Relationships among feed efficiency traits across production segments and production cycles in cattle

Phillip A. Lancaster,[†] Michael E. Davis,[‡,1] Jack J. Rutledge,[‖] and Larry V. Cundiff[$]

[†]Beef Cattle Institute, Kansas State University, Manhattan, KS 66506, USA [‡]Department of Animal Sciences, The Ohio State University, Columbus, OH 43210, USA [‖]Department of Animal and Dairy Sciences, University of Wisconsin, Madison, WI 53706, USA [$]U.S. Meat Animal Research Centre, Clay Centre, NE 68933, USA

ABSTRACT: Understanding the relationships between feed efficiency traits measured in different stages of production is necessary to improve feed efficiency across the beef value chain. The objective of this study was to evaluate relationships among feed efficiency traits measured as growing heifers and breeding females and in their progeny in three full production cycles, and relationships of dam residual feed intake (RFI) with lifetime and lifecycle cow efficiency traits. Data were collected on 160 mixed-breed heifers from 240 d of age to weaning of their third progeny, and postweaning performance of progeny until harvest in experiments initiated in 1953, 1954, 1959, 1964, 1969, and 1974. Individual feed offered was recorded daily, and feed refusals measured every 28 d. Milk yield was measured at 14-d intervals throughout lactation by machine or hand milking. Females and progeny were weighed at 28-d intervals and progeny were harvested at a constant endpoint of live grade or age depending upon the experiment. Feed efficiency traits of RFI and residual BW gain (RG) were computed as the residual from linear regression for developing heifers, dams (RFI and residual energy-corrected milk [RECM]), and postweaning progeny. Feed:gain ratio (FCR) was computed for developing heifers and postweaning progeny, and feed:milk energy ratio (FME) was computed for dams. Various measures of cow efficiency were calculated on either a life cycle or lifetime basis using ratios of progeny and dam weight outputs to progeny and dam feed inputs. Pearson correlations were computed among traits adjusted for a random year-breed-diet group effect. Heifer RFI (0.74) and RG (−0.32) were correlated ($P \le 0.05$) with dam RFI in parity 1 only, but were not correlated ($P > 0.05$) with dam RECM in any parity. Heifer RFI was correlated ($P \le 0.05$) with progeny RFI (0.17) in parity 3 only. Heifer FCR was not correlated with dam FME or progeny FCR in any parity. Dam RFI was weakly correlated ($r = 0.25$ to 0.36; $P \le 0.05$) among parities, whereas dam FME and RECM were strongly correlated ($r = 0.49$ to 0.72; $P \le 0.05$) among parities. Dam RFI in parity 1 and 2 was weakly correlated ($r = -0.20$ to −0.33; $P \le 0.05$) with cow efficiency ratios that included dam weight as an output, whereas dam RFI in parity 3 was not correlated with any cow efficiency ratio. In conclusion, feed efficiency traits were poorly correlated across production segments, but moderately repeatable across production cycles.

Key words: cows, heifers, progeny, residual feed intake, residual gain

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[1]Corresponding author: davis.28@osu.edu

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INTRODUCTION

Selection for feed efficiency can improve the sustainability of beef production (Basarab et al., 2013), but improvements in feed efficiency are needed in all segments of the beef industry, which will require a highly repeatable trait. Residual feed intake (RFI) has been the focus of selection programs for feed efficiency (Arthur and Herd, 2012). Early research focussed on the association between RFI in growing cattle early postweaning on high-roughage diets and more physiologically mature cattle on high-concentrate diets. Several studies reported substantial reranking of cattle for RFI between these two phases of production (Arthur et al., 2001; Kelly et al., 2010; Durunna et al., 2011). More recent studies indicate that the reranking may be due to the physiological stage of the animal more than diet (Durunna et al., 2012; Asher et al., 2018; Ferriman et al., 2018).

Cattle are generally measured for feed efficiency during a postweaning test, and the difference in physiological stage between a growing animal and a gestating/lactating cow is considerable. The breeding female consumes 70% of the feed required from birth to slaughter, expends 70% of that feed energy for maintenance (Johnson, 1984), and accounts for 75% of the carbon footprint for beef production (Johnson et al., 2002; Beauchemin et al., 2010; Asem-Hiablie et al., 2019). Selection programs should improve feed efficiency in the cow–calf segment of the beef industry. RFI measured in growing heifers postweaning and again as gestating or open females is moderately, phenotypically correlated (Arthur et al., 1999; Archer et al., 2002; Herd et al., 2006; Hafla et al., 2013), but the relationship is nonexistent or weak in lactating females (Nieuwhof et al., 1992; Black et al., 2013).

Previously mentioned studies measured feed efficiency in gestating or lactating cows over short (~70 days) periods relative to a full production cycle and only in a single production cycle. The objective of this study was to evaluate relationships among feed efficiency traits measured as growing heifers and breeding females and in their progeny in three full production cycles, and relationships of cow RFI with lifetime and lifecycle cow efficiency traits. We hypothesised that feed efficiency traits will be positively correlated across production segments and repeatable across production cycles.

MATERIALS AND METHODS

Animal care and use committee approval was not required for this study because no animals were used. Data from Davis et al. (1983) were used.

Source of Data

Data were collected from identical and fraternal twin heifers purchased between 8 and 224 d of age in 1953, 1954, 1959, 1964, 1969, and 1974, and their progeny (Christian et al., 1965; Kress et al., 1969, 1971a, 1971b; Hohenboken et al., 1972, 1973; Towner, 1975; Baik, 1980). Dams from the 1964, 1969, and 1974 datasets that produced at least one progeny that survived to the harvest endpoint (n = 37, 45, and 56, respectively) were included in the first analysis (analysis I) to compute cow efficiency ratios on a lifecycle basis. Dams that produced three calves that survived to the harvest endpoint were 6, 8, 8, 22, 33, and 33 in the 1953, 1954, 1959, 1964, 1969, and 1974 datasets, respectively, and were included in a second analysis (analysis II) to compute cow efficiency ratios on a lifetime basis. Dams in the 1953, 1954, and 1959 datasets were included in analysis II only to be consistent with previous papers from this dataset even though data from these dams could be included in computation of lifecycle efficiency ratios (analysis I). Breed composition and numbers of dams used in each dataset are shown in Table 1.

Feeding and Management Systems

Feeding and management of females and their progeny have been recently described in detail by Davis et al. (2016, 2018). Briefly, all females of the same breed were mated to bulls of a common breed composition, although not necessarily the same breed as the females (Table 2). Females in the 1953 and 1954 experiments were bred by natural service, whereas females in all subsequent experiments were bred by artificial insemination. For parity 1, breeding began at the first oestrus after 15 mo of age (1953, 1954, 1959, 1964, and 1969) or at the first detected oestrus (1974) and continued until conception occurred. For parities 2 and 3, breeding began at the first oestrus after calving and continued until conception occurred. Age at calving was recorded for each dam during each parity.

Females in the 1953, 1954, and 1959 experiments were fed a common diet within an experiment (Table 2). Females in the 1953 and 1954 experiments were fed a mixture of corn silage and chopped alfalfa hay, and were fed chopped alfalfa hay in the 1959 experiment plus 1.81 kg/d of a grain supplement (75.4% TDN) during lactation. In the 1964, 1969, and 1974 experiments, females were randomly assigned within breed to either a low- or high-energy diet. The high-energy diet in the 1964 experiment consisted of 50% chopped mixed hay, 25% cracked corn, 20% crimped oats, and 5% linseed meal, and in the 1969 and 1974 experiments consisted of 75% chopped mixed hay, 20% crimped oats, and 5% linseed meal. The low-energy diet in the 1964, 1969, and 1974 experiments consisted of 100% chopped mixed hay. Mineral and salt were allowed free choice. All diets were formulated to meet digestible protein requirements and TDN concentration computed from values for individual feedstuffs according to Morrison (1956). Metabolisable energy was computed from diet TDN values using equations of National Academies of Science, Engineering, and Medicine (2016). Females and their nursing progeny were randomly assigned to separate individual self-feeders during lactation and feed offered was recorded daily. Progeny were fed individually from weaning until harvest and feed offered was recorded daily. Females and progeny were tied to the self-feeder for 2 h in the morning and afternoon, and allowed to consume feed ad libitum. Recent work indicates that feeding duration ranges from 48 to 209 min/d (Nkrumah et al., 2006; Lancaster et al., 2009b; Green et al., 2013; Hafla et al., 2013; Fitzsimons et al., 2014a; McGee et al., 2014), which is less than the 240 min/d allowed in the current study. Feed refusals were weighed at 28-d intervals and feed consumption was calculated for dams, and progeny pre-and postweaning.

