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Heritability and genetic correlations of feed intake, body weight gain, residual gain, and residual feed intake of beef cattle as heifers and cows

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Abstract

The cow herd consumes approximately 70% of the annual feed resources. To date, most genetic evaluations of feed intake in beef cattle have been made in growing animals and little information is available for mature cows. Genetic evaluations in mature cows have predominately been confined to lactating dairy cows and the relationship between feed intake as growing heifers and mature cows has not been addressed. It was the purpose of this study to estimate the heritability of feed intake when measured as growing heifers and mature cows and determine the genetic correlation between these measurements. Individual feed intake and BW gain were measured on 687 heifers and 622 5-yr-old cows. The heritability of average daily DMI (ADDMI) estimated in heifers was 0.84 ± 0.12 and 0.53 ± 0.12 in cows. The heritability of ADG estimated in heifers was 0.53 ± 0.12 and 0.34 ± 0.11 in cows. The genetic correlation between heifer and cow ADDMI was 0.84 ± 0.09 . The genetic correlation between heifer and cow ADG was 0.73 ± 0.19 . Heritability of residual feed intake in heifers was 0.25 ± 0.11 and 0.16 ± 0.10 in cows. Heritability for residual gain in heifers was 0.21 ± 0.11 and 0.14 ± 0.10 in cows. Feed intake and ADG are heritable and genetically correlated between heifers and cows. Selection for decreased feed intake and ADG in growing animals will probably have the same directional effects on mature cows.

Key words: beef cattle, feed intake, gain, heritability

Introduction

The cow herd consumes approximately 70% of the annual feed resources. To date, most genetic evaluations of feed intake in beef cattle have been made in growing animals, and little information is available for mature cows. Genetic evaluations in mature cows have predominately been confined to lactating dairy cows, and the relationship between feed intake as growing heifers and mature cows has not been addressed. It was the purpose of this study to estimate the heritability of feed intake, BW gain, and restricted indices for intake and gain when

measured in growing heifers and mature cows and determine the genetic correlation associated with these measurements.

Materials and Methods

Research protocols were approved and monitored by the U.S. Meat Animal Research Center Institutional and Animal Care Committee in accordance with the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (FASS, 1999).

Cattle

Crossbred cows that were progeny of cattle sampled from industry AI sires were used in the study. The original matings were Angus, Hereford, and MARC III composite ($\frac{1}{4}$ Angus, $\frac{1}{4}$ Hereford, $\frac{1}{4}$ Pinzgauer, $\frac{1}{4}$ Red Poll) cows bred by AI to Angus ($n = 21$), Hereford ($n = 21$), Simmental ($n = 20$), Limousin ($n = 20$), Charolais ($n = 24$), Gelbvieh ($n = 21$), and Red Angus ($n = 21$) bulls sampled from the industry in 1998 to produce the F_1 generation. The cows used in this study were the result of mating F_1 bulls ($n = 47$) that had Angus and Hereford dams and were sired by a subset of the AI sires described above to F_1 cows ($n = 485$) from all 3 dam breeds in multiple-sire pastures to produce 2-, 3-, and 4-breed cross progeny. Parentage was determined using various SNP array (primarily Illumina BovineSNP50, Illumina, San Diego, CA). Heifers from 4 consecutive years calf crops were retained and kept as cows: year 1 ($n = 277$), year 2 ($n = 431$), year 3 ($n = 240$), and year 4 ($n = 220$). Heifers were bred to have their first calves as 2-yr-olds and given the opportunity to produce 4 calf crops. A cow was removed from the study after she failed to give birth to a calf twice. In total, 0, 240, 229, and 218 heifers were evaluated for feed intake and growth in years 1 through 4, respectively, and 158, 179, 154, and 131 cows were evaluated for feed intake and BW change from years 1 through 4, respectively.

