth; CWT = carcass weight.

expected, RFI and RG were phenotypically independent of the components production traits of ADG and MMWT, and FI and MMWT, respectively (Table 5). For RFI, there were positive, unfavorable genetic associations with ADG (0.34) and MMWT (0.18). These findings are contrary to those found by Arthur et al. (2001b), who found weak negative, favorable associations between RFI and its component traits. Furthermore, the genetic correlation between RFI and FI (0.83) was stronger than the estimate of 0.51 published by Mao et al. (2013). The correlations estimated in this study suggest that although RFI is phenotypically independent of ADG and MMWT, it is not genetically independent of older animals as observed in this study. It also implies that selection for more feed efficient animals would reduce FI, but would also decrease ADG. Although contrary to Arthur et al. (2001b), similar findings have been observed in other cattle breeds (Berry and Crowley, 2013; Ceacero et al., 2016). Following the same trend as the correlation between RFI and FI, the genetic correlation between RG and ADG was strongly positive which has been observed previously by Crowley et al. (2010). Similarly, the genetic correlation estimated between FCR and ADG ( $-0.69 \pm 0.09$ ) was negative and favorable, in agreement with other studies in beef cattle (Arthur et al., 2001a; Arthur et al., 2001b; Schenkel et al., 2004). The genetic correlation between FCR and RFI

was moderate ( $0.20 \pm 0.16$ ) and lower than those reported by Arthur et al. (2001b) and Mao et al. (2013) in younger growing cattle. Interestingly, Berry and Crowley (2013) in a meta-analysis documented that this correlation can range widely from  $-0.62$  to  $0.76$  with an average of  $0.39$ . A possible explanation for the large differences is that RFI and FCR are unique traits across studies where the animals used range in age and growth stages from young growing cattle to more mature animals (as used in this study).

Among carcass traits, the genetic correlation between CRIB and P8FAT was the highest and positive ( $0.50 \pm 0.12$ ), followed by the association between P8FAT and CWT ( $0.27 \pm 0.11$ ), and IMF and CWT ( $0.21 \pm 0.12$ ). Our estimated genetic correlation between CRIB with P8FAT was similar to the estimate from Robinson and Oddy (2004) in feedlot-finished beef cattle. Genetic correlations between CWT with the other carcass traits were weak to moderate, suggesting that selection for heavier CWTs would result in higher values for IMF, CRIB, and P8FAT (Table 6). These positive genetic correlations agreed with the estimates published by Hoque et al. (2006) in Japanese Black cattle.

Of specific interest in the present work were the genetic correlations between feed efficiency traits with growth and carcass traits. In general, RFI presented stronger genetic associations with growth traits compared with RG and FCR (Table 7). The

**Table 7.** Estimates of genetic and phenotypic correlations with their standard errors for growth and carcass traits with feed efficiency traits

