

Phenotypic and genetic relationships for feed intake, feed efficiency, body composition and cow milk yield measured postweaning and in mature beef cows

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ABSTRACT

Context. Providing feed is the largest cost in beef production. Genetic variation exists in feed efficiency traits in young cattle but the genetic associations with feed efficiency traits in cows are poorly understood, but if strong and favourable, they might be used to improve feed efficiency of cows. **Aim.** To examine the phenotypic and genetic relationships among feed intake, feed efficiency, body composition and cow milk yield measured in young cattle and in cows. **Methods.** Data on 1783 young Angus, Hereford, Polled Hereford and Shorthorn bulls and heifers, and for 751 of the females as cows, were used to calculate the phenotypic and genetic relationships among feed efficiency traits, body composition and cow milk yield measured postweaning and in mature cows. The young cattle were tested for feed intake and feed efficiency at approximately 9 months of age and the females, after two calvings, were tested again as non-pregnant, non-lactating cows at approximately 4 years of age. **Key results.** At the postweaning test, the heritability estimates for feed intake, average daily gain, test weight, residual feed intake (RFI), feed conversion ratio, rump fat depth and eye-muscle area were 0.47, 0.32, 0.46, 0.42, 0.28, 0.47 and 0.20 respectively. Corresponding heritability estimates in the cow test were 0.27, 0.35, 0.74, 0.22, 0.30, 0.47 and 0.12. Heritability estimates for 400-day weight, cow 4-year weight and cow milk yield were 0.47, 0.62 and 0.15 respectively. Genetic correlations between traits measured postweaning and the same traits measured in the cow were moderate to high, and for the feed efficiency trait, RFI, was very high (0.95), close to unity. **Conclusions.** Inclusion of postweaning RFI as a selection criterion in beef cattle breeding can be expected to lead to improvement in cow feed efficiency. **Implications.** Most breeding decisions in beef cattle are based on traits measured early in life and for replacement heifers are made with an aim to improve their productivity and profitability as cows. The strong and favourable associations measured between postweaning RFI and cow RFI mean that feed efficiency measured in young cattle can be used as a selection trait to improve cow feed efficiency.

Keywords: ADG, EMA, fat, FCR, heritability, milk, RFI, weight.

Introduction

Phenotypic and genetic variation exists in feed intake by beef cattle and is independent of their weight and growth rate (Koch *et al.* 1963). Measured as residual feed intake (RFI), breeding for lower RFI has been suggested as a means to reduce feed requirements by young growing cattle and by cows without changing their size (Archer *et al.* 1999). Internationally, for beef cattle, most experiments have investigated RFI in young growing/finishing animals in confinement and fed medium and high energy-dense rations (Kenny *et al.* 2018). In Australia, measurement of RFI has largely been conducted on young cattle during a postweaning test (RFI_{pw}; Arthur *et al.* 2001) or in a feedlot test (RFI_f; for example, Robinson and Oddy 2004; Torres-Vázquez *et al.* 2018). Divergent selection of sires and dams based on RFI_{pw} has been shown to be effective in changing the feed efficiency of their progeny in postweaning tests (Herd *et al.* 1997), at pasture (Herd *et al.* 2005) and in the feedlot (Herd *et al.* 2003, 2018). Depending on the production system, it has been

calculated that the cow herd uses 65–85% of the feed energy required for beef production (Gregory 1972; Montaño-Bermudez *et al.* 1990), making genetic improvement in feed efficiency of cows an attractive target. Despite the fact that the greatest benefits of improved RFI may be realised in the cow herd when compared with growing cattle, few studies have examined the effect of RFI status on maternal productivity traits (Kenny *et al.* 2018).

Prediction of the responses in cow feed intake, cow RFI (RFI_{cow}), body composition and milk production to selection on RFI_{pw} or RFI_f requires knowledge of their phenotypic and genetic correlations. The objective of this study was to examine the phenotypic and genetic relationships, and heritabilities, between feed intake, feed efficiency and body composition traits recorded postweaning in young cattle and those for the females again as cows, including with milk yield of the cows. A preliminary report on the feed efficiency traits only (Archer *et al.* 2002) was based on postweaning test data that due to original sampling of sires had created inflated genetic variances for weight traits, and parameter estimates were presented without standard errors. This new analysis used additional performance and pedigree data from the Australian Angus and Hereford cattle databases. This publication presents updated phenotypic and genetic correlations and heritabilities, now with standard errors, for the feed efficiency traits, and results for traits describing body composition and cow milk yield not included in the earlier preliminary report.

Materials and methods

Animals and their management

The animal data used in this paper were collected under approval from the local Animal Experimentation Ethics Committee: Project No. 93/5.

The data used for this study were from a major research project, which started in 1993 at the New South Wales (NSW) Department of Primary Industries Agricultural Research Centre, Trangie, NSW, Australia, to investigate genetic variation in postweaning feed efficiency and its associations with feed efficiency traits in mature cows. The design of that project has been described in detail by Arthur *et al.* (2001).