Feed intake measurements

Heifers

Feed intake and growth measurements were taken on heifers born in years 2 through 4. Feed intake and growth were determined for an 84-d period. Each year heifers were randomly split into 2 contemporary groups to determine feed intake of all heifers using available equipment capacity. At the beginning of the feed intake study, group 1 heifers averaged 228 d of age and group 2 heifers averaged 333 d. Heifers had ad libitum access to a ration that contained as a percent of DM 64.8% corn silage, 30% chopped alfalfa hay, 5% soybean meal, and 0.2% salt. Feed intake was measured with Calan Gates (American Calan, Northwood, NH). Heifers were offered feed each day and orts were determined weekly. Feed was subsampled daily and DM of a weekly composite sample was determined. Weekly intakes were multiplied by weekly feed DM to determine weekly DMI. Total DMI was calculated by summing DMI for the feeding period, and average daily DMI (ADDMI) were calculated by dividing total DMI by days on study. Year 2 group 1 heifers were weighed on days 0, 1, 14, 28, 42, 56, 70, 83, and 84, and year 2 group 2 heifers were weighed on days 0, 1, 17, 28, 42, 56, 70, 80, and 84. Year 3 group 1 heifers were weighed on days 0, 1, 14, 28, 43, 56, 70, 83, and 84, and year 3 group 2 heifers were weighed on days 0, 1, 14, 28, 42, 56, 70, 80, and 84. Year 4 group 1 heifers were weighed on days 0, 1, 14, 28, 43, 56, 70, 83, and 84, and year 4 group 2 heifers were weighed on days 0, 1, 14, 28, 42, 56, 70, 80, and 84. A quadratic function was used to regress BW on days on study. The regression equation was used to calculate total BW gain, and ADG was calculated as the total BW gain divided by days on study.

Cows

At 5 yr of age, cows were not bred and were moved to an individual feed intake facility equipped with Calan Gates (American Calan, Northwood, NH) the week after they weaned their fourth calf. Within year, cows were a single contemporary group. Cows were fed a ration that contained as a percent of DM 27.0% ground alfalfa hay, 5.5% corn, 67.3% corn silage, and 0.2% salt. Twenty-one days after weaning, cows were weighed on 2

consecutive days. Body weight was averaged and feed offered was set to provide 120 kcal ME/kg BW^{0.75}. Cows were fed the same amount of feed for 112 d. At 112 d, cows had ad libitum access to the same ration. Cows were fed once a day and feed refusal were measured weekly. Average daily DMI was calculated for each period as described for heifers. In the first year, feed intake and BW gain were measured for 84 d during the ad libitum feeding period. Cows were weighed on days 0, 14, 28, 42, 56, 70, and 84. In subsequent years, cows were fed for 98 d and weighed on days 0, 14, 28, 42, 56, 70, 84, 97, and 98 except in year 3 cows were weighed on day 86 instead of 84. An additional weight was taken on day 7 of the refeed in year 2 (Fig. 1). A quadratic function was used to regress BW on days on study. The regression equation was used to calculate total BW gain, and ADG was calculated as the total BW gain divided by days on study.

Data analysis

(Co)variance components were estimated using REML procedures of ASReml (version 4.1; VSN International, Ltd., Hemel Hempstead, UK). The multiple-trait model included heifer ADDMI, heifer ADG, cow ADDMI, and cow ADG. Fixed independent variables in the model for each trait were birth year, direct heterosis (fraction of expected breed heterozygosity to account for heterosis), and proportions of each breed. Details of expected breed heterozygosity and breed proportions were described in Ahlberg et al. (2016). Briefly, the Angus, Hereford, and MARC III cows that contributed to the population were subdivided into 10 genetic groups that reflected different selection histories at USMARC within breed and those genetic groups were treated as distinct from the 7 breeds from which AI sires were sampled explicitly for the purpose of estimating breed differences. The models for heifer ADDMI and heifer ADG also included a fixed effect for feed intake recording group (1 or 2) as described above. The models for cow ADDMI and cow ADG also included a fixed effect for whether the cow was lactating or dry during the season prior to feed intake recording.

The random effects for each trait were additive breeding values of 7,269 animals in the pedigree and residuals. Covariances among breeding values within trait were assumed proportional to the numerator relationship matrix.

Restricted indices

Restricted indices were computed from ADDMI and ADG, both as heifers and as cows. For residual ADG (RADG), the relative economic value (REV) assigned to ADG was 1.0, and the REV assigned to ADDMI was the negative of the genetic regression of ADG on ADDMI (Eisen, 1977; Lin, 1980). Similarly, REV for residual feed intake (RFI) were 1.0 for ADDMI and the negative of the genetic regression of ADDMI on ADG (Lin, 1980).

Breed effect estimates of the restricted indices and their standard errors were computed using the !CONTRAST statement of ASREML. Genetic parameter estimates (and their standard errors) of the restricted indices, including their covariances with the underlying traits, were computed using the VPREDICT statement for estimating functions of variance component parameters in ASREML.