Trait <sup>1</sup>	ADG	MMWT	FI	FCR	RFI	RG
Genetic correlations						
BWT	0.27 ± 0.12	0.30 ± 0.10	0.20 ± 0.10	-0.09 ± 0.15	0.00 ± 0.12	0.19 ± 0.15
200dWT	0.45 ± 0.14	0.92 ± 0.04	0.68 ± 0.09	0.05 ± 0.18	0.25 ± 0.14	-0.06 ± 0.18
400dWT	0.27 ± 0.14	0.90 ± 0.04	0.42 ± 0.11	0.10 ± 0.17	-0.02 ± 0.14	-0.12 ± 0.17
600dWT	0.53 ± 0.10	0.98 ± 0.01	0.61 ± 0.07	-0.12 ± 0.15	0.15 ± 0.11	0.09 ± 0.15
CEMA	0.06 ± 0.15	0.12 ± 0.14	-0.05 ± 0.13	-0.05 ± 0.18	-0.19 ± 0.14	0.08 ± 0.18
IMF	0.11 ± 0.15	0.20 ± 0.13	0.30 ± 0.12	0.06 ± 0.18	0.31 ± 0.14	-0.12 ± 0.18
CRIB	0.23 ± 0.17	-0.23 ± 0.15	0.11 ± 0.15	-0.23 ± 0.20	0.18 ± 0.16	0.28 ± 0.20
P8FAT	0.27 ± 0.14	-0.03 ± 0.13	0.20 ± 0.12	-0.12 ± 0.17	0.24 ± 0.13	0.24 ± 0.17
CWT	0.71 ± 0.09	0.78 ± 0.05	0.73 ± 0.07	-0.26 ± 0.16	0.40 ± 0.12	0.33 ± 0.16
Phenotypic correlations						
BWT	0.13 ± 0.02	0.33 ± 0.02	0.20 ± 0.02	0.01 ± 0.02	0.01 ± 0.03	0.01 ± 0.02
200dWT	0.14 ± 0.02	0.64 ± 0.01	0.33 ± 0.02	0.07 ± 0.02	0.01 ± 0.02	-0.08 ± 0.02
400dWT	0.10 ± 0.03	0.82 ± 0.01	0.34 ± 0.03	0.11 ± 0.03	-0.08 ± 0.03	-0.15 ± 0.03
600dWT	0.34 ± 0.02	0.90 ± 0.00	0.48 ± 0.02	-0.07 ± 0.02	-0.01 ± 0.02	0.05 ± 0.02
CEMA	-0.03 ± 0.03	-0.11 ± 0.03	-0.09 ± 0.03	0.00 ± 0.03	-0.05 ± 0.03	0.01 ± 0.03
IMF	0.03 ± 0.03	0.05 ± 0.03	0.08 ± 0.03	0.01 ± 0.03	0.07 ± 0.03	-0.01 ± 0.03
CRIB	0.02 ± 0.03	-0.11 ± 0.03	0.04 ± 0.03	-0.02 ± 0.03	0.06 ± 0.03	0.02 ± 0.03
P8FAT	0.09 ± 0.03	0.11 ± 0.03	0.17 ± 0.03	-0.01 ± 0.03	0.12 ± 0.03	0.02 ± 0.03
CWT	0.43 ± 0.02	0.72 ± 0.01	0.52 ± 0.02	-0.14 ± 0.03	0.11 ± 0.03	0.17 ± 0.03

<sup>1</sup>BWT = birth weight; 200dWT = 200-d weight; 400dWT = 400-d weight; 600dWT = 600-d weight; ADG = average daily gain; MMWT = metabolic midweight; FI = feed intake; FCR = feed conversion ratio; RFI = residual feed intake; RG = residual gain; CEMA = carcass eye muscle area; IMF = carcass intramuscular fat; CRIB = subcutaneous fat depths at the 12th/13th rib; P8FAT = rump P8 fat depth; CWT = carcass weight.

genetic correlation between RFI with 200dWT and 600dWT was slightly positive. This result contrasts those found by [Arthur et al. \(2001b\)](#) and [Jeyaruban et al. \(2009\)](#) who have published negative but favorable genetic associations between RFI with 200dWT and 600dWT. The genetic correlation between RFI and 400dWT was close to zero. In Angus cattle, negative and favorable genetic correlations have been published by [Arthur et al. \(2001b\)](#) and [Jeyaruban et al. \(2009\)](#). The differences observed between the current study and those by [Arthur et al. \(2001b\)](#) and [Jeyaruban et al. \(2009\)](#) may be attributed to the difference in performance between bulls and steers. The previous mentioned studies included many bull records from industry seedstock herds, whereas the current study is limited to commercial steers and heifers. It also suggests that the environments where steers were recorded (from essentially commercial environments) may be different from those where bulls were raised. In this study, the genetic correlations for FCR and RG with growth and carcass traits were very similar but of the opposite sign, which reflects the direction of selection (increases in RG and decreases in FCR are desired), which further confirms the strong relationship between FCR and RG observed in this study.

Regardless of the high standard errors for RFI, positive but undesirable genetic associations of these traits with carcass traits were estimated, meaning that selecting more efficient animals would decrease values for CRIB and P8FAT ([Table 7](#)). [McDonagh et al. \(2001\)](#) documented, after 1 generation of divergent selection, that high-efficient steers fed for between 112 and 180 d had less subcutaneous fat over their rib and rump, but similar cross-sectional area of the eye muscle than low efficient steers. This phenomenon has also been observed by several others ([Arthur et al., 2001b](#); [Robinson and Oddy, 2004](#); [Ceacero et al., 2016](#)), and our results further confirm that fat animals tended to be less efficient when efficiency is defined using RFI. In contrast, there were positive and unfavorable genetic correlations for RFI with IMF ( $0.31 \pm 0.14$ ). Similar findings have been reported in other beef cattle populations where more efficient cattle tend to reduce carcass quality traits ([Archer et al., 1999](#); [Nkrumah et al., 2007](#); [Berry and Crowley, 2013](#)). Positive, but unfavorable, genetic correlations were estimated between RFI and CWT ( $0.40 \pm 0.12$ ), which is different from the correlations between RFI and CWT ( $0.12 \pm 0.20$ ) observed by [Mao et al. \(2013\)](#). One potential reason for the differences observed between this study and [Mao et al. \(2013\)](#) is that