Postweaning data for 1783 young animals (by 206 sires) tested in 10 groups for postweaning feed efficiency were available. The animals from Groups 1, 3, 5, and 7 consisted of bulls and heifers that were progeny of the Angus cow herd at the research centre and Angus bulls obtained from the Australian industry. Animals from Groups 8, 9 and 10 were also born at the research centre and consisted of Angus bulls and heifers and were progeny of sires and dams that had been divergently selected for high or low RFI_{pw}. Animals in Groups 2, 4, and 6 were all heifers purchased after weaning from industry Angus, Hereford, Poll Hereford and Shorthorn

herds. These animals were fully pedigreed and approximately seven progeny per sire were purchased.

Mature-cow data were collected for females only from postweaning Test groups 1–7, yielding a total of 751 females with cow feed efficiency test records. After their postweaning test, the heifers entered the breeding herd of the research centre. They were mated to produce their first calves as 2-year-olds and their second calves as 3-year-olds. Cows and their calves grazed perennial pastures, with supplementary feed (chopped hay and oats) offered during prolonged periods of limited pasture growth. The cows were not mated as 3-year-olds, and approximately 3 months after the weaning of their second calf, they were entered the cow feed efficiency test. The seven postweaning test groups were tested separately.

Postweaning traits

For the postweaning feed efficiency-test feed intake by each animal was measured using an automated feeding system (Herd 1992). A pre-test adjustment period of at least 21 days was allowed for the animals to adapt to the feeding system and diet. The average age at the start of test was 267 days (± 7 days, s.d.). For Tests groups 1–7, the adjustment period was followed by a 120-day test. On the basis of the recommendations reported by Archer *et al.* (1997), a 70-day test was instituted for Groups 8–10. For this study, the efficiency test traits for all groups have been recalculated using only data from the first 70 days of the test. During the test, animals had *ad libitum* access to a pelleted diet composed of 70% alfalfa hay and 30% wheat plus monensin, vitamins, and mineral supplements. The pellets had an average energy content of 10.5 MJ metabolisable energy (ME) per kilogram dry matter (DM) and 15–17% crude protein. Straw with an average ME content of 9 MJ per kg DM was provided to the group of animals at the rate of 0.5 kg per animal per day. The ME content of the pellets and straw were determined on multiple subsamples taken across each test. More information about the composition of the feeds has been provided in Herd (1995). All animals were weighed weekly without fasting. At the start and end of each test, the same accredited technician used real-time ultrasound scanning to measure subcutaneous fat depth over the rump (Australian P8 site; P8FAT) and the cross-sectional area of the eye-muscle (*M. longissimus dorsi*; EMA) between the 12th and 13th ribs; both measurements have been described in Upton *et al.* (2001). The end-of-test scan measurements were used in this study. For Test groups 1–7, which had a 120-day test, a mid-test (approximately 70 days) ultrasound measurement was taken and is used for the end-of-test record. Following the test, the animals were returned to pasture and weighed at approximately 400 days of age (400dWT) after an overnight curfew. Additional information on testing facility and protocols can be obtained from Arthur *et al.* (2001).

Cow traits

After the weaning of their second calf, the cows were tested again for feed efficiency. The average age at the start of the cow feed efficiency test was 1454 days (± 13 days, s.d.). The cow tests were conducted in a manner similar to the postweaning tests, with a 14–21-day adjustment period and a 70-day test. The cow test used the same pelleted ration as did the postweaning test and the cows received a straw allowance of 0.5 kg/day. The start-of-test ultrasound-scan measurements on the cows were used. The 4-year weight of cows was taken at the weaning of their second calf, and records on other cows in the research herd that did not undergo the cow feed intake test when cow numbers exceeded the capacity of the test facility were included in the genetic parameter estimation, bringing the total number of records to 919 for this trait. Cows were mated again as 4-year-olds. Milk yield by the cow was measured using the weigh–suckle–weigh method at approximately 81 days (± 2 days, s.d.) after calving. The 1994 autumn-born cows were not measured for milk yield. The 1993 spring-born cows were measured for milk yield after their third calving, while all the other cows were measured after their second calving, yielding a total of 679 cows with milk yield records. The protocol used to measure milk yield was the same as described in [Herd \(1990\)](#).

Derived traits

Derived traits studied were daily DM intake (DMI), average daily gain in weight (ADG), metabolic mid-test weight (MMWT), RFI and feed conversion ratio (FCR). Feed DMI for each animal was calculated by adding together the daily intake of the pelleted ration and straw, and then adjusting to a common concentration of 10 MJ ME/kg DM, using ME values specific to each test. The growth of each animal over the test period was modelled by linear regression of weight on test day, and the regression estimates were used to calculate ADG and weight at start and end of test. The average of the computed start and end-of-test weights for an animal was used as the mean weight of an animal during the test and MMWT was calculated as $(\text{mean weight})^{0.73}$. To calculate RFI, a linear regression model of DMI on MMWT and ADG, with test group and sex included as class variables, was performed and the intercept and regression coefficients from this model were used to predict feed intake of each animal. RFI for each animal was then calculated as the actual (measured) DMI minus that predicted using the regression equation. In calculating RFI of cows, the regression model used was the same as that used for postweaning animals, except that the intercept and regression coefficients were generated from the cow test data. FCR was calculated as DMI divided by ADG.