Results

Descriptive statistics for DMI and BW gain for heifers and cows are presented in Table 1. Estimates of heritability and genetic and residual correlations for heifer DMI, heifer ADG, Cow DMI, and Cow ADG are presented in Table 2. There were

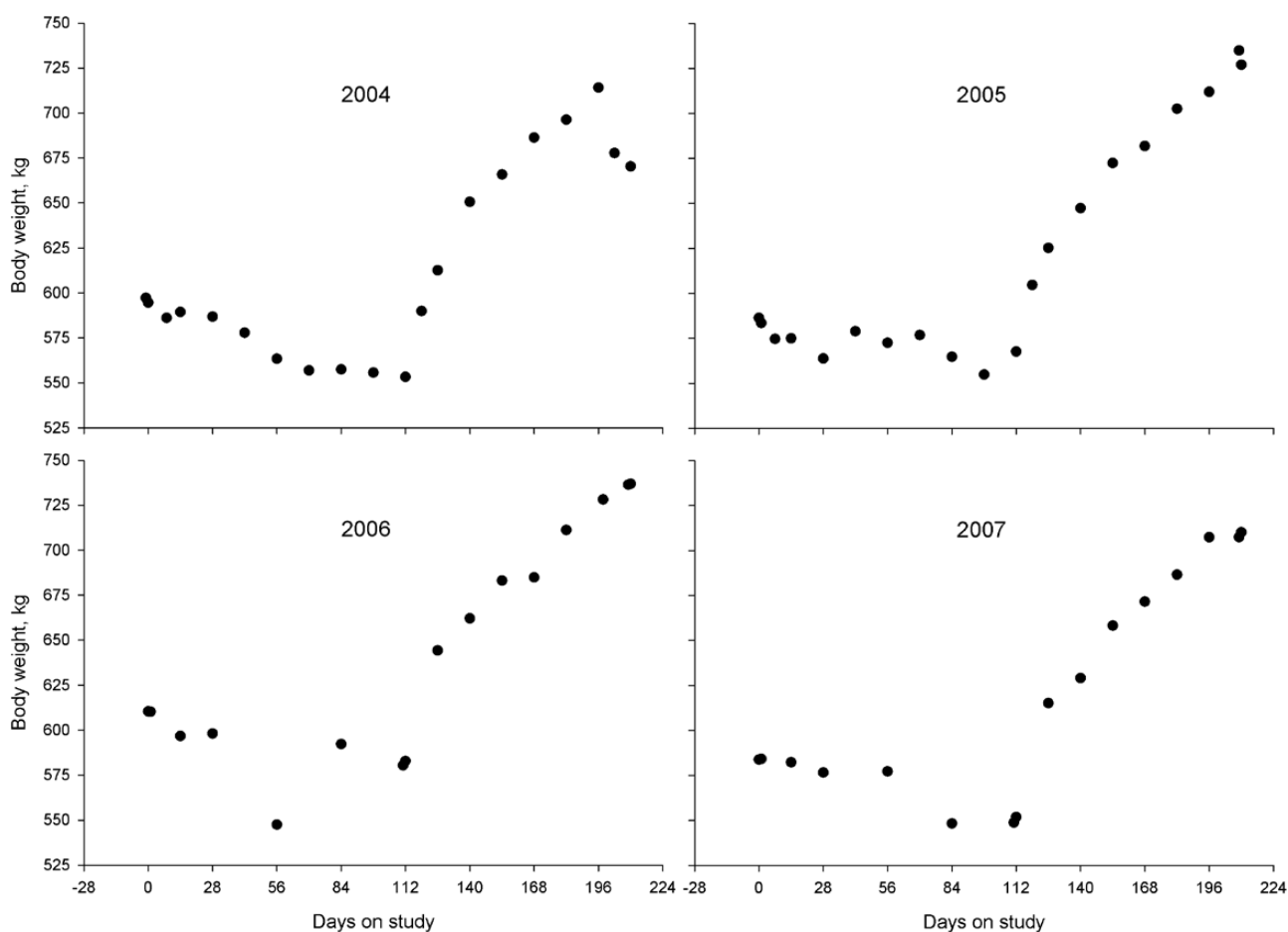


Figure 1. Body weight of 5-yr-old cows restricted for 112 d to 120 kcal ME/kg BW^{0.75} of their initial BW followed by ad libitum access to feed.