Milk yield was measured twice daily at 14-d intervals throughout the lactation period by machine or hand milking one half of the udder while the calf nursed the other half. Calves were separated at 0800 h, then one side of the udder was milked at 1630 h. The calf was again separated following nursing at 1630 h, then the other side of the udder was milked at 0800 h the next day. Twice the sum of the two milkings were considered the daily milk production. Butterfat percentage was measured and used to compute milk yield adjusted to 4%

Table 1. Source of data for analysis I and analysis II

Experiment	Dam breed composition	*N*	Singles/twins	Analysis I	Analysis II
1953	Hereford	6	Twins	No	Yes
1954	Hereford	8	Twins	No	Yes
1959	Hereford	8	Twins	No	Yes
1964	Hereford	33	Twins	Yes	Yes
	Hereford × Guernsey	1	Twins	Yes	Yes
	Hereford × Shorthorn	1	Twins	Yes	Yes
	Hereford × Holstein	1	Twins	Yes	Yes
	Hereford × Brown Swiss	1	Twins	Yes	Yes
1969	Hereford	17	Twins	Yes	Yes
	Hereford × Shorthorn	2	Twins	Yes	Yes
	Hereford × Charolais	2	Twins	Yes	Yes
	Holstein	24	Twins	Yes	Yes
1974	Hereford × Holstein	14	Singles	Yes	Yes
	Angus × Holstein	14	Singles	Yes	Yes
	Simmental × Holstein	15	Singles	Yes	Yes
	Chianina × Holstein	13	Singles	Yes	Yes

Table 2. Breed composition of sire mated to females and metabolisable energy concentration (MEC, Mcal/kg DM) of diets fed to dams and progeny postweaning for each experiment

Experiment	Dam MEC	Progeny MEC	Dam breed composition	Sire breed composition
1953 1954 1959	2.05	2.35	Hereford	Hereford
1964	Low energy = 1.82 High energy = 2.28	2.33	Hereford, Hereford crosses	Hereford
1969	Low energy = 1.84 High energy = 1.99	2.47	Hereford, Hereford crosses Holstein	Holstein Hereford
1974	Low energy = 1.84 High energy = 1.96	2.47	All breed crosses[a]—parity 1 All breed crosses—parity 2, 3	Jersey Charolais

[a]All breed crosses includes Hereford × Holstein, Angus × Holstein, Simmental × Holstein, and Chianina × Holstein cross females used in 1974 experiment.

butterfat equivalent (Davis et al., 1983). Length of lactation was 240 d in all experiments except 1974, and milk yield for the 1974 dams was adjusted from 224 d to 240 d according to Rutledge et al. (1972).

Dams were weighed at 28-d intervals as well as within 12 h following parturition. Progeny were weighed at 28-d intervals from birth to harvest. For the 1953, 1954, and 1959 experiments, progeny were harvested at a constant live grade of USDA Choice based on grading standards at the time (United States Department of Agriculture, 1996), whereas progeny in the 1964 and 1969 experiments were harvested at constant age of 532 d and in 1974 at a constant age of 364 d. Progeny were removed from feed 24 h before harvest and weighed at the University of Wisconsin Meat Laboratory. Carcases were weighed, chilled for 48 h, and the right side processed into whole-sale cuts trimmed to 0.95 cm of external fat thickness. Progeny weaning weight, slaughter weight, carcase weight, and weight of trimmed wholesale cuts, as well as pre- and postweaning feed consumption were adjusted to a steer basis (Davis et al., 1983).

Data Calculations

Feed consumption data that were available in the datafile was the accumulated feed consumption converted to metabolisable energy intake. For developing heifers, feed consumption was accumulated from 240 d of age to first calving, and average daily dry matter intake (DMI) was computed as the accumulated feed consumption divided by the number of days as previously described (Davis et al., 2016). For dams, feed consumption was accumulated from weaning to weaning (1 production cycle); for parity 1, feed consumption was accumulated from 240 d of age of the dam to weaning of the first progeny. Average daily DMI of dams for each production cycle was calculated by dividing the accumulated feed consumption by the number of days from weaning of the previous progeny to weaning of the current progeny and then divided by the metabolisable energy concentration of the diet. For progeny, the postweaning feed consumption was accumulated from weaning until harvest. Average daily DMI of progeny was calculated by dividing the accumulated feed consumption by the number of days from weaning until harvest and then divided by the metabolisable energy concentration of the diet.

Body weight data available in the datafile were the weights at specific time points extrapolated from the weights collected at 28-d intervals. For developing heifers, body weight at 240 d of age and first parturition was used to compute average daily gain (ADG) as weight at parturition minus weight at 240 d of age divided by age at parturition minus 240 as previously described (Davis et al., 2016). Weight change of dams during late gestation (WTGAINGEST) was computed as dam weight at parturition minus dam weight at weaning of previous progeny. Weight change of dams during lactation (WTGAINLACT) was computed as dam weight at weaning of the current progeny minus dam weight after parturition. Average dam weight (MCWT) for a given parity was computed as the average of dam weights at weaning of previous progeny, parturition, and weaning of current progeny. The postweaning ADG of progeny was computed as harvest weight minus weaning weight divided by the number of days from weaning to harvest.

For dams, the milk yield data available in the datafile was the total milk yield for the entire 240-d lactation adjusted to an energy corrected basis (4% butterfat). The average energy-corrected milk yield (ECM) was calculated as the total milk energy yield divided by 240 d of lactation.

Efficiency Traits

Cow efficiency ratios were calculated using two approaches, the first based on life cycle (analysis I) and the second based on the lifetime approach for dams with three calves that survived to harvest (analysis II). Calculation of cow efficiency ratios has been described previously (Davis et al., 1983, 1984, 2016, 2018) and is shown in Table 3.

Additional feed efficiency traits of RFI for all production segments, postweaning feed:gain ratio, residual gain (RG), and residual intake and gain (RIG) for progeny, and feed:milk ratio, residual energy-corrected milk (RECM), and residual intake and milk (RIM) for dams were computed. Feed:gain ratio (FCR) of developing heifers and progeny was calculated as DMI divided by ADG. Feed:milk ratio of dams (FME) was computed as DMI divided by ECM.

RFI and residual gain of developing heifers were previously computed (Davis et al., 2016). RIG of heifers was calculated as $-1 \times \text{RFI} + \text{RG}$, both standardised to variance of 1 (Berry and Crowley, 2012). Mid-test body weight of progeny was calculated as the average of weaning and harvest weights raised to the 0.75 power. RFI of progeny was computed as the residual from mixed-model linear regression (lmer function; R Core Team, 2019) of

Table 3. Definitions of cow efficiency ratios, and associated symbols and acronyms

Item	Definition
PW_1, PW_2, PW_3	Progeny weaning weights. Sex-adjusted weaning weight (240-d weight) of the first, second, and third calf from each cow.
$CARCPW_1$, $CARCPW_2$, $CARCPW_3$	Carcase progeny weights. Sex-adjusted sum of chilled weight of right and left half of carcase of first, second, and third calf from each cow.
$WHOLPW_1$, $WHOLPW_2$, WHOLPW3	Wholesale progeny weights. Sex-adjusted sum of trimmed wholesale cuts (chuck, rib, plate, foreshank, brisket, flank, sirloin, shortloin, round, hindshank, and rump) of first, second, and third calf from each cow.
PF_1, PF_2, PF_3	Progeny feed consumptions. Sex-adjusted feed consumption of the first, second, and third calf from 60 to 240 d of age.
PPF_1, PPF_2, PPF_3	Postweaning progeny feed consumptions. Sex-adjusted feed consumption of the first, second, and third progeny from 240 d of age to slaughter.
DW_1, DW_2, DW_3	Dam weights. Weight of the cow when her first, second, and third calf was weaned.
DF_0	An estimate of the feed consumed by the dam from her birth to 240 d of age.
DF_1, DF_2, DF_3	Dam feed consumptions. Feed consumed by the cow from 240 d of age to the weaning of the first calf, from the weaning of the first calf to the weaning of the second calf, and from the weaning of the second calf to the weaning of the third calf.
k_1, k_2, k_3	Weighting factors to accumulate first, second, and third (subscripts 1, 2, and 3) progeny weights on a life cycle basis.
l_1, l_2, l_3	Weighting factors to estimate average weight of the dam on a life cycle basis where subscripts 1, 2, and 3 denote first, second, and third parity, respectively.
m_1, m_2, m_3	Weighting factors to accumulate first, second, and third (subscripts 1, 2, and 3) progeny feed consumptions on a life cycle basis.
n_0, n_1, n_2, n_3	Weighting factors to accumulate feed consumption of the dam on a life cycle basis where subscripts 0, 1, 2, and 3 denote periods from birth to 240 d and first, second, and third parity, respectively.
R1	Progeny and dam output divided by progeny and dam input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i PW_i + (0.5714) \sum_{i=1}^{3} l_i DW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=0}^{3} n_i DF_i}$
R2	Progeny output divided by progeny and dam input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i PW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=0}^{3} n_i DF_i}$
R3	Progeny and dam output divided by progeny and dam input computed on a lifetime basis for cows weaning 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} PW_i + (0.5714) DW_3}{\sum_{i=1}^{3} PF_i + \sum_{i=0}^{3} DF_i}$
R4	Progeny output divided by progeny and dam input computed on a lifetime basis for cows weaning 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} PW_i}{\sum_{i=1}^{3} PF_i + \sum_{i=0}^{3} DF_i}$
R5	Progeny and dam slaughter weight output divided by progeny and dam feed input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i SLPW_i + (0.690) \sum_{i=1}^{3} l_i DW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=1}^{3} m_i PPF_i + \sum_{i=0}^{3} n_i DF_i}$
R6	Progeny slaughter weight output divided by progeny and dam feed input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i SLW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=1}^{3} m_i PPF_i + \sum_{i=0}^{3} n_i DF_i}$
R7	Progeny and dam carcase weight output divided by progeny and dam feed input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i CARCPW_i + (0.439) \sum_{i=1}^{3} l_i DW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=1}^{3} m_i PPF_i + \sum_{i=0}^{3} n_i DF_i}$
R8	Progeny carcase weight output divided by progeny and dam feed input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i CARCPW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=1}^{3} m_i PPF_i + \sum_{i=0}^{3} n_i DF_i}$