Previous experience analysing postweaning data from this project showed that in the sampling of the original sires used to generate progeny for feed intake measurement had created inflated genetic variances for weight traits ([Arthur *et al.* 2001](#)). An additional 28 158 performance and pedigree records from

the Australian Angus and Hereford cattle databases were used in a new genetic parameter estimation to account for any selection bias that may have occurred in the original sampling of sires. To restrict the amount of data, only performance records from herds that had ultrasound-scan P8FAT and EMA records and large contemporary groups (greater than 15 records for 400dWT) were used.

Statistical analyses

Descriptive statistics of the traits studied are presented in [Table 1](#). Genetic variances and covariances were estimated by REML by using VCE4.2.5 ([Groeneveld and Garcia-Cortes 1998](#)). Data were analysed in a series of tri-variate animal models, with 400dWT being always included as one of the three traits. All 400dWT records were pre-adjusted for age of animal and age of dam, by using standard BREEDPLAN adjustments ([Graser *et al.* 2005](#)). In all analyses, 400dWT was modelled with a random additive genetic and residual component and a fixed contemporary group effect. Contemporary group for 400dWT records from the Australian Angus and Hereford databases was as defined for a BREEDPLAN analysis ([Graser *et al.* 2005](#)). The analytical method used that was to overcome the computational limitations that existed at the time of this research project are more fully described in [Reverter *et al.* \(2000\)](#) and [Arthur *et al.* \(2001\)](#). In addition, only two generations of pedigree for each animal with a record were used.

For the tri-variate analyses involving 400dWT and pair-wise combinations of postweaning traits, the model used included fixed contemporary group effect, random additive genetic and residual effects, and linear covariate for age at the start of the test. Contemporary group for research centre animals was defined as all animals from the same breed–herd–sex–test–group–management–group subclass. For the tri-variate analyses involving 400dWT and pair-wise combinations of cow traits only, the model used was similar to the one used for postweaning traits, except that the linear age covariate used was the age at the start of the cow feed intake test. For the milk yield trait, the number of days post-calving at which milk yield was measured was used as an additional covariate. The same basic model was used for tri-variate analyses involving 400dWT and pair-wise combinations of a postweaning trait and a cow trait. However, in these analyses, both postweaning feed intake test age and cow feed intake test age were used as linear covariates, and for milk yield the number of days post-calving at which milk yield was measured was used as a third covariate.

Results

The additive genetic variances and heritability estimates of the traits are presented in [Table 2](#). The minimum and maximum values for the series of trivariate analyses indicated that, for a

Table 1. Number of animals with records and descriptive statistics of the traits studied.

Trait		Number	Minimum	Maximum	Mean	s.d.
Full name and units	Abbreviation					
Postweaning traits						
Dry-matter intake (kg/day)	DMI _{pw}	1783	3.96	14.98	9.51	1.38
Average daily gain (kg/day)	ADG _{pw}	1783	0.56	2.40	1.29	0.25
Metabolic mid-weight (kg)	MMWT _{pw}	1783	40.41	95.80	67.17	8.17
Residual feed intake (kg/day)	RFI _{pw}	1783	-4.28	2.95	0.04	0.78
Feed conversion ratio (kg/kg)	FCR _{pw}	1783	3.71	15.22	7.56	1.36
Rump P8 fat depth (mm)	P8FAT _{pw}	1778	2.00	31.00	10.32	3.49
Eye-muscle area (cm ²)	EMA _{pw}	1700	42.6	112.40	68.75	9.54
400-day weight (kg)	400dWT _{pw}	29 941	147.90	654.33	372.34	71.45
Cow traits						
Dry-matter intake (kg/day)	DMI _{cow}	751	8.56	21.87	15.74	1.89
Average daily gain (kg/day)	ADG _{cow}	751	0.17	2.47	1.19	0.31
Metabolic mid-weight (kg)	MMWT _{cow}	751	83.68	140.32	110.22	9.08
Residual feed intake (kg/day)	RFI _{cow}	751	-8.14	5.30	-0.54	1.69
Feed conversion ratio (kg/kg)	FCR _{cow}	751	5.25	70.23	14.31	5.09
Rump P8 fat depth (mm)	P8FAT _{cow}	751	1.00	41.00	13.23	7.49
Eye-muscle area (cm ²)	EMA _{cow}	677	50.00	124.00	81.29	12.78
Milk yield (kg/day)	MILK _{cow}	679	1.10	14.53	5.76	2.16
4-year weight (kg)	4yWT _{cow}	919	334.00	736.00	498.34	56.21

particular trait, the additive variances were stable from one analysis to the other. Direct heritability estimates for cow EMA and MILK were low (0.12, 0.15), moderate for postweaning ADG, FCR and EMA (0.32, 0.28 and 0.20) and cow DMI, RFI and FCR (0.27, 0.22 and 0.30), and high (>0.40) for the remaining traits in Table 2.