Table 1. Descriptive statistics of heifers and cow traits

Trait	Mean	SD
Heifer average daily DM intake, kg/d	8.14	1.06 ¹
Heifer ADG, kg/d	1.05	0.19 ¹
Cow average daily DM intake, kg/d	15.34	1.64 ²
Cow ADG, kg/d	1.54	0.29 ²

Heifers were fed 84 d, and cows were fed 84 or 98 d.

¹n = 719.

²n = 666.

positive genetic correlations among similar traits observed on heifers and cows. Residual correlations were positive within heifer or cow traits, but slightly negative between traits of heifers and cows. Heritabilities and genetic correlations among heifer RFI, heifer RADG, cow RFI and cow RADG, and their genetic correlations with the underlying traits are presented in Table 2. The genetic correlations between RFI and ADG were exactly zero in both heifers and cows because the restricted indices were intentionally designed to make it so. Similarly, the genetic correlations between RADG and ADDMI were exactly zero in both heifers and cows for the same reason. The genetic correlations between RFI and RADG within heifers and within cows were each -0.86 because the favorable directions of these 2 measures of efficiency are of opposite sign. The genetic correlations between heifers and

cows of RFI and RADG, respectively, were 0.41 ± 0.36 and 0.31 ± 0.46 . The regressions of ADG on DMI were 0.123 ± 0.017 and 0.113 ± 0.022 in heifers and cows, respectively. The regressions of DMI on ADG were 5.97 ± 0.96 and 6.59 ± 1.41 in heifers and cows, respectively.

Breed differences for ADDMI and ADG in heifers and cows are presented in Table 3. Breed differences for traits and indices of heifers were taken from Retallick et al. (2017) because that analysis included all of the heifers in the present study, as well as many others, resulting in standard errors of breed differences of approximately half the magnitude of standard errors of the same differences in the present study. Heifer breed difference estimates of ADDMI, ADG, and RADG were taken directly from Retallick et al. (2017), although RADG was referred to in that paper as the “restricted index.” Estimates of RFI were not included in Retallick et al. (2017), but the estimates reported here were computed directly from results of the analysis used by Retallick et al. (2017), interchanging ADDMI and ADG in the computation of the “restricted index.”

Breed differences and P-values reported in Table 3 reflect only the AI sires representing the 7 breeds. Consequently, the P-values for heifer traits reported in Table 3 are different (and more significant) than those reported by Retallick et al. (2017), which incorporated differences among the 10 genetic groups of USMARC base cows. Breeds differed as heifers for ADDMI ($P = 0.000003$), ADG ($P = 0.004$), RFI ($P = 0.0004$), and RADG ($P = 0.048$), but did not differ significantly as cows.

Table 2. Heritability (diagonal), genetic correlations (above diagonal), and residual correlations (below diagonal) of average daily DM intake, ADG, residual feed intake, and residual ADG of beef cattle as heifers and 5-year-old cows¹

	Heifer ADDMI	Heifer ADG	Cow ADDMI	Cow ADG	Heifer RFI	Heifer RADG	Cow RFI	Cow RADG
Heifer ADDMI	0.84 ± 0.12	0.86 ± 0.07	0.84 ± 0.09	0.83 ± 0.14	0.52 ± 0.10	0 ± 0	0.25 ± 0.22	0.20 ± 0.26
Heifer ADG	0.05 ± 0.32	0.53 ± 0.12	0.66 ± 0.16	0.73 ± 0.19	0 ± 0	0.52 ± 0.11	0.04 ± 0.29	0.33 ± 0.30
Cow ADDMI	-0.08 ± 0.35	-0.08 ± 0.18	0.53 ± 0.12	0.86 ± 0.10	0.54 ± 0.19	-0.13 ± 0.28	0.50 ± 0.14	0 ± 0
Cow ADG	-0.40 ± 0.36	-0.15 ± 0.16	0.43 ± 0.10	0.34 ± 0.11	0.39 ± 0.25	0.05 ± 0.30	0 ± 0	0.50 ± 0.16
Heifer RFI					0.25 ± 0.11	-0.86 ± 0.40	0.41 ± 0.36	-0.16 ± 0.43
Heifer RADG						0.21 ± 0.11	-0.33 ± 0.42	0.31 ± 0.46
Cow RFI							0.16 ± 0.10	-0.86 ± 0.57
Cow RADG								0.14 ± 0.10

¹Heifer ADDMI, average daily feed intake kg/d over 84 d when feed was offered with ad libitum access; Heifer ADG, average heifer BW gain kg/d during feeding period; Cow ADDMI, average daily feed intake kg/d over feeding period when feed was offered with ad libitum access; Cow ADG, average cow BW gain kg/d during feeding period. Residual feed intake and residual average daily gain were restricted indices of ADDMI and ADG in which the weight on ADDMI or ADG, respectively, was set equal to 1, and the weight on ADG or ADDMI, respectively, was set equal to the negative of the genetic regression of ADDMI on ADG or ADG on ADDMI, respectively.