Table 3. Continued

Item	Definition
R9	Progeny and dam trimmed wholesale cut output divided by progeny and dam feed input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i WHOLPW_i + (0.289) \sum_{i=1}^{3} l_i DW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=1}^{3} m_i PPF_i + \sum_{i=0}^{3} n_i DF_i}$
R10	Progeny trimmed wholesale cut output divided by progeny and dam feed input computed on a life cycle basis (analysis I) as: $\frac{\sum_{i=1}^{3} k_i WHOLPLW_i}{\sum_{i=1}^{3} m_i PF_i + \sum_{i=1}^{3} m_i PPF_i + \sum_{i=0}^{3} n_i DF_i}$
R11	Progeny and dam slaughter weight output divided by progeny and dam feed input computed on a lifetime basis for dams producing 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} SLPW_i + (0.690) DW_3}{\sum_{i=1}^{3} PF_i + \sum_{i=1}^{3} PPF_i + \sum_{i=0}^{3} DF_i}$
R12	Progeny slaughter weight output divided by progeny and dam feed input computed on a lifetime basis for dams producing 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} SLPW_i}{\sum_{i=1}^{3} PF_i + \sum_{i=1}^{3} PPF_i + \sum_{i=0}^{3} DF_i}$
R13	Progeny and dam carcase weight output divided by progeny and dam feed input computed on a lifetime basis for dams producing 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} CARCPW_i + (0.439) DW_3}{\sum_{i=1}^{3} PF_i + \sum_{i=1}^{3} PPF_i + \sum_{i=0}^{3} DF_i}$
R14	Progeny carcase weight output divided by progeny and dam feed input computed on a lifetime basis for dams producing 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} CARCPW_i}{\sum_{i=1}^{3} PF_i + \sum_{i=1}^{3} PPF_i + \sum_{i=0}^{3} DF_i}$
R15	Progeny and dam trimmed wholesale cut output divided by progeny and dam feed input computed on a lifetime basis for dams producing 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} WHOLPW_i + (0.289) DW_3}{\sum_{i=1}^{3} PF_i + \sum_{i=1}^{3} PPF_i + \sum_{i=0}^{3} DF_i}$
R16	Progeny trimmed wholesale cut output divided by progeny and dam feed input computed on a lifetime basis for dams producing 3 calves (analysis II) as: $\frac{\sum_{i=1}^{3} WHOLPW_i}{\sum_{i=1}^{3} PF_i + \sum_{i=1}^{3} PPF_i + \sum_{i=0}^{3} DF_i}$

DMI on mid-test metabolic body weight and ADG having random intercept for a year-progeny breed group variable. The year-progeny breed group variable accounts for dam birth year and breed composition of the calf such that RFI is independent of these variables. Random slopes for mid-test metabolic body weight and ADG were not significant ($P > 0.10$). The coefficient of determination for the progeny RFI model was 0.69, 0.70, and 0.47 for progeny from 1st, 2nd, and 3rd parities, respectively, calculated using the *r.squaredGLMM* function in R, which is similar to the methodology described by Lancaster et al. (2009b). Residual ADG of progeny was computed as the residual from mixed-model linear regression of ADG on mid-test metabolic body weight and DMI having random intercept for the year-progeny breed group. Random slopes for mid-test metabolic body weight and DMI were not significant ($P > 0.10$). The coefficient of determination for the progeny RG model was 0.59, 0.52, and 0.38 for progeny from 1st, 2nd, and 3rd parities, respectively. Progeny RIG was calculated as described for heifers.

Mid-test metabolic body weight of dams was calculated as MCWT raised to the 0.75 power. RFI of dams was computed as the residual from mixed-model linear regression of DMI on mid-test metabolic body weight, WTGAINGEST, WTGAINLACT, and ECM having random intercept for the year-diet-dam breed group, which accounts for dam birth year, diet of the dam within year, and breed composition of the dam. Random slopes for mid-test metabolic body weight, WTGAINGEST, WTGAINLACT, and ECM were not significant ($P > 0.10$) for the 1st parity and were removed from the model. For the 2nd parity, random slopes for ECM and WTGAINLACT were not significant ($P > 0.10$) and were removed from

Table 4. Summary statistics of growth, intake, and feed efficiency traits of mature cows and progeny

Trait[a]	N	Mean	SD	Min	Max
Dam performance					
MCWT1[b], kg	160	372	35	290	498
WTGAINGEST1, kg/d	160	0.48	0.06	0.37	0.68
WTGAINLACT1, kg/d	160	0.21	0.11	−0.10	0.53
DMI1, kg/d	160	9.08	0.79	6.30	13.16
ECM1, Mcal/d	122	3.42	0.68	2.13	5.30
CALVINT1, d	138	335	56	262	637
MCWT2, kg	160	505	49	386	655
WTGAINGEST2, kg/d	160	0.01	0.23	−0.70	1.17
WTGAINLACT2, kg/d	160	0.16	0.11	−0.20	0.55
DMI2, kg/d	160	12.86	1.19	9.12	17.83
ECM2, Mcal/d	147	4.26	0.94	1.95	6.88
CALVINT2, d	160	375	55	301	601
MCWT3, kg	159	544	51	417	726
WTGAINGEST3, kg/d	159	−0.04	0.25	−0.82	0.44
WTGAINLACT3, kg/d	159	0.13	0.13	−0.27	0.47
DMI3, kg/d	159	13.56	1.36	7.81	21.48
ECM3, Mcal/d	139	4.44	0.93	2.15	7.47
CALVINT3, d	159	371	62	290	702
Progeny performance					
PW1, kg	125	256	26	150	311
PSLW1, kg	123	417	35	312	503
ADG1, kg/d	123	0.64	0.11	0.32	1.01
DMI1, kg/d	123	7.66	0.68	6.13	9.43
PW2, kg	152	285	28	163	341
PSLW2, kg	152	453	44	282	564
ADG2, kg/d	152	0.73	0.13	0.25	1.17
DMI2, kg/d	152	8.21	0.94	5.03	10.57
PW3, kg	160	294	21	239	362
PSLW3, kg	160	462	35	372	591
ADG3, kg/d	160	0.73	0.11	0.44	1.06
DMI3, kg/d	160	8.37	0.88	5.93	10.24
Feed efficiency					
Heifer RIG	160	0.00	1.71	−6.49	4.92
Dam FME1, kg/Mcal	122	2.75	0.56	1.73	4.53
Dam RFI1, kg/d	122	0.00	0.38	−1.11	1.79
Dam RECM1, Mcal/d	122	0.00	0.56	−1.25	1.63
Dam RIM1	122	0.00	1.62	−6.95	4.68
Dam FME2, kg/Mcal	147	3.18	0.78	1.89	6.40
Dam RFI2, kg/d	147	0.00	0.81	−3.10	3.02
Dam RECM2, Mcal/d	147	0.00	0.85	−2.29	2.35
Dam RIM2	147	0.00	1.68	−5.70	4.66
Dam FME3, kg/Mcal	139	3.20	0.76	1.81	6.02
Dam RFI3, kg/d	139	0.00	1.00	−4.62	5.20
Dam RECM3, Mcal/d	139	0.00	0.87	−2.36	2.97
Dam RIM3	139	0.00	1.68	−7.91	5.78
Progeny FCR1, kg/kg	123	12.28	1.87	8.03	20.66
Progeny RFI1, kg/d	123	0.00	0.50	−1.51	1.35
Progeny RG1, kg/d	123	0.00	0.08	−0.26	0.29
Progeny RIG1	123	0.00	1.72	−5.83	6.52
Progeny FCR2, kg/kg	152	11.56	2.32	7.49	31.04
Progeny RFI2, kg/d	152	0.00	0.56	−1.78	1.63
Progeny RG2, kg/d	152	0.00	0.10	−0.49	0.33
Progeny RIG2	152	0.00	1.35	−4.86	4.37
Progeny FCR3, kg/kg	160	11.57	1.69	7.62	18.57

Table 4. Continued

Trait[a]	N	Mean	SD	Min	Max
Progeny RFI3, kg/d	160	0.00	0.58	−2.03	1.83
Progeny RG3, kg/d	160	0.00	0.09	−0.25	0.33
Progeny RIG3	160	0.00	1.60	−4.89	5.02

[a]MCWT, mid-cycle dam weight; WTGAINGEST, dam weight change from weaning to calving; WTGAINLACT, dam weight change from calving to weaning; ECM, average daily energy-corrected milk yield during lactation; DMI, average daily dry matter intake during the production cycle or postweaning period; CALVINT, number of days from puberty to first parturition for parity 1, and from birth of previous progeny to parturition for parities 2 and 3; PW, progeny weaning weight; PSLW, progeny slaughter weight; ADG, postweaning average daily gain; RIG, residual intake and gain; FME, feed:milk energy ratio of dams; RFI, residual feed intake; RECM, residual energy-corrected milk yield; RIM, residual intake and milk; FCR, postweaning feed:gain ratio; RG, postweaning residual gain.