Genetic and phenotypic correlations among postweaning traits are presented in Table 3. The growth traits (ADG_{pw}, MMWT_{pw} and 400dWT_{pw}) were correlated with each other and with feed intake, both genetically (r_g) and phenotypically (r_p). By definition, RFI_{pw} should not be phenotypically correlated with its component traits. ADG_{pw} and MMWT_{pw}; and the results confirmed this. In addition, the results showed that RFI_{pw} was genetically independent of the component traits (ADG_{pw} and MMWT_{pw}). This implies that selection against RFI to improve feed efficiency is not likely to result in changes in the two-component traits. In contrast, negative phenotypic and genetic correlations ($r_p = -0.69$ and $r_g = -0.56$) were observed between FCR_{pw} and its component trait, ADG_{pw}. These indicated that faster-growing animals tended to have better (lower) FCR_{pw} and that selection against FCR_{pw} to improve feed efficiency is likely to result in faster-growing cattle. Postweaning feed intake was genetically correlated with both feed efficiency traits but was more strongly correlated with RFI_{pw} ($r_g = 0.70$) than with FCR_{pw} ($r_g = 0.28$). The genetic correlations between the feed efficiency traits, RFI_{pw} and FCR_{pw}, with P8FAT_{pw}

or EMA_{pw} were either low or close to zero ($r_g = 0.08$ – 0.22). Positive correlations ($r_p = 0.55$ and $r_g = 0.67$) were obtained between the two feed efficiency traits in young animals.

Genetic and phenotypic correlations among cow traits are presented in Table 4. In general, the results for the cow traits were similar to those between equivalent postweaning traits, with some exceptions. In the cows, the genetic correlations between RFI_{cow} and FCR_{cow}, between RFI_{cow} and EMA_{cow}, and between ADG_{cow} and EMA_{cow} were close to zero, whereas at postweaning age, these correlations were positive and different from zero. The genetic correlation between feed intake and FCR_{cow} was negative in the cow but positive at postweaning age. Another difference is the genetic correlation between P8FAT_{cow} and EMA_{cow}, which was close to zero at postweaning age but was medium to high and negative in the cow. In terms of genetic correlations, milk yield was strongly correlated with cow feed intake and RFI_{cow} ($r_g = 0.77$ and 0.99 respectively), weakly correlated with FCR_{cow} ($r_g = 0.25$) and generally uncorrelated with the other cow traits. Weak genetic correlations were observed between cow RFI_{cow} and 4-year weight ($r_g = -0.29$), and between cow feed intake and 4-year weight ($r_g = 0.34$). However, the genetic correlation between FCR_{cow} and 4-year weight was close to zero ($r_g = -0.13$).

Phenotypic and genetic correlations between postweaning traits and cow traits are presented in Tables 5 and 6 respectively. In general, genetic correlations were higher than

Table 2. Estimates of additive variance and heritability (\pm s.e.) for postweaning and cow traits.

Trait Full name	Additive variance ^A			Heritability ^B
	Mean	Minimum	Maximum	
Postweaning traits				
Dry-matter intake	0.391	0.388	0.398	0.47 \pm 0.03
Average daily gain	0.009	0.009	0.009	0.32 \pm 0.03
Metabolic mid-weight	6.03	5.93	6.07	0.46 \pm 0.02
Residual feed intake	0.186	0.184	0.190	0.42 \pm 0.03
Feed conversion ratio	0.263	0.237	0.280	0.28 \pm 0.04
Rump P8 fat depth	2.79	2.75	2.82	0.47 \pm 0.03
Eye-muscle area	7.21	7.01	8.08	0.20 \pm 0.03
400-day weight	381.12	378.51	383.67	0.47 \pm 0.01
Cow traits				
Dry-matter intake	0.718	0.643	0.777	0.27 \pm 0.07
Average daily gain	0.023	0.021	0.025	0.35 \pm 0.07
Metabolic mid-weight	24.48	24.02	26.21	0.74 \pm 0.05
Residual feed intake	0.427	0.377	0.485	0.22 \pm 0.08
Feed conversion ratio	5.820	5.389	6.189	0.30 \pm 0.07
Rump P8 fat depth	8.94	8.56	9.16	0.47 \pm 0.07
Eye-muscle area	5.35	4.04	9.66	0.12 \pm 0.09
Milk yield	0.360	0.330	0.418	0.15 \pm 0.06
4-year weight	1204.3	1174.9	1225.8	0.62 \pm 0.04

^AMean and range from 120 different tri-variate analyses for 400-day weight and from 15 different tri-variate analyses for each of the other traits.

^BMaximum s.e. from tri-variate analyses.

phenotypic correlations. Genetic correlations between traits measured postweaning and the same traits measured in the cow were moderate to high, except for FCR, which had a correlation close to zero ($r_g = 0.09$). In contrast, for the other feed efficiency trait, RFI, the genetic correlation between the postweaning and cow measurement was 0.95, which is close to unity.