animals in the current study were older, heavier, and fed grain for a longer period. This also suggests that as animals are fed for longer periods the adjustment for growth (ADG) and MMWT no longer ensure low correlations between RFI and other growth-related production traits.

Several authors have documented negative properties for ratio traits such as FCR because they do not guarantee the selection for the most efficient animals (Gunsett, 1984; Bishop et al., 1991; Arthur et al., 2001b; Berry and Crowley, 2013). The genetic correlations estimated in this study were close to zero or slightly negative (favorable) between FCR and carcass traits. This has been observed previously by Arthur et al. (2001b) and Mao et al. (2013). The strong genetic correlations between FCR and RG ( $-0.92 \pm 0.04$ ), and between RG with ADG ( $0.81 \pm 0.06$ ) were consistent with those published by Crowley et al. (2010). This suggests that RG targeted similar outcomes to FCR whilst avoiding the negative properties of ratio traits.

Genetic and phenotypic correlations between FI and growth and carcass traits were all higher than those estimated for RFI. This is not surprising given that RFI is essentially FI with the phenotypic variation due to growth (ADG) and maintenance (MMWT) removed. Such results agree with previous studies by Arthur et al. (2001b) and Mao et al. (2013) and those summarized by Berry and Crowley (2013).

Medium and high positive genetic correlations between growth traits and CWT were found in this study (Table 8), and have also been published by other authors in beef cattle (Crews et al., 2004; Bouquet et al., 2010). Genetic correlations between P8FAT and CRIB with growth traits were negative, from moderate to weak, indicating that selection for

faster growth rates would slightly decrease carcass rib and rump fat for this population. There were low, near zero phenotypic correlations between IMF and growth traits (and CWT), which is in agreement with previous studies (Reverter et al., 2003; Meyer et al., 2004). In contrast, previous studies that estimated the genetic correlation between growth traits and IMF suggested that there was a negative correlation between such traits (Meyer et al., 2004). In this study, CWT was positively correlated with growth traits. In addition, IMF was positively associated with 200dWT, 400dWT, and 600dWT (Table 8). In Australia, both growth and marbling (IMF) have been a large part of the breeding objective for Angus cattle, and the trend of selection for high growth and high marbling may be observed in these genetic correlations.

Genetic parameters estimated in the current study may be useful for calculating the prediction of genetic values, direct and correlated selection response, and for developing economic selection indices. They are also key to understanding the current makeup of the Australia Angus population. It is important to acknowledge that information on genetic parameters for feed efficiency traits is still limited when compared with that available for growth traits. Fewer studies are available because feed efficiency traits and carcass quality traits are expensive and difficult to measure in beef cattle. This has meant that there are limited studies that have attempted to quantify the genetic relationships between feed efficiency traits and carcass traits. These studies are limited by the number of observations and therefore large standard errors have been reported. Such large standard errors have also made it difficult to generalize conclusions across relatively underpowered studies. Large standard

**Table 8.** Estimates of genetic and phenotypic correlations with their standard errors for carcass traits with growth traits