[b]Numerals 1, 2, and 3 refer to traits for parity 1, 2, and 3, respectively

the model to compute RFI. For the 3rd parity, WTGAINGEST did not account for significant ($P > 0.10$) variation in DMI, and random slopes for ECM and WTGAINLACT were not significant ($P > 0.10$) and were removed from the model to compute RFI. The covariance structure was modelled assuming independent random effects which produced the least Bayesian information criteria. The coefficient of determination for the dam RFI model was 0.89, 0.79, and 0.77 for dams during 1st, 2nd, and 3rd parities, respectively. Residual milk energy yield of dams was computed as the residual from mixed-model linear regression of ECM on DMI and WTGAINLACT having random intercept for the year-diet-dam breed group similar to that described by Guinguina et al. (2020). Fixed effect of mid-test metabolic body weight and random slopes were not significant ($P > 0.10$) in any parity and were removed from the model. The coefficient of determination for the RECM model was 0.64, 0.63, and 0.63 for dams during 1st, 2nd, and 3rd parities, respectively. Dam RIM was calculated as −1 × RFI + RECM, both standardised to a variance of 1, similar to the calculation for RIG described by Berry and Crowley (2012).

Statistical Analysis

All dam traits were adjusted to remove the random effect of year-diet-dam breed group using a one-way random-effect treatment structure (*lmer* function of R) with year-diet-dam breed group as the random effect (Littell et al., 2006; Lancaster et al., 2009b). Similarly, all progeny traits were adjusted to remove the random effect of year-progeny breed group using a one-way random-effect treatment structure (*lmer* function of R) with year-progeny breed group as the random effect. This allows the relationships among variables to be assessed independent of the effects of year, diet, and breed. Phenotypic Pearson correlation coefficients (*corr.test* function of R) were computed among the adjusted traits. Significance was determined at $P \leq 0.05$ and tendencies if $0.05 < P \leq 0.10$.

RESULTS AND DISCUSSION

Results for performance and feed efficiency traits in developing heifers from 240 d of age to first parturition are presented in Davis et al. (2016) and are only included here in comparison with feed efficiency traits of dams and progeny.

Mature cow weight (505 and 544 kg), DDMI (12.86 and 13.56 kg/d), and MEY (4.26 and 4.44 Mcal/d) for parities 2 and 3 (Table 4), respectively, are similar to previous studies evaluating feed intake and efficiency in beef cows age 3–6 yr that have reported BW ranging from 435 to 757 kg, DMI ranging from 9.08 to 12.97 kg/d, and energy-corrected milk yield ranging from 4.7 to 11.6 kg/d (Basarab et al., 2007; Black et al., 2013; Lawrence et al., 2013; Wood et al., 2014; Broleze et al., 2020). A previous analysis with the current dataset estimated the energy-corrected peak milk yield to be 10.03 (5.21) kg/d (Lancaster et al., 2020). The SD of RFI in previous studies with beef cows ranged from 1.00 to 3.18 kg/d with three out of five estimates between 1.0 and 1.5 kg/d (Basarab et al., 2007; Black et al., 2013; Lawrence et al., 2013; Wood et al., 2014; Broleze et al., 2020), which is slightly larger than 0.81 and 1.00 kg/d in the current dataset.

ADG (0.64–0.73 kg/d) and DMI (7.66–8.37 kg/d) of progeny were lesser than previous studies in growing/finishing cattle that reported a range from 0.82 to 1.65 kg/d in ADG and a range from 7.62 to 10.81 kg/d in DMI (Basarab et al., 2003; Nkrumah et al., 2007; Lancaster et al., 2009a, 2009b; Crowley et al., 2010; Kelly et al., 2010; Durunna et al., 2012; Black et al., 2013; Hafla et al., 2013). The SD of RFI in previous studies of growing/finishing cattle ranged from 0.34 to 0.94 kg/d but seven of eight estimates were between

0.59 and 0.94 kg/d (Basarab et al., 2003; Nkrumah et al., 2007; Lancaster et al., 2009a, 2009b; Crowley et al., 2010; Kelly et al., 2010; Durunna et al., 2012; Black et al., 2013; Hafla et al., 2013) which is greater than 0.50–0.58 kg/d in the current dataset. The dataset used in this analysis is dated concerning cattle genetics and management practices but is unique in that individual monthly feed intake of breeding females was measured from 240 days of age through three production cycles, and in that milk yield was determined fortnightly during each 240-d lactation. Even though somewhat different from current cattle genetics, this dataset can provide useful information on the relationships between feed intake and efficiency among production segments and production cycles.

Relationships Among Dam Traits

Dam MCWT was strongly, positively correlated ($P \leq 0.05$) with WTGAINGEST in parities 1 and 2, but not in parity 3, and was not correlated ($P > 0.10$) with WTGAINLACT or ECM, except in parity 1 (Table 5). Dam WTGAINGEST was not correlated ($P > 0.10$) with WTGAINLACT in parity 1 but was negatively correlated ($P \leq 0.05$) in parities 2 and 3. Dam WTGAINGEST was weakly, negatively correlated ($P \leq 0.05$) with CALVINT in parity 1 but moderately, positively correlated ($P \leq 0.05$) with CALVINT in parities 2 and 3. Dam WTGAINLACT was weakly, negatively correlated ($P \leq 0.05$) with CALVINT and moderately, negatively correlated ($P \leq 0.05$) with ECM in all parities.

Dam DMI was positively correlated ($P \leq 0.05$) with MCWT and ECM in each parity, positively correlated ($P \leq 0.05$) in parity 1, and tended ($P \leq 0.10$) to be positively correlated with WTGAINGEST in parity 2 but was not correlated ($P > 0.10$) with WTGAINLACT. Dam FME was weakly, positively correlated ($P \leq 0.05$) with MCWT in parities 2 and 3, was moderately, positively correlated ($P \leq 0.05$) with WTGAINLACT in each parity, was strongly, negatively correlated ($P \leq 0.05$) with ECM in each parity, and was or tended to be weakly, positively correlated ($P \leq 0.10$) with dam DMI in each parity. In contrast to FME, dam RFI was not correlated ($P > 0.10$) with MCWT, WTGAINGEST, WTGAINLACT, or ECM as expected based on the use of regression to compute RFI. Additionally, dam RFI was strongly, positively correlated ($P \leq 0.05$) with dam DMI and weakly, positively correlated ($P \leq 0.05$) with dam FME in each parity. Correlations of dam RFI with DMI (r = 0.65–0.83) in gestating and lactating beef cows (Basarab et al., 2007; Walker et al., 2015), and with DMI (0.38) and feed:milk ratio (0.39) in lactating dairy cows (Potts et al., 2015) are similar to those in the current dataset. Additionally, Lawrence et al. (2013) reported 28% greater silage DMI for high versus low RFI cows, and Freetly et al. (2020) reported a genetic correlation of 0.50 between DMI and RFI in gestating beef cows. Dam RECM was strongly, positively correlated ($P \leq 0.05$) with ECM, but not ($P > 0.10$) with dam DMI or WTGAINLACT as expected based on use of regression to compute RECM; however, RECM was weakly, negatively correlated ($P \leq 0.05$) with MCWT in parities 2 and 3 and with WTGAINGEST in parity 1 even though these traits were not significant predictors of variation in ECM. Correlations of dam RIM with dam DMI, ECM, MCWT, WTGAINGEST, and WTGAINLACT were intermediate compared with those of dam RFI and RECM being moderately, negatively correlated ($P \leq 0.05$) with dam DMI, moderately, positively correlated ($P \leq 0.05$) with ECM, and not correlated ($P > 0.10$) with MCWT, WTGAINGEST, or WTGAINLACT.