Table 3. Genetic (above diagonal, \pm s.e.) and phenotypic correlations (below diagonal) among postweaning traits.

Trait	DMI _{pw}	ADG _{pw}	MMWT _{pw}	RFI _{pw}	FCR _{pw}	P8FAT _{pw}	EMA _{pw}	400dWT _{pw}
DMI _{pw}		0.61 \pm 0.05	0.69 \pm 0.02	0.70 \pm 0.02	0.28 \pm 0.06	0.29 \pm 0.05	0.49 \pm 0.07	0.70 \pm 0.02
ADG _{pw}	0.43		0.67 \pm 0.05	0.02 \pm 0.06	-0.56 \pm 0.05	0.09 \pm 0.07	0.42 \pm 0.00	0.78 \pm 0.04
MMWT _{pw}	0.63	0.26		0.03 \pm 0.01	-0.05 \pm 0.06	0.24 \pm 0.04	0.46 \pm 0.05	0.96 \pm 0.00
RFI _{pw}	0.75	-0.01	0.05		0.67 \pm 0.05	0.22 \pm 0.06	0.21 \pm 0.03	0.01 \pm 0.04
FCR _{pw}	0.28	-0.69	0.19	0.55		0.18 \pm 0.01	0.08 \pm 0.10	-0.19 \pm 0.05
P8FAT _{pw}	0.28	0.03	0.24	0.20	0.18		-0.01 \pm 0.08	0.21 \pm 0.04
EMA _{pw}	0.36	0.18	0.44	0.11	0.09	0.11		0.41 \pm 0.05
400dWT _{pw}	0.67	0.46	0.94	0.05	0.02	0.23	0.43	

See Table 1 for explanation of traits.

Standard errors of phenotypic correlations ranged from 0.01 to 0.02.

Subscript 'pw' denotes postweaning trait.

Postweaning RFI was genetically correlated with feed intake of the cow ($r_g = 0.74$). However, it was not genetically correlated with MMWT_{cow} and 4-year weight of cows ($r_g = 0.02$ and -0.03 respectively). In addition, the genetic correlation between postweaning RFI_{pw} and ADG_{cow} was low and close to zero ($r_g = 0.19$). These results indicated that selection for lower RFI_{pw} will result in replacement females that consume less feed as cows but still have growth characteristics that are similar to those of females selected for higher RFI_{pw}. Although the genetic correlations were low to moderate (0.30–0.41), their direction indicated that selection for a lower RFI_{pw} could result in replacement females that tend to be leaner, have smaller EMA_{cow} and produce less milk. Postweaning FCR had a moderate and positive genetic correlation with cow feed intake, but negative genetic correlations with MMWT_{cow} and 4-year weight of cows. These results indicated that, in contrast to selection for lower RFI_{pw}, selection based on lower FCR_{pw} will result in replacement heifers that are heavier as cows (r_g of -0.33 to -0.43 for FCR_{pw} versus near zero for RFI_{pw}) and consume more feed (r_g of 0.39 versus 0.74) and produce less milk (r_g of 0.53 versus 0.30).

Discussion

The magnitude of the genetic relationships among the postweaning traits was similar to those reported by Arthur *et al.* (2001) and because that paper presents a comprehensive discussion of them it will not be repeated here. The new results for mature cows presented here showed that significant additive genetic variation exists in the population studied for most traits recorded. The genetic parameter estimates presented here represent one of the few data sets available for beef cattle on feed intake and feed efficiency in young cattle because it relates to feed efficiency of breeding cows.

The relationships between postweaning traits and cow traits are important because most selection in beef cattle is

Table 4. Genetic (above diagonal, \pm s.e.) and phenotypic (below diagonal) correlations among cow traits.

Trait	DMI _{cow}	ADG _{cow}	MMWT _{cow}	RFI _{cow}	FCR _{cow}	P8FAT _{cow}	EMA _{cow}	MILK _{cow}	4yWT _{cow}
DMI _{cow}		0.56 \pm 0.06	0.56 \pm 0.09	0.74 \pm 0.07	-0.51 \pm 0.19	0.21 \pm 0.08	0.40 \pm 0.23	0.77 \pm 0.27	0.34 \pm 0.11
ADG _{cow}	0.31		0.40 \pm 0.08	-0.04 \pm 0.18	-0.86 \pm 0.05	0.03 \pm 0.14	0.06 \pm 0.08	0.04 \pm 0.07	0.33 \pm 0.11
MMWT _{cow}	0.37	0.20		-0.03 \pm 0.13	-0.14 \pm 0.11	0.22 \pm 0.05	0.49 \pm 0.17	-0.07 \pm 0.12	0.97 \pm 0.01
RFI _{cow}	0.89	0.04	0.05		-0.02 \pm 0.22	0.09 \pm 0.16	-0.06 \pm 0.35	0.99 \pm 0.05	-0.29 \pm 0.12
FCR _{cow}	-0.06	-0.73	-0.02	0.23		-0.02 \pm 0.14	-0.04 \pm 0.28	0.25 \pm 0.10	-0.13 \pm 0.11
P8FAT _{cow}	-0.01	-0.10	0.23	-0.05	0.08		-0.65 \pm 0.30	-0.17 \pm 0.18	0.22 \pm 0.02
EMA _{cow}	0.07	-0.05	0.37	-0.02	0.09	0.17		0.20 \pm 0.41	0.73 \pm 0.15
MILK _{cow}	0.12	0.09	-0.06	0.12	-0.02	-0.13	-0.01		-0.28 \pm 0.12
4yWT _{cow}	0.12	0.03	0.88	-0.15	0.03	0.25	0.40	-0.19	

See Table 1 for explanation of traits.