Trait <sup>1</sup>	CEMA	IMF	CRIB	P8FAT	CWT
Genetic correlations					
BWT	0.05 ± 0.13	-0.09 ± 0.12	-0.27 ± 0.14	-0.03 ± 0.12	0.26 ± 0.11
200dWT	0.07 ± 0.15	0.18 ± 0.15	-0.47 ± 0.16	-0.06 ± 0.15	0.64 ± 0.09
400dWT	0.05 ± 0.15	0.21 ± 0.14	-0.39 ± 0.16	-0.23 ± 0.14	0.56 ± 0.10
600dWT	0.10 ± 0.12	0.19 ± 0.12	-0.26 ± 0.14	-0.08 ± 0.12	0.75 ± 0.05
Phenotypic correlations					
BWT	-0.08 ± 0.03	-0.04 ± 0.03	-0.17 ± 0.03	-0.06 ± 0.03	0.23 ± 0.03
200dWT	-0.07 ± 0.03	-0.05 ± 0.03	-0.09 ± 0.03	0.11 ± 0.03	0.46 ± 0.02
400dWT	-0.12 ± 0.04	0.04 ± 0.04	-0.09 ± 0.04	0.10 ± 0.03	0.54 ± 0.02
600dWT	-0.13 ± 0.03	0.04 ± 0.03	-0.14 ± 0.03	0.08 ± 0.03	0.66 ± 0.01

<sup>1</sup>BWT = birth weight; 200dWT = 200-d weight; 400dWT = 400-d weight; 600dWT = 600-d weight; CEMA = carcass eye muscle area; IMF = carcass intramuscular fat; CRIB = subcutaneous fat depths at the 12th/13th rib; P8FAT = rump P8 fat depth; CWT = carcass weight.

errors could be, in part, due to small number of animal being measured but also due to inaccuracies in the measurement of FI and growth (Hill, 2012).

RFI has been the preferred feed efficiency trait for genetic improvement of feed efficiency in beef cattle. RFI and RG as linear indexes increase the response to selection compared with some disadvantages of ratio traits (Gunsett, 1984). A major difference between most studies is related to the differences in age of measurements for feed efficiency and carcass traits. It is often difficult to generalize and compare the impact of selecting for RFI across populations because for most studies RFI may in fact be a different unique trait, with all studies being influenced by differences in management conditions, diets (e.g., *ad libitum* feeding, restricted feeding, and composition or diet type), finishing systems, and breeds, making it difficult to generalize conclusions across studies.

Results of this study suggest the existence of low and positive (unfavorable) genetic associations between feed efficiency measured as RFI with meat quality traits measured under a long feeding (~270 d) production system. This implies that long-term selection for RFI could negatively affect meat quality carcass traits which are highly valuable for the markets targeted in this production system. It also illustrates the need for a balanced selection index, considering all other economically important traits and that single trait selection for RFI may have undesirable outcomes for many production traits. Further studies that expand the number of records and test different production systems (pasture based and short grain feeding) are essential to elucidate the direction of genetic correlations to design optimal breeding programs.

In conclusion, all traits were from moderately to highly heritable, indicating that all traits would respond favorably to selection. Response to selection could be higher for RFI compared with FCR and RG. However, selection for feed efficient animals based on RFI would result in cattle with lighter weights and lower meat quality. To avoid these problems, it would be necessary to build selection indices to select efficient animals with favorable weights and beef quality.