Interestingly, dam DMI, FME, and RFI were weakly to moderately, negatively correlated ($P \leq 0.05$) and dam RIM moderately, positively correlated ($P \leq 0.05$) with CALVINT, but RECM was not correlated ($P > 0.10$). The negative relationships are like those found in previous studies indicating that the onset of puberty and age at first calving are delayed in heifers identified as more efficient during a postweaning feeding trial (Crowley et al., 2011; Donoghue et al., 2011; Shaffer et al., 2011). However, heifer RFI was not correlated ($P = 0.30$) with age at first calving ($r = -0.08$) in the current data set like the study of Callum et al. (2018). Basarab et al. (2007) reported that calving interval was similar between dams that produced low or high RFI progeny; however, theirs nor any other studies have reported the relationship between dam RFI and calving interval. The negative correlation of CALVINT with dam DMI and WTGAINLACT indicates that dams with lesser feed intake and weight gain during lactation took longer to rebreed, which is consistent with the effect of negative energy balance postpartum on the postpartum interval (Hess et al., 2005). The correlation between CALVINT and dam RFI is likely the result of the strong dependency of RFI on DMI. Further research is needed to investigate the relationship between RFI measured in mature cows and reproductive performance.

Table 5. Pearson correlations among performance and feed efficiency traits of cows

Trait[a]	MCWT	WTGAINGEST	WTGAINLACT	ECM	DMI	FME	RFI	RECM	RIM	PW
CALVINT	0.43*[b]	−0.16*	−0.16*	0.29*	−0.01	−0.20*	−0.09	0.11	0.12	0.11
	0.09	0.48*	−0.19*	0.10	−0.22*	−0.17*	−0.40*	0.13	0.32*	−0.03
	0.07	0.45*	−0.32*	0.06	−0.40*	−0.21*	−0.48*	0.10	0.35*	0.02
MCWT		0.51*	0.09	0.17†	0.61*	0.13	−0.01	−0.14	−0.07	0.16
		0.51*	0.08	−0.04	0.51*	0.22*	−0.04	−0.20*	−0.10	0.15†
		−0.01	0.05	−0.07	0.36*	0.27*	−0.02	−0.28*	−0.15†	0.09
WTGAINGEST			0.01	0.05	0.66*	0.18*	−0.01	−0.18*	−0.10	0.10
			−0.36*	0.15†	0.15†	−0.08	−0.01	−0.05	−0.02	0.03
			−0.53*	0.24*	−0.06	−0.22	0.01	0.04	0.02	0.03
WTGAINLACT				−0.47*	−0.03	0.50*	0.01	−0.02	−0.02	−0.08
				−0.36*	0.11	0.42*	−0.01	0.00	0.00	−0.10
				−0.32*	−0.04	0.35*	0.00	0.02	0.01	−0.07
ECM					0.24*	−0.89*	−0.04	0.80*	0.52*	0.23*
					0.23*	−0.87*	−0.06	0.83*	0.54*	0.24*
					0.16*	−0.83*	−0.06	0.84*	0.54*	0.24*
DMI						0.16†	0.58*	−0.09	−0.42*	0.26*
						0.17*	0.70*	−0.12	−0.49*	0.35*
						0.33*	0.72*	−0.16†	−0.52*	0.20*
FME							0.24*	−0.81*	−0.65*	−0.14
							0.34*	−0.83*	−0.70*	−0.09
							0.37*	−0.85*	−0.73*	−0.14†
RFI								−0.31*	−0.81*	0.13
								−0.40*	−0.84*	0.26*
								−0.41*	−0.84*	0.12
RECM									0.81*	0.13
									0.84*	0.06
									0.84*	0.13
RIM										0.01
										−0.12
										0.01

[a]CALVINT, number of days from puberty to first parturition for parity 1, and from birth of previous progeny to parturition for parities 2 and 3; MCWT, mid-cycle dam weight; WTGAINGEST = dam weight change from weaning to calving; WTGAINLACT, dam weight change from calving to weaning; ECM, average daily energy-corrected milk yield during lactation; DMI, average daily dry matter intake during the production cycle; FME, feed:milk energy ratio; RFI, residual feed intake; RECM, residual energy-corrected milk; RIM, residual intake and milk; PW, progeny weaning weight.

[b]Correlation coefficients are in top to bottom order from 1st to 3rd parity

*Pearson correlation coefficient is different from zero at $P \leq 0.05$.

†Pearson correlation coefficient tends to differ from zero at $0.05 < P \leq 0.10$.

Dam ECM and DMI were weakly, positively correlated ($P \le 0.05$) with PW in each parity, but dam FME only tended ($P \le 0.10$) to be correlated with PW in parity 3, and dam RFI was only weakly, positively correlated ($P \le 0.05$) with PW in parity 2, but RECM and RIM were not correlated ($P > 0.10$) with PW. Increased weaning weight with increased milk energy yield is expected (Clutter and Nielsen, 1987; Beal et al., 1990; Meyer et al., 1994), and cows with greater milk yield are expected to have greater DMI (National Academies of Sciences, Engineering, and Medicine, 2016). The relationship between postweaning RFI and cow productivity in the form of weaning weight is mixed with most studies indicating no relationship (Arthur et al., 2005; Basarab et al., 2007; Morris et al., 2014; Callum et al., 2018); however, Copping et al. (2018) reported greater calf weaning weight for cows from a low RFI selection line, whereas, Hebart et al. (2018) reported that cows from a high RFI selection line had greater weaning weight under high nutrition, but not under low nutrition. In the current dataset, heifer RFI was not correlated with PW for any parity (Davis et al., 2016). In contrast to the positive correlation between dam RFI and PW in parity 2, Broleze et al. (2020) reported no effect of dam RFI determined during lactation on calf weight, which is the only published study evaluating the relationship of mature cow RFI with calf performance traits.

Correlations among dam feed efficiency traits were generally moderate to strong as expected based on the use of the same component traits in the calculations. Dam FME was moderately, positively correlated ($P \le 0.05$) with dam RFI, but strongly, negatively correlated ($P \le 0.05$) with RECM and RIM in all parities (Table 5). Dam RFI was moderately, negatively correlated ($P \le 0.05$) with RECM. Since RIM is a standardised combination of dam RFI and RECM, the correlations of dam RFI and RECM with RIM were equally strong ($P \le 0.05$) in opposite directions. Similar phenotypic correlations have been reported between cow RFI and feed:gain ratio in beef cows (0.23; Archer, 2002), and RFI and feed:milk ratio in dairy cows (0.51; Manafiazar et al., 2016). Additionally, Connor et al. (2013) reported greater milk:feed ratio in dairy cows with low than high RFI. Few reports on residual milk yield are available, but Guinguina et al. (2020) reported that low RFI dairy cows had greater RECM yield and energy-corrected milk to DMI ratio than high RFI cows.

Relationships Among Progeny Traits

In progeny, PSLW was strongly, positively correlated ($P \le 0.05$) with progeny ADG and DMI, and progeny ADG was strongly, positively correlated ($P \le 0.05$) with DMI in each parity (Table 6), which is similar to previous studies (Basarab et al., 2003; Nkrumah et al., 2007; Lancaster et al., 2009a, 2009b). Progeny FCR was weakly, negatively correlated ($P \le 0.05$) with PSLW and strongly, negatively

Table 6. Pearson correlations among growth, intake, and feed efficiency traits of progeny

Trait[a]	ADG	DMI	FCR	RFI	RG	RIG
SLPW	0.56*,[b] 0.67* 0.59*	0.59* 0.76* 0.46*	−0.28* −0.26* −0.28*	−0.08 0.02 −0.04	0.18* 0.17* 0.19*	0.15 0.09 0.14
ADG		0.61* 0.67* 0.40*	−0.81* −0.73* −0.72*	−0.02 0.02 0.01	0.80* 0.74* 0.86*	0.47* 0.42* 0.53*
DMI			−0.10 −0.11 0.32*	0.69* 0.61* 0.69*	0.02 0.01 0.00	−0.39* −0.35* −0.43*
FCR				0.44* 0.38* 0.48*	−0.95* −0.89* −0.86*	−0.80* −0.74* −0.84*
RFI					−0.48* −0.44* −0.28*	−0.86* −0.85* −0.80*
RG						0.86* 0.85* 0.80*

[a]PSLW, progeny slaughter weight; ADG = postweaning average daily gain; DMI = postweaning daily dry matter intake; FCR = postweaning feed:gain ratio; RFI = postweaning residual feed intake; RG = postweaning residual gain; RIG = postweaning residual intake and gain.

[b]Correlation coefficients are in top to bottom order from 1st to 3rd parity.

*Pearson correlation coefficient is different from zero at $P \le 0.05$.