Standard errors of phenotypic correlations ranged from 0.02 to 0.04.

Subscript 'cow' denotes cow trait.

Table 5. Phenotypic correlations between postweaning and cow traits.

Cow trait	Postweaning trait							
	DMI _{pw}	ADG _{pw}	MMWT _{pw}	RFI _{pw}	FCR _{pw}	P8FAT _{pw}	EMA _{pw}	400dWT _{pw}
DMI _{cow}	0.46	0.26	0.23	0.35	0.08	0.04	0.13	0.30
ADG _{cow}	0.17	0.23	0.12	0.05	-0.11	0.02	0.06	0.17
MMWT _{cow}	0.45	0.52	0.56	0.00	-0.20	0.05	0.23	0.63
RFI _{cow}	0.34	0.06	0.06	0.39	0.20	0.02	0.06	0.09
FCR _{cow}	0.04	-0.08	0.01	0.08	0.10	0.03	0.03	0.00
P8FAT _{cow}	0.10	-0.09	0.03	0.15	0.14	0.42	-0.06	0.00
EMA _{cow}	0.15	0.15	0.16	0.03	-0.06	-0.01	0.31	0.16
MILK _{cow}	0.06	0.07	0.00	0.05	-0.01	-0.03	0.06	0.02
4yWT _{cow}	0.33	0.35	0.52	-0.06	-0.12	0.03	0.21	0.53

See Table 1 for explanation of traits.

Standard errors of phenotypic correlations ranged from 0.03 to 0.04.

Subscript 'pw' denotes postweaning trait.

Subscript 'cow' denotes cow trait.

Table 6. Genetic correlations (\pm s.e.) between postweaning and cow traits.

Cow trait	Postweaning trait							
	DMI _{pw}	ADG _{pw}	MMWT _{pw}	RFI _{pw}	FCR _{pw}	P8FAT _{pw}	EMA _{pw}	400dWT _{pw}
DMI _{cow}	0.94 \pm 0.08	0.58 \pm 0.12	0.49 \pm 0.09	0.74 \pm 0.10	0.39 \pm 0.15	0.27 \pm 0.13	0.23 \pm 0.15	0.60 \pm 0.08
ADG _{cow}	0.41 \pm 0.10	0.42 \pm 0.09	0.28 \pm 0.08	0.19 \pm 0.08	-0.11 \pm 0.13	0.22 \pm 0.10	0.09 \pm 0.14	0.29 \pm 0.07
MMWT _{cow}	0.54 \pm 0.03	0.74 \pm 0.05	0.62 \pm 0.04	0.02 \pm 0.07	-0.43 \pm 0.07	0.00 \pm 0.06	0.26 \pm 0.09	0.68 \pm 0.03
RFI _{cow}	0.87 \pm 0.14	0.18 \pm 0.13	0.15 \pm 0.09	0.95 \pm 0.02	0.81 \pm 0.15	0.20 \pm 0.14	0.11 \pm 0.04	0.27 \pm 0.09
FCR _{cow}	0.01 \pm 0.10	-0.08 \pm 0.11	0.12 \pm 0.08	-0.01 \pm 0.11	0.09 \pm 0.13	-0.13 \pm 0.11	0.12 \pm 0.14	0.12 \pm 0.07
P8FAT _{cow}	0.18 \pm 0.06	-0.06 \pm 0.02	-0.07 \pm 0.06	0.32 \pm 0.08	0.32 \pm 0.12	0.74 \pm 0.07	-0.45 \pm 0.12	-0.04 \pm 0.06
EMA _{cow}	0.61 \pm 0.18	0.54 \pm 0.25	0.46 \pm 0.22	0.41 \pm 0.15	0.12 \pm 0.24	-0.04 \pm 0.17	0.99 \pm 0.01	0.40 \pm 0.17
MILK _{cow}	0.23 \pm 0.08	-0.21 \pm 0.09	0.17 \pm 0.09	0.30 \pm 0.11	0.53 \pm 0.16	0.04 \pm 0.12	0.19 \pm 0.20	0.20 \pm 0.09
4yWT _{cow}	0.47 \pm 0.05	0.58 \pm 0.06	0.64 \pm 0.04	-0.03 \pm 0.07	-0.33 \pm 0.08	-0.03 \pm 0.07	0.45 \pm 0.09	0.62 \pm 0.04

See Table 1 for explanation of traits.