Table 3. Across breed comparison of average daily DM intake, average daily gain, residual feed intake, and residual average daily gain of heifers and cows compared with Angus¹

Breed	Heifer ² ADDMI	Heifer ² ADG	Cow ADDMI	Cow ADG	Heifer ² RFI	Heifer ² RADG	Cow RFI	Cow RADG
Angus	0	0	0	0	0	0	0	0
Red Angus	-684 ± 255	-86 ± 42	-604 ± 940	-17 ± 143	-299 ± 214	-18 ± 35	-491 ± 760	51 ± 106
Charolais	-876 ± 270	-75 ± 45	-977 ± 1,046	-55 ± 163	-543 ± 227	13 ± 37	-617 ± 882	56 ± 124
Gelbvieh	-723 ± 253	-114 ± 42	-1,070 ± 990	139 ± 153	-215 ± 212	-42 ± 34	-1,987 ± 824	260 ± 116
Hereford	-962 ± 266	-21 ± 44	-756 ± 1,003	37 ± 157	-868 ± 225	75 ± 36	-1,003 ± 849	123 ± 119
Limousin	-1,471 ± 255	-160 ± 42	-1,327 ± 1,000	-67 ± 155	-760 ± 214	-13 ± 35	-882 ± 830	83 ± 116
Simmental	-530 ± 275	-68 ± 45	82 ± 1,030	265 ± 160	-228 ± 232	-15 ± 38	-1,662 ± 860	255 ± 121
P _{breed differed}	0.000003	0.004	0.74	0.27	0.0004	0.048	0.22	0.15

¹Residual feed intake and residual average daily gain were restricted indices of ADDMI and ADG in which the weight on ADDMI or ADG, respectively, was set equal to 1 and the weight on ADG or ADDMI, respectively, was set equal to the negative of the genetic regression of ADDMI on ADG or ADG on ADDMI, respectively. All traits expressed in g/d of DM intake or BW gain.

²Breed effect estimates for all traits and indices as heifers were taken from [Retallick et al. \(2017\)](#).

Cows that weaned a calf in the year prior to the intake study had 615 ± 314 g/d greater ($P = 0.051$) ADDMI and 275 ± 47 g/d greater ($P = 0.0000002$) ADG than cows that did not wean a calf.

Discussion

Feed represents the largest input cost in beef production, and within a production year, the majority of the feed is used by the cow herd. It has been established in multiple studies that feed intake is a heritable trait in beef cattle ([Koch et al., 1963](#); [Fan et al., 1995](#); [Herd and Bishop, 2000](#); [Arthur et al., 2001](#); [Schenkel et al., 2004](#); [Nkrumah et al., 2007](#); [Elzo et al., 2009](#); [Mujibi et al., 2011](#); [Rolfe et al., 2011](#); [Mao et al., 2013](#); [Retallick et al., 2017](#)). All of these studies have estimated the heritability of feed intake in the growing animal and estimates have ranged between 0.28 ± 0.11 and 0.44 ± 0.06 ([Koch et al., 1963](#); [Schenkel et al., 2004](#)). Our estimate in the growing heifer (0.84 ± 0.12) is greater than those previously reported including what we reported earlier for the same population for growing steers (0.40 ± 0.02; [Rolfe et al., 2011](#)). Numerous factors may be associated with regulation of satiety in growing cattle including composition of the test ration. The signals for satiety in high concentrate rations are probably associated with chemical signals while those in high fiber diets are probably associated with gut fill. In our heifer study, the diet was approximately 30% concentrate; where, in our steer study, the ration was approximately 88% concentrate ([Rolfe et al., 2011](#)). The studies of [Arthur et al. \(2001\)](#) and [Schenkel et al.](#)

(2004) reported heritabilities for feed intake of 0.37 ± 0.05 and 0.44 ± 0.06, respectively, which were lower than our estimate in heifers. Their studies used rations with a similar metabolizable energy density of the diet that we used; however, [Arthur et al. \(2001\)](#) used a pelleted ration.