Table 7. Pearson correlations among feed efficiency traits at different stages of production

	Dam traits			Progeny traits		
RFI trait[a]	RFI1	RFI2	RFI3	RFI1	RFI2	RFI3
Heifer RFI	0.74*	0.11	−0.06	−0.03	0.11	0.17*
Dam RFI1		0.25*	0.25*	0.02	−0.05	0.19*
Dam RFI2			0.36*	−0.04	0.07	0.16*
Dam RFI3				0.06	−0.13	0.06
Progeny RFI1					0.15†	0.14
Progeny RFI2						0.25*
FE Trait[b]	FME1	FME2	FME3	FCR1	FCR2	FCR3
Heifer FCR	0.00	0.03	0.11	−0.08	0.02	0.09
FME1		0.56*	0.63*	0.06	−0.13	−0.08
FME2			0.72*	−0.03	0.05	0.06
FME3				0.02	−0.09	0.04
Progeny FCR1					0.06	0.18*
Progeny FCR2						0.23*
RG Trait[c]	RECM1	RECM2	RECM3	RG1	RG2	RG3
Heifer RG	−0.10	−0.03	0.03	−0.06	0.07	0.04
RECM1		0.49*	0.50*	0.02	−0.18*	−0.14
RECM2			0.66*	−0.01	−0.04	−0.10
RECM3				−0.03	−0.12	−0.08
Progeny RG1					0.13	0.15†
Progeny RG2						0.24*
RIG Trait[d]	RIM1	RIM2	RIM3	RIG1	RIG2	RIG3
Heifer RIG	0.34*	0.05	0.04	−0.10	0.08	0.14
RIM1		0.33*	0.37*	0.06	−0.06	0.06
RIM2			0.47*	−0.05	0.08	0.09
RIM3				0.03	−0.11	0.09
Progeny RIG1					0.16†	0.17†
Progeny RIG2						0.24*

[a]RFI, residual feed intake; RFI1,2,3 = residual feed intake for parity 1, 2, or 3.

[b]FCR = feed:gain ratio; FME1,2,3 = feed:milk energy ratio of dams for parity 1, 2, or 3; FCR1,2,3 = postweaning feed:gain ratio for parity 1, 2, or 3.

[c]RG = residual gain; RECM1,2,3 = residual energy-corrected milk yield of dams for parity 1, 2, or 3; RG1,2,3 = residual gain for parity 1, 2, or 3.

[d]RIG = residual intake and gain; RIM1,2,3 = residual intake and milk of dams for parity 1, 2, or 3; RIG1,2,3 = postweaning residual intake and gain for parity 1, 2, or 3.

*Pearson correlation coefficient is different from zero at $P \le 0.05$.

†Pearson correlation coefficient tends to differ from zero at $0.05 < P \le 0.10$.

correlated ($P \le 0.05$) with progeny ADG in each parity, but weakly, positively correlated ($P \le 0.05$) with progeny DMI only in the 3rd parity. Likewise, progeny RG was weakly, positively correlated ($P \le 0.05$) with PSLW and strongly, positively correlated ($P \le 0.05$) with progeny ADG, but not correlated ($P > 0.10$) with progeny DMI as expected based on regression methods used to compute RG. In contrast, progeny RFI was not correlated ($P > 0.10$) with PSLW or ADG but was strongly positively correlated ($P \le 0.05$) with progeny DMI. As progeny RIG is a combination of progeny RFI and RG, RIG was moderately, positively correlated ($P \le 0.05$) with progeny ADG and moderately, negatively correlated ($P \le 0.05$) with progeny DMI. Additionally, progeny RFI was moderately, positively correlated ($P \le 0.05$) with progeny FCR and moderately, negatively correlated ($P \le 0.05$) with progeny RG in each parity. Progeny RG was strongly, negatively correlated ($P \le 0.05$) with progeny FCR in each parity, and progeny RIG was strongly, negatively correlated ($P \le 0.05$) with FCR and RFI, and strongly, positively correlated ($P \le 0.05$) with RG. Previous studies have reported similar correlation coefficients of FCR with ADG (−0.69 to −0.81), RFI with DMI (0.58 to 0.80), FCR (0.29 to 0.59), RG (−0.40 to −0.46) and RIG (−0.82 to −0.99), and RG with ADG (0.70 to 0.88), FCR (−0.71 to −0.97) and RIG (0.85) in growing/finishing cattle (Basarab et al., 2003; Nkrumah et al., 2007; Lancaster et al., 2009a, 2009b; Crowley et al., 2010; Kelly et al., 2010; Berry and Crowley, 2012; Hafla et al., 2013; Asher et al.,

2018) indicating that relationships among component traits in the current dataset are typical of studies using current genetics.

Comparison Across Production Segments

Heifer RFI was strongly, positively correlated ($P \leq 0.05$) with dam RFI1, moderately, negatively correlated ($P \leq 0.05$) with dam RIM1 (−0.49), but not correlated ($P > 0.10$) with dam RECM1 (Table 7). Heifer RG was weakly, negatively correlated ($P \leq 0.05$) with dam RFI1 (−0.32), but not dam RECM1 or RIM1. Heifer RIG was strongly, negatively correlated ($P \leq 0.05$) with dam RFI1 (−0.59) and moderately, positively correlated ($P \leq 0.05$) with dam RIM1 (0.34), but not dam RECM1. Heifer FCR was not correlated ($P > 0.10$) with dam FME1, and heifer feed efficiency traits were not correlated ($P > 0.10$) with any of the cow feed efficiency traits in parity 2 or 3. The significant correlations between heifer traits and dam RFI1 are likely due to the fact that accumulated feed intake during parity 1 overlapped with heifer feed intake from 240 d of age to first parturition, and is more due to partially using the same data to compute each trait than it is of biological significance. Heifer RFI was weakly, positively correlated ($P \leq 0.05$) with progeny RFI3, but not progeny RFI1 or RFI2. Heifer FCR was not correlated ($P > 0.10$) with dam FME or progeny FCR, and heifer RG was not correlated ($P > 0.10$) with progeny RG in any parity. As with these results, Nieuwhof et al. (1992) and Black et al. (2013) reported no correlation between RFI in growing heifers and lactating beef cows. In contrast, Davis et al. (2014) reported weak positive correlations ($r = 0.28$ and 0.36) between the genomic prediction of RFI in growing animals and measured RFI in lactating dairy cows, and weak to moderate correlations ($r = 0.30$ to 0.42) have been reported between RFI in growing heifers and gestating or open, nonlactating beef cows (Archer et al., 2002; Herd et al., 2006; Basarab et al., 2007; Adcock et al., 2011; Hafla et al., 2013).

Within parity, dam RFI was not correlated ($P > 0.10$) with progeny RFI or RG. Likewise, dam FME was not correlated ($P > 0.10$) with progeny FCR within parity. However, across parity, dam RFI1 and RFI2 were weakly, positively correlated ($P \leq 0.05$) with progeny RFI3, and dam RFI2 was weakly, positively correlated ($P \leq 0.05$) with progeny RG1. Few studies have compared the RFI of dams with that of their progeny, but in contrast to the current results, Basarab et al. (2007) reported that RFI in mid-gestation, non-lactating dams was correlated (0.30) with postweaning RFI of their progeny. The reason for a lack of correlation in the current study may be due to the inclusion of both gestation and lactation periods in the calculation of dam RFI as the relationship between RFI in growing heifers and lactating cows is near zero (Nieuwhof et al., 1992; Black et al., 2013).

Comparison Across Production Cycles

Dam RFI was weakly, positively correlated ($P \leq 0.05$) among parities, dam FME and RECM were strongly, positively correlated ($P \leq 0.05$) among parities, and dam RIM was moderately, positively correlated ($P \leq 0.05$) among parities. Progeny RFI in parity 1 tended ($P \leq 0.10$) to be positively correlated with progeny RFI2, but not RFI3, and progeny RFI2 was weakly, positively correlated ($P \leq 0.05$) with progeny RFI3. Progeny FCR in parity 1 and 2 were weakly positively correlated ($P \leq 0.05$) with progeny FCR3, but progeny FCR1 and FCR2 were not correlated ($P > 0.10$). Similarly, progeny RG1 and RG2 tended to be ($P \leq 0.10$) or were weakly, positively correlated ($P \leq 0.05$) with progeny RG3, but progeny RG1 and RG2 were not correlated ($P > 0.10$). No previous studies have compared feed efficiency traits across multiple production cycles, but the comparison of the same animals in different stages of growing/finishing indicates a positive correlation ($r_p = 0.42$ to 0.52) in calves fed the same diet (Arthur et al., 2001; Durunna et al., 2011 , 2012). In contrast to our results, the correlation ($r = 0.06$ to 0.38) between FCR in different stages of growing/finishing was lower than for RFI (Arthur et al., 2001; Durunna et al., 2011, 2012). Additionally, Asher et al. (2018) reported that the repeatability of RG was lower than for RFI. The lack of or low correlation of feed efficiency traits of progeny in parity 1 with those in parities 2 and 3 could be due to the use of a different sire breed in the first parity in the 1974 experiment, but the correlation coefficients are not that much lower than those between parities 2 and 3, which used the same sires in each respective experiment, indicating that the primary reason for the poor correlation is likely the environment (i.e., nutrition, management, and weather) differences between production cycles.