Subscript 'pw' denotes postweaning trait.

Subscript 'cow' denotes cow trait.

based on traits measured early in life and for replacement heifers with an aim to improve their productivity and profitability as cows. In general, the genetic correlations were higher than corresponding phenotypic correlations due to low environmental correlations between postweaning and cow traits. There are a plethora of environmental influences that can occur over the intervening period and, as a consequence, low environmental correlations might be expected. Importantly, the genetic correlations of RFI_{pw} with the cow traits suggested that selection for lower RFI_{pw} (for improved feed efficiency) will lead to corresponding reduction in cow feed intake, with little change in cow weight. Similar results were obtained by Nieuwhof *et al.* (1992) who reported genetic correlations for ME intake and for RFI between growing dairy heifers and then as lactating cows, of 0.69 and 0.58 respectively. Both values are lower than observed in the present study, but were estimated on the basis of a much smaller number of females ($n = 350$ compared with $n = 751$ in the present study). Calculated across a range of beef breeds, Davis *et al.* (2016) reported significant phenotypic correlations between feed intake and RFI of growing heifers and their feed intake from 240 days of age to weaning of their first calf (0.65 and 0.31 respectively), which remained significant for heifer feed intake (but not RFI) for feed intake between the weaning of first and second calf, and the second and third calf (0.19 and 0.14). Beef cows classified for having progeny with low postweaning RFI had themselves significantly lower feed intake and RFI as cows, whereas cows classified for having progeny with high RFI had significantly higher feed intake and RFI as cows (Basarab *et al.* 2007). A positive phenotypic correlation for RFI measured postweaning on young heifers from a range of beef breeds and their subsequent feed intake, but not RFI, as 3-year-old cows was reported by Black *et al.* (2013). Taken together, these results showed that selection for lower RFI measured on young beef animals can be expected to result in improved feed efficiency, as lower RFI, in beef cows.

Of particular note are the very high genetic correlations between postweaning feed intake and cow feed intake, and between postweaning RFI and cow RFI. Phenotypic analyses of maturity patterns have generally found that feed intake matures much faster than does bodyweight, and that animals achieve their 'mature feed intake' quite early in life, such as, for example, described for sheep by Thompson *et al.* (1985). The results of the present study support these findings at a genetic level, as the high genetic correlation DMI_{pw} and DMI_{cow} (0.94) suggest that essentially the same set of genes determines *ad libitum* feed intake from postweaning to maturity. Variation in RFI has been attributed to a large number of physiological processes as was documented in the reviews by Kenny *et al.* (2018) and Cantalapiedra-Hijar *et al.* (2018). The high genetic correlation between RFI_{pw} and RFI_{cow} (0.95) suggests that whatever genetic variation in physiological processes underlies the observed genetic variation in RFI_{pw} , the same (or similar) variation in

physiological processes is also acting to control feed efficiency of cows. This supports the hypothesis by Archer *et al.* (1999) that cattle possess an intrinsic efficiency that is genetically determined and may influence lifetime feed efficiency.

The genetic correlation reported herein between RFI_{pw} and $P8FAT_{cow}$ indicated that selection to reduce RFI_{pw} may result in a correlated decrease in cow fatness, although the correlation is not strong at 0.32. Many individual experiments have reported positive phenotypic and genotypic associations between RFI and measures of body fat content in growing cattle, but a meta-analysis of seven phenotypic studies by Kenny *et al.* (2018) found no consistent statistically significant differences in either live-animal or carcass measures of fat depth between cattle of high- or low-RFI status. Divergent selection lines for RFI_{pw} were established from within the animals used in the present study (described in Arthur *et al.* 2001) and a correlated response in fatness of females was observed, with females from the high-RFI line being fatter than those from the low-RFI line across their first and subsequent reproductive cycles (Copping *et al.* 2018; Laurence *et al.* 2018). A low but positive genetic correlation (0.19) between the RFI of growing steers and $P8FAT$ of young cow relatives at the end of their first 'wet' season, but which became zero at the end of the following 'dry' seasons, in two tropical beef breeds, was reported by Barwick *et al.* (2009). In phenotypic studies on cows from a range of beef breeds, no difference in subcutaneous rib or rump fat depth was observed in pregnant females that had previously been phenotypically ranked as extreme in RFI measured in postweaning tests (Hafla *et al.* 2013). Black *et al.* (2013) also reported a lack of phenotypic correlations for RFI measured postweaning on young heifers with their subsequent backfat thickness or rib-eye area as 3-year-old cows. Low but significant phenotypic correlations have been reported between RFI measured on growing heifers and backfat thickness as cows at their first, second and third calving (0.13, 0.17 and 0.15 respectively; Davis *et al.* 2016). In contrast, Basarab *et al.* (2007) reported that beef cows classified for having progeny with a low postweaning RFI had a greater backfat thickness across their first two production cycles than did cows classified for having progeny with a high RFI. These results indicate that the strength of association for RFI_{pw} with cow fatness is inconsistent and is likely to be population or breed specific, but should be considered in implementing breeding programs that include RFI_{pw} .