## LITERATURE CITED

- Archer, J. A., E. C. Richardson, R. M. Herd, and P. F. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. *Aust. J. Agric. Res.* 50:147–161. doi:10.1071/A98075
- Arthur, P. F., J. A. Archer, and R. M. Herd. 2004. Feed intake and efficiency in beef cattle: overview of recent Australian research and challenges for the future. *Aust. J. Exp. Agric.* 44:361–369. doi:10.1071/EA02162
- Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001b. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in angus cattle. *J. Anim. Sci.* 79:2805–2811. doi:10.2527/2001.79112805x
- Arthur, J. P. F., and R. M. Herd. 2008. Residual feed intake in beef cattle. *R. Bras. Zootec.* 37 (Suppl.):269–279. doi:10.1590/S1516-35982008001300031
- Arthur, P. F., G. Renand, and D. Krauss. 2001a. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young charolais bulls. *Livest. Prod. Sci.* 68:131–139. doi:10.1016/S0301-6226(00)00243-8
- Banks, R. G. 2011. Progress in implementation of beef information nucleus portfolio in the Australian beef industry. *Proc. Assoc. Adv. Anim. Breed. Genet.* 19:399–402. <http://www.aaabg.org/livestocklibrary/2011/banks399.pdf> (accessed June 5 2018).
- Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. *Can. J. Anim. Sci.* 83:189–204. doi:10.4141/A02-065
- Basarab, J. A., K. Toogood, K. L. Lyle, and V. Ohama. 2002. Validation of the GrowSafe® System for determining individual animal feed intake. Final report. In *Net feed intake in young growing cattle*. Canadian Alberta Beef Industry Development Fund, Project Number: 98AB249. Alberta Agriculture, Food and Rural Development, Lacombe Research Centre, Lacombe, Alberta, AB. Final Report. p. 13–32.
- Berry, D. P., and J. J. Crowley. 2012. Residual intake and body weight gain: a new measure of efficiency in growing cattle. *J. Anim. Sci.* 90:109–115. doi:10.2527/jas.2011-4245
- Berry, D. P., and J. J. Crowley. 2013. Cell biology symposium: genetics of feed efficiency in dairy and beef cattle. *J. Anim. Sci.* 91:1594–1613. doi:10.2527/jas.2012-5862
- Bishop, M. D., M. E. Davis, W. R. Harvey, G. R. Wilson, and B. D. VanStavern. 1991. Divergent selection for postweaning feed conversion in Angus beef cattle: II. Genetic and phenotypic correlations and realized heritability estimate. *J. Anim. Sci.* 69:4360–4367. doi:10.2527/1991.69114360x
- Bouquet, A., M.-N. Fouilloux, G. Renand, and F. Phocas. 2010. Genetic parameters for growth, muscularity, feed efficiency and carcass traits of young beef bulls. *Livest. Sci.* 129:38–48. doi:10.1016/j.livsci.2009.12.010
- Ceacero, T. M., M. E. Mercadante, J. N. Cyrillo, R. C. Canesin, S. F. Bonilha, and L. G. de Albuquerque. 2016. Phenotypic and genetic correlations of feed efficiency traits with growth and carcass traits in Nelore cattle selected for postweaning weight. *PLoS ONE* 11:e0161366. doi:10.1371/journal.pone.0161366
- Crews, D. H., Jr., M. Lowerison, N. Caron, and R. A. Kemp. 2004. Genetic parameters among growth and carcass traits of Canadian Charolais cattle. *Can. J. Anim. Sci.* 84:589–597. doi:10.4141/A04-019
- Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr, R. D. Evans, and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. *J. Anim. Sci.* 88:885–894. doi:10.2527/jas.2009-1852