Comparison with Lifecycle and Lifetime Cow Efficiency Ratios

Dam RFI in parity 1 was weakly, negatively correlated with cow efficiency ratios R3, R4, R11, R13, and R15, and tended to be negatively correlated with R12, R14, and R16 (Table 8) such that more efficient dams based on RFI were also more efficient based on cow efficiency ratios. Similarly, dam RFI2 was weakly, negatively corrected with cow efficiency ratios R1, R3, R4, R5, R7, R9, R11, R13, R15, and R16, and tended to be negatively correlated with R12. In contrast, dam RFI3 was not correlated with any of the cow efficiency ratios. The reason for differences in correlations may be due to the independent variables included in the dam RFI models. In general, dam RFI1 and RFI2 were correlated with ratios that include dam weight in the numerator (output) except for R4 and R16, and dam RFI1 and RFI2 included WTGAINGEST in the RFI model, whereas WTGAINGEST was not a significant predictor in the model for dam RFI3. Dam MCWT was not correlated ($P > 0.10$) with WTGAINGEST and had a weaker correlation with dam DMI in parity 3 indicating the RFI model in the 3rd parity was less influenced by average dam weight and weight gain, which are important drivers of the variation in the cow efficiency ratios. Additionally, dam RFI, which is computed based on dam weight and feed intake, is primarily correlated with the cow efficiency ratios that include both dam weight and feed intake. Thus, the correlation of dam RFI with cow efficiency ratios is analogous to a correlation with dam gain:feed ratio, which has been observed in many studies of growing cattle (Basarab et al., 2003; Nkrumah et al., 2004; Lancaster et al., 2009a, 2009b).

General Discussion

In general, relationships among RFI measured in different stages of production are weak to moderate as discussed above and have little usefulness in predicting the feed efficiency of an animal across stages of production. For example, the phenotypic correlations between RFI measured in growing heifers and again as gestating or lactating cows range from 0.07 to 0.42 (Nieuwhof et al., 1992; Archer et al., 2002; Herd et al., 2006; Basarab et al., 2007; Adcock et al., 2011; Black et al., 2013; Hafla et al., 2013) indicating that RFI measured in growing heifers explains 0.5% to 17.6% of the variation in RFI of mature females. Phenotypic correlations between growing/finishing phases are slightly stronger (r_p = 0.42–0.52; Arthur et al., 2001; Durunna et al., 2011, 2012), but the variation in finishing phase RFI explained by growing phase RFI is low (17.6% to 27%). Genetic correlations (r_g = 0.41–0.98; Nieuwhof et al., 1992; Arthur et al., 2001, 2002; Durunna et al., 2011; Freetly et al., 2020) across stages of production are stronger than reported phenotypic correlations, although, except for the genetic correlation of 0.98 (Archer et al., 2002), genetic correlations indicate that RFI is not genetically the same trait across stages of production. Thus, although positively correlated, when

Table 8. Pearson correlations between dam RFI and lifetime efficiency traits of cows

Trait[a]	Dam RFI1	Dam RFI2	Dam RFI3
R1	−0.08	−0.29*	−0.08
R2	−0.03	−0.09	−0.02
R3	−0.28*	−0.27*	0.07
R4	−0.22*	−0.22*	0.11
R5	−0.08	−0.29*	−0.08
R6	−0.02	−0.09	−0.07
R7	−0.08	−0.33*	−0.09
R8	−0.02	−0.11	−0.09
R9	−0.07	−0.30*	−0.08
R10	−0.03	−0.13	−0.08
R11	−0.22*	−0.21*	0.07
R12	−0.18†	−0.17†	0.10
R13	−0.22*	−0.20*	0.06
R14	−0.18†	−0.15	0.08
R15	−0.20*	−0.22*	0.06
R16	−0.17†	−0.19*	0.08

[a]RFI1,2,3 = residual feed intake for parity 1, 2, or 3; R1, R2, R5–R10 = cow efficiency ratios on lifecycle basis; R3, R4, R11–R16 = cow efficiency ratios on lifetime basis, see text for details.

*Pearson correlation coefficient is different from zero at $P \le 0.05$.

†Pearson correlation coefficient tends to differ from zero at $0.05 < P \le 0.10$.

selecting individuals from a population the probability of the most efficient animal in one stage of production also being the most efficient animal in another stage of production is small.

RFI is strongly correlated with DMI and the strength of the correlation between RFI in different stages of production follows the strength of the correlation between DMI in different stages of production (Nieuwhof et al., 1992; Arthur et al., 2001, 2002; Kelly et al., 2010; Durunna et al., 2011). Additionally, heifers with low RFI typically eat less as cows even though RFI as cows may not be different (Black et al., 2013; Hafla et al., 2013; Manafiazar et al., 2015; Hebart et al., 2018), but not always (Meyer et al., 2008; Lawrence et al., 2012, 2013). Mechanisms regulating feed intake have been implicated in RFI (Perkins et al., 2014; Lines et al., 2018; Pitchford et al., 2018). Thus, factors affecting and regulating DMI are likely factors affecting RFI.

Feed intake is controlled by both physical and metabolic mechanisms, and the balance between these mechanisms is related to the size of the animal and the metabolizability of the feed (Forbes, 1996; Allen, 2014). In the case of cattle fed a high-roughage growing diet versus a high-concentrate finishing diet, physical mechanisms would likely exert more control when fed the high-roughage diet and metabolic mechanisms would likely exert more control when fed the high-concentrate diet, which can be seen in the lower correlation when fed high-roughage versus high-concentrate than when fed the same diet both early and late postweaning (r_p = 0.33 vs. 0.43; Durunna et al., 2011). However, the moderate correlation even when fed the same diet indicates physiological changes are influencing feed intake and/or growth. Phenotypic correlations between growing and finishing phases are lower for ADG (0.02–0.38) than for DMI (0.61–0.63) indicating that changes in gain are the primary cause for the low correlation between RFI in growing and finishing phases (Arthur et al., 2001; Kelly et al., 2010; Durunna et al., 2011). In the current study, heifer ADG was not correlated ($P > 0.10$) with progeny ADG in any parity, but heifer DMI was weakly, positively correlated (0.15; $P \leq 0.05$) with progeny DMI2 and DMI3. As cattle become heavier and fatter the amount of energy used for maintenance increases and the relationship between retained energy and weight gain changes (National Academies of Sciences, Engineering, and Medicine, 2016) and thus the relationship between feed intake and weight gain changes. This is supported by the stronger correlation between RFI and body fat in finishing cattle than growing cattle (Arthur et al., 2001; Basarab et al., 2003; Nkrumah et al., 2004; Schenkel et al., 2004; Lancaster et al., 2009a). Correlations among serial ultrasound rib fat thickness measurements are weak to strong with stronger correlations between measurements closer in time (Clement, 2009) indicating that ranking among animals for composition of gain is not constant throughout a feeding period. Additionally, the less than perfect correlation between growing and finishing phases for DMI also indicates physiological effects on DMI, which are known to occur (National Academies of Sciences, Engineering, and Medicine, 2016). Greater fat deposition will utilize more glucose and acetate (Smith and Crouse, 1984), which in turn will decrease hepatic oxidation of propionate (Allen et al., 2009) and synthesis of malonyl-CoA in the hypothalamus (Black et al., 2009) that induce satiety signals in the paraventricular nucleus. Thus, changes in body composition between cattle early postweaning versus late postweaning that alter growth and feed intake may explain the weak correlation between RFI in growing versus finishing cattle.

The differences in feed intake regulation between growing cattle and lactating cows are likely greater than the differences between growing cattle fed high-roughage and high-concentrate diets. In growing cattle, growth is thought to be a consequence of energy intake above maintenance rather than an energy demand, whereas milk production is an energy demand causing increased feed intake. The National Academies of Science, Engineering, and Medicine (2016) indicates that expected feed intake should be increased by 0.2 kg/d for each kg/d of milk yield. Milk synthesis utilizes glucose for lactose synthesis and acetate for lipid synthesis, which reduces satiety signals through hepatic oxidation of propionate and malonyl-CoA synthesis (Allen et al., 2009; Black et al., 2009). Growth rate of a heifer postweaning is not correlated with milk yield during lactation as a cow (Nieuwhof et al., 1992; Black et al., 2013); however, the primary driver of feed intake, BW, is strongly correlated between growing heifers and cows (Nieuwhof et al., 1992; Koots et al., 1994; Hafla et al., 2013). Thus, the correlation of DMI between growing heifers and lactating cows is moderate (r_p = 0.18–0.63; Nieuwhof et al., 1992; Black et al., 2013) resulting in a poor correlation between RFI measured in growing heifers and lactating cows.