There is a well established influence of body fatness on key reproductive events, such as the onset of puberty and resumption of postpartum ovarian cyclicity (Kenny *et al.* 2018). Even though the associations between RFI_{pw} and cow fatness may not be strong, any decrease in cow fatness could have an adverse impact on fertility traits. Studies on females from the Trangie divergent RFI_{pw} lines mentioned above found no difference in pregnancy rates between the selection lines at the first and subsequent reproductive cycles (Copping *et al.* 2018; Laurence *et al.* 2018), but heifers from the low-RFI

line attained puberty at a slightly older age than did those from the high-RFI line (Jones *et al.* 2018). Similar results have been reported in separate studies on these selection lines (Arthur *et al.* 2005; Donoghue *et al.* 2011). In another experiment, Basarab *et al.* (2007) reported that cows that had produced low-RFI progeny did not differ in pregnancy rates, calving rates, weaning rates or in production efficiency across a number of production cycles from cows that had produced high-RFI progeny, but that they calved 5–6 days later than did the cows that produced high-RFI progeny. In beef cows previously tested for RFI as replacement heifers, Callum *et al.* (2019) reported a significant and favourably higher index for production of birth weight over nine joining cycles in cows with a low RFI than in cows with a high RFI, but found no significant differences in indices for production of weaning weight or for lifetime productivity. Results of another phenotypic study with Black Angus females that were tested postweaning for RFI and then grouped as low, average or high found that classification of RFI had little to no effect on subsequent reproductive efficiency through the weaning of the third calf (Parsons *et al.* 2019). It is therefore recommended that breeding programs including selection for lower RFI_{pw} also place appropriate weighting on estimated breeding value for fertility traits.

The relationships between cow feed intake, RFI_{cow} and MILK_{cow} at the genetic level are of particular interest. Cow DMI and RFI_{cow} were strongly correlated with each other, and both were positively correlated with MILK_{cow}, meaning that cows with higher feed intakes and higher RFI_{cow}, both measured when non-lactating, tended to have higher milk production. The genetic correlation between RFI_{pw} and MILK_{cow} suggests that some antagonism may exist between postweaning feed efficiency and cow milk production. This is supported by the association between RFI_{pw} and the maternal genetic component of weight at 200 days in the Trangie Angus heifers reported by Arthur *et al.* (2001), which was of a similar magnitude (0.22). In contrast, Nieuwhof *et al.* (1992) found a slight favourable correlation ($r_g = -0.10$) between RFI in the growing dairy heifer and her subsequent milk production (corrected for fat and protein), although this correlation is unlikely to be significantly different from zero. No significant phenotypic correlations calculated across a range of beef breeds between RFI of growing heifers and their milk production during each of their first three lactations were reported by Davis *et al.* (2016). Black *et al.* (2013) also reported a lack of phenotypic correlation for RFI measured postweaning on young heifers from a range of beef breeds and their subsequent production of milk as 3 year-old cows. In contrast, Parsons *et al.* (2021) reported that cows that had been ranked as phenotypically high or low for postweaning RFI subsequently displayed a cow age by RFI interaction for milk production, where both 5–6-year-olds and 8–9-year-olds, but not 9–10-year-olds, phenotypically low-RFI cows produced more milk than did high-RFI cows. These studies indicated that the relationship

between postweaning RFI and cow milk production is weak, and in beef cattle breeding programs, any antagonism between these traits could be managed by inclusion of the maternal genetic influence on 200-day weight in a selection index, along with RFI_{pw}.

Overall, the results showed that the inclusion of RFI measured postweaning as a selection criterion in beef cattle would lead to improvements in cow feed efficiency. Females from the Trangie RFI-divergent lines were used to examine the impact of genetic divergence in RFI_{pw} on cow feed efficiency and productivity in pasture-based systems under conditions more akin to commercial cattle production systems (Pitchford *et al.* 2018). That study included periods of constrained feed intake, where variation in efficiency might be seen as differential weight loss, and periods where the processes of gestation and lactation place additional energetic demands on the cow. The results showed that heifers selected for low RFI_{pw} were more feed efficient at pasture than were those selected for high RFI_{pw} (Hebart *et al.* 2018), naturally produced less enteric methane (a potent greenhouse gas; Jones *et al.* 2011), did not differ significantly in reproductive performance (as described above), and as cows with calves were more profitable on pasture (Anderton *et al.* 2018).

This study has demonstrated that feed intake and efficiency traits measured on young cattle are strongly genetically related to similar traits in cows. Feed efficiency of both young animals and cows is of considerable economic importance to beef production, and inclusion of feed intake and feed efficiency measured in young animals as a selection criterion can improve cow feed efficiency. Selection decisions need to be cognisant of the possible antagonist associations with heifer age-at-puberty, and with cow fatness and milk production. Examples of methods and consequences of including feed intake and RFI in genetic selection for multiple-trait merit are described in Barwick *et al.* (2018).

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

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