- Davis, G. P. 1993. Genetic parameters for tropical beef cattle in northern Australia: a review. *Aust. J. Agric. Res.* 44:179–198. doi:10.1071/AR9930179
- Duff, C., J. H. J. van der Werf, and S. A. Clark. 2018. Comparison of two live-animal ultrasound systems to predict carcass intramuscular fat and marbling in Australian Angus cattle. In: *Proc. 11th World Congr. Genet. Appl. Livest. Prod.* No. Electronic Poster Session. Auckland, NZ. p. 262. <http://www.wcgalp.org/system/files/proceedings/2018/comparison-two-live-animal-ultrasound-systems-predict-carcass-intramuscular-fat-and-marbling.pdf> (accessed June 5 2018).
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2009. ASReml user guide release 3.0. VSN Int. Ltd., Hemel Hempstead, UK.
- Graser, H.-U., B. Tier, D. J. Johnston, and S. A. Barwick. 2005. Genetic evaluation for the beef industry in Australia. *Aust. J. Agric. Res.* 45:913–921. doi:10.1071/EA05075
- Gunsett, F. C., 1984. Linear index selection to improve traits defined as ratios. *J. Anim. Sci.* 59:1185–1193. doi:10.2527/jas1984.5951185x
- Hetzel, D. J. S., R. L. Quaas, G. W. Seifert, K. G. Bean, H. M. Burrow, and W. J. Aspden. 1990. Genetic parameters for growth of tropical beef cattle. *Proc. Aust. Assoc. Anim. Breed. Genet.* 8:517–520. <http://www.aaabg.org/livestocklibrary/1990/ab90107.pdf> (accessed June 4 2018).
- Hill, R. A. 2012. *Feed efficiency in the beef industry*. John Wiley & Sons, Ames, IA.
- Hoque, M. A., P. F. Arthur, K. Hiramoto, A. R. Gilmour, and T. Oikawa. 2007. Variance components due to direct genetic, maternal genetic and permanent environmental effect for growth and feed-efficiency traits in young male Japanese black cattle. *J. Anim. Breed. Genet.* 124:102–107. doi:10.1111/j.1439-0388.2007.00648.x
- Hoque, M. A., P. F. Arthur, K. Hiramoto, and T. Oikawa. 2006. Genetic parameters for carcass traits of field progeny and their relationships with feed efficiency traits of their sire population for Japanese Black cattle. *Livest. Sci.* 100:251–260. doi:10.1016/j.livsci.2005.09.006
- Jeyaruban, M. G., D. J. Johnston, and H. U. Graser. 2009. Genetic association of net feed intake measured at two stages with insulin-like growth factor-I, growth and ultrasound scanned traits in Angus cattle. *Proc. Assoc. Adv. Anim. Breed. Genet.* 18:584–587. <http://www.aaabg.org/proceedings18/files/jeyaruban584.pdf> (accessed June 1, 2018).
- Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22:486–494. doi:10.2527/jas1963.222486x
- Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. *Anim. Breed. Abstr.* 62:826–853.
- Mao, F., L. Chen, M. Vinsky, E. Okine, Z. Wang, J. Basarab, D. H. Crews, Jr, and C. Li. 2013. Phenotypic and genetic relationships of feed efficiency with growth performance, ultrasound, and carcass merit traits in Angus and Charolais steers. *J. Anim. Sci.* 91:2067–2076. doi:10.2527/jas.2012-5470
- Mateescu, R. G., D. J. Garrick, A. J. Garmyn, D. L. VanOverbeke, G. G. Mafi, and J. M. Reecy. 2015. Genetic parameters for sensory traits in longissimus muscle and their associations with tenderness, marbling score, and intramuscular fat in Angus cattle. *J. Anim. Sci.* 93:21–27. doi:10.2527/jas.2014-8405
- McDonagh, M. D., R. M. Herd, E. C. Richardson, V. H. Oddy, J. A. Archer, and P. F. Arthur. 2001. Meat quality and the Calpain system of feedlot steers following a single generation of divergent selection for residual feed intake. *Aust. J. Exp. Agric.* 41:1013–1021. doi:10.1071/EA00024
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31:179–204. doi:10.1016/0301-6226(92)90017-X
- Meyer, K. 2005. Estimates of covariance functions for growth of Angus cattle from random regression analyses fitting B-spline functions. *Proc. Aust. Assoc. Anim. Breed. Genet.* 16:52–55. <http://www.aaabg.org/livestocklibrary/2005/052meyer.pdf> (accessed June 5 2018).
- Meyer, K., D. J. Johnston, and H.-U. Graser. 2004. Estimates of the complete genetic covariance matrix for traits in multi-trait genetic evaluation of Australian Hereford cattle. *Aust. J. Agric. Res.* 55:195–210. doi:10.1071/AR03164
- Nkrumah, J. D., D. H. Keisler, D. H. Crews Jr., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, and S. S. Moore. 2007. Genetic and phenotypic relationships of serum leptin concentration with performance, efficiency of gain, and carcass merit of feedlot cattle. *J. Anim. Sci.* 85:2147–2155. doi:10.2527/jas.2006-767
- Reverter, A., D. J. Johnston, D. Perry, M. E. Goddard, and H. M. Burrow. 2003. Genetic and phenotypic characterisation of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds. 2. Abattoir carcass traits. *Aust. J. Agric. Res.* 54:119–134. doi:10.1071/AR02086
- Rios-Utrera, A., and L. D. Van Vleck. 2004. Heritability estimates for carcass traits of cattle: a review. *Genet. Mol. Res.* 3:380–394. <https://digitalcommons.unl.edu/animalscifacpub/242/> (accessed March 1, 2018).
- Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Livest. Prod. Sci.* 90:255–270. doi:10.1016/j.livprodsci.2004.06.011
- Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth and body composition traits of young beef bulls. *Can. J. Anim. Sci.* 84:177–185. doi:10.4141/A03-085
- Torres-Vázquez, J. A., and M. L. Spangler. 2016. Genetic parameters for docility, weaning weight, yearling weight, and intramuscular fat percentage in hereford cattle. *J. Anim. Sci.* 94:21–27. doi:10.2527/jas.2015-9566
- Trus, D., and J. W. Wilton. 1988. Genetic parameters for maternal traits in beef cattle. *Can. J. Anim. Sci.* 68:119–128. doi:10.4141/cjas88-011