As mentioned above, RFI is strongly correlated with DMI and most of the differences in feed utilization can be attributed simply to differences in feed intake. Dry matter digestibility is greater for low RFI cattle when low RFI cattle consume 17% to 22% less feed than high RFI cattle (Brown, 2005; Krueger, 2009), but not significantly greater when consuming only 13% less feed (Cruz et al., 2010; Fitzsimons et al., 2013, 2014b), and almost identical when fed at similar amounts (Vining, 2015; Lines et al., 2018). The difference in feed intake explains 60% to 100% of the difference in dry matter digestibility between RFI phenotypes (Krueger, 2009; Cruz et al., 2010; Fitzsimons et al., 2014b; Potts et al., 2017). Results on methane yield (g, CH4/kg DMI) are somewhat mixed with only a couple of studies indicating that low RFI phenotypes have less methane yield (Nkrumah et al., 2006; Sharma et al., 2014), but most studies (White, 2004; Hegarty et al., 2007; Fitzsimons et al., 2013; Freetly and Brown-Brandl, 2013; Gomes et al., 2013) report no difference between RFI phenotypes. Even differences in some molecular mechanisms between RFI phenotypes may be related to differences in intake as mitochondrial oxidative stress and coupling of electron transport with ATP synthesis are influenced by caloric intake (Bevilacqua et al., 2004, 2005). To date, differences in energy metabolism between low and high RFI cattle independent of differences in feed intake have been difficult to elucidate.

Developing a feed efficiency trait within the framework of classical dietary energy partitioning could allow for selection of more efficient animals in both growing and finishing, and breeding and lactating stages of production, but depends on similarities between maintenance and efficiency of metabolisable energy use for different physiological functions. Regression of DMI on metabolic body weight and gain results in meaningless and inconsistent coefficients (Davis et al., 2014) as has been discussed previously with the use of regression techniques to determine efficiency of energy and protein gain (Koong, 1977; van Milgen and Noblet, 1999; Moraes, 2019). Models with intake as the dependent variable do not accurately account for heat of support metabolism for energy gain instead including it in the coefficient for metabolic body weight inflating the estimate of the maintenance energy requirement (Marcondes et al., 2013). Computation of RFI using metabolisable energy intake as the dependent variable resulted in regression coefficients for metabolic body weight of 160 to 180 kcal/kg$^{0.75}$ in growing heifers and 240 to 330 kcal/kg$^{0.75}$ in lactating dairy cows (Connor et al., 2019), which are greater than expected values for metabolisable energy required for maintenance (National Research Council, 2001). Regression of output (energy as protein, fat, or milk) on metabolic body weight and metabolisable energy intake results in more accurate regression coefficients for metabolic body weight as estimates of maintenance energy requirement (Moe et al., 1971, 1972; van Milgen and Noblet, 1999).

Changes in weight are a poor representation of energy gain or loss. Guinguina et al. (2020) reported more accurate regression coefficients when using calorimetry data and energy balance to compute RFI. However, in growing animals, regressing feed intake on retained energy as protein and fat results in coefficients that overestimate efficiency of metabolisable energy use (Strathe et al., 2012; Moraes, 2019). In accordance, Guinguina et al. (2020) reported greater accuracy of regression coefficients when using an energy-corrected milk dependent model than a DMI dependent model to compute feed efficiency. Løvendahl et al. (2018) also reported more consistent regression coefficients with an energy-corrected milk than a DMI dependent model.

Accurate selection of energy efficient mature cows through measurement of growing heifers may be possible. Heifers with low net energy for maintenance requirements would be expected to become mature cows with low net energy for maintenance requirements. Net energy for maintenance requirement varies with breed (Solis et al., 1988) and within groups of genetically similar animals (van Es, 1961; Hotovy et al., 1991) suggesting that genetic variation exists for selection, although further research to determine whether differences exist independent of body composition are warranted (DiCostanzo et al., 1990; Herd, 1995; Birnie et al., 2000). Research in other species suggests that genetic variation exits in molecular mechanisms of protein turnover and mitochondrial function important in energy metabolism (Oddy, 1999; Tieleman et al., 2009; Eya et al., 2012) indicating that genetic selection to increase the efficiency of these molecular mechanisms is possible. The potential to increase the efficiency of metabolisable energy use for growth and lactation simultaneously is less clear. First, there is not clear evidence whether genetic variation in partial efficiencies for growth and lactation exist (Veerkamp and Emmans, 1995). However, Guinguina et al. (2020) reported that more efficient lactating dairy cows based on RECM from calorimetry data had greater partial efficiencies of lactation. Second, there is minimal evidence that efficiency of metabolisable energy use for gain is positively correlated with efficiency of metabolisable energy use for lactation. Bath et al. (1966) measured net energy for gain in Hereford steers and net energy for lactation in Holstein cows fed the same diets. Although only three different diets were fed, net energy for gain and lactation were positively correlated. Using the feed composition table (120 feedstuffs) from the National Research Council (2001), the conversion of metabolisable energy to net energy for gain (ratio of net energy for gain to metabolisable energy concentrations) was strongly correlated (0.78) with the conversion of metabolisable energy to net energy for lactation (ratio of net energy for lactation to metabolisable energy concentrations). Given that net energy values of feedstuffs represent the biological efficiency of energy transformation in growing and lactating animals consuming those feedstuffs, it is expected that partial efficiency of gain would be positively correlated with partial efficiency of lactation.

In conclusion, there was a lack of correlation for RFI across different production segments when feed intake was measured during the entire production cycle. Additionally, RFI was poorly correlated across consecutive production cycles. Many physiological and environmental factors affect feed intake, which is likely the primary reason for the poor relationships across production segments and cycles. Thus, although genetically correlated, phenotypic expression of DMI and RFI potential may be highly dependent upon the environment (i.e., nutrition, management, and weather). Developing feed efficiency traits in the framework of dietary energy partitioning could overcome these issues, but there is a need to determine the existence of genetic variation in maintenance energy requirements independent of feed intake level and body composition, and in partial efficiencies of maintenance, gain and lactation. Otherwise, any improvements in feed efficiency are only possible as a dilution of maintenance energy requirements.

Definition of abbreviations

Abbreviation	Definition
ADG, ADG1, ADG2, ADG3	Average daily gain. For heifers, average daily gain from 240 d of age to first parturition (Davis et al., 2016). For progeny, average daily gain from weaning to harvest for the first, second, and third progeny from each dam
DMI, DMI1, DMI2, DMI3	Dry matter intake. For heifers, average daily dry matter intake from 240 d of age to first parturition (Davis et al., 2016). For dams, average daily dry matter intake of dams from weaning of previous calf to weaning of current calf for the first, second, and third parity. For progeny, average daily dry matter intake from weaning to harvest for the first, second, and third progeny from each dam
ECM1, ECM2, ECM3	Energy-corrected milk yield. Average daily energy-corrected milk yield for the first, second, and third parity
FCR, FCR1, FCR2, FCR3	Feed conversion ratio. For heifers, ratio of daily dry matter intake to average daily gain from 240 d of age to first parturition (Davis et al., 2016). For progeny, ratio of daily dry matter intake to average daily gain from weaning to harvest for the first, second, and third progeny from each dam
FME1, FME2, FME3	Feed:milk energy ratio. Ratio of daily dry matter intake during the entire production cycle to daily energy-corrected milk yield of dams for the first, second, and third parity
RECM1, RECM2, RECM3	Residual energy-corrected milk yield. Residual energy-corrected milk yield for the entire production cycle for the first, second, and third parity
RFI, RFI1, RFI2, RFI3	Residual feed intake. For heifers, residual dry matter intake for the time from 240 d of age to first parturition (Davis et al., 2016). For dams, residual dry matter intake for the entire production cycle for the first, second, and third parity. For progeny, residual dry matter intake for the time from weaning to harvest for the first, second, and third progeny from each dam
RG, RG1, RG2, RG3	Heifer residual gain. Residual average daily gain for the time from 240 d of age to first parturition (Davis et al., 2016). For progeny, residual average daily gain for the time for weaning to harvest for the first, second, and third progeny from each dam
RIG, RIG1, RIG2, RIG3	Heifer residual intake and gain. Residual dry matter intake plus residual average daily gain from 240 d of age to first parturition for each dam. For progeny, residual dry matter intake plus residual average daily gain from weaning to harvest for the first, second, and third progeny from each dam
RIM1, RIM2, RIM3	Residual intake and milk. Residual dry matter intake plus residual energy-corrected milk of dams for the entire production cycle for the first, second, and third parity
MCWT1, MCWT2, MCWT3	Mid-cycle dam weight. Average weight of dam during the production cycle for the first, second, and third parity
PSLW1, PSLW2, PSLW3	Progeny harvest weight. Sex-adjusted shrunk harvest weight of first, second, and third progeny from each dam
WTGAINGEST1, WTGAINGEST2, WTGAINGEST3	Dam gestational weight change. Weight change per day from weaning of previous calf to parturition for the first, second, and third parity
WTGAINLACT1, WTGAINLACT2, WTGAINLACT3	Dam lactational weight change. Weight change per day from parturition to weaning for the first, second, and third parity

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