Like feed intake, numerous studies have reported that growth is a heritable trait in beef cattle ([Koch et al., 1963](#); [Fan et al., 1995](#); [Herd and Bishop, 2000](#); [Arthur et al., 2001](#); [Schenkel et al., 2004](#); [Nkrumah et al., 2007](#); [Elzo et al., 2009](#); [Mujibi et al., 2011](#); [Rolfe et al., 2011](#); [Mao et al., 2013](#); [Retallick et al., 2017](#)). Our estimate (0.53 ± 0.12) is within the range previously reported 0.26 ± 0.10 and 0.62 ± 0.12 ([Koch et al., 1963](#); [Rolfe et al., 2011](#)), and is greater than those previously reported for growing steers (0.26 ± 0.10; [Rolfe et al., 2011](#)) in the same population. The primary difference between the 2 studies was that the steers received a diet to promote fat gain; where, the heifers were fed to support lean gain. It is possible that heritability of lean and fat gain differ; however, that speculation may not be supported by heritability estimates of component traits of gain. [Schenkel et al. \(2004\)](#) reported a heritability of 0.36 ± 0.03 for back fat compared with 0.30 ± 0.04 for longissimus muscle area. [Mao et al. \(2013\)](#) reported a heritability for back fat of 0.33 ± 0.10 and 0.50 ± 0.13 compared with heritability of lean meat yields of 0.41 ± 0.13 and 0.32 ± 0.14.

Our estimate of the genetic correlation between ADG and feed intake (0.86 ± 0.07) is at the higher end of the range reported 0.34 ± 0.10 and 0.88 ± 0.10 ([Elzo et al., 2009](#); [Retallick et al., 2017](#)),

and is greater than what we reported for steers in the same population (Rofe et al., 2011). In a larger study that included the heifers in this study, Retallick et al. (2017) reported that heifers had greater genetic correlations between feed intake and gain than steers. Stage of maturity and diet density may contribute to the variation in the reported correlations between ADG and feed intake.

There are fewer studies that have estimated heritability of feed intake in the mature cow and many of those estimates have been made in lactating dairy cows (Veerkamp and Thompson, 1999; Archer et al., 2002; Berry et al., 2007; Buttchereit et al., 2011). Archer et al. (2002) reported a heritability of 0.28 in nonpregnant, nonlactating beef cattle of a similar age that is less than what we estimated. The studies differed in the form of the feed where their study used a pelleted diet and we used a diet that was primarily chopped. In our study, cows were not pregnant or lactating and our heritability estimate for ADDMI (0.53 ± 0.12) was greater than those typically estimated in the dairy cow (0.20 to 0.40). There is evidence that the heritability for feed intake differs from the days in milk (Tetens et al., 2014; Li et al., 2016). Biologically we would predict feed intake would be associated with the cow's maintenance and her level of milk production in the lactating cow. Manafiazar et al. (2016) reported a genetic correlation between DMI and milk yield of 0.71 ± 0.15 .

The model used in this study removes feed intake associated with the support of milk production and pregnancy and represents the feed intake associated with maintenance and BW gain. Cows were limit fed for 112 d to allow all cows to reach a baseline associated with a common feed intake (Fig. 1). Based on our previous studies in mature cows, it takes approximately 112 d for a cow to move into zero energy balance following a feed restriction (Freetly and Nienaber, 1998). Although ADDMI heritability estimates are lower in the cow than the heifer the genetic correlation between heifer ADDMI and cow ADDMI is high (0.84 ± 0.09). Archer et al. (2002) reported a lower heritability for cow feed intake (0.28) than ours, but like our study, they reported a high genetic correlation (0.94) between postweaning feed intake and cow feed intake. Black et al. (2013) reported that there was a phenotypic correlation between heifer and cow feed intake. These findings suggest that selection pressure in heifers for feed intake would have the same directional effect on mature cow feed intake. The heritability estimate for ADG in cows is less than half of the heritability for heifers; however, like heifers, the genetic correlation between ADG and ADDMI is high (0.86 ± 0.10). These findings suggest that selecting for lower feed intake as either heifers or cows would also result in a reduction in ADG in mature cows.

Efficiency of feed utilization is commonly expressed as RFI or RADG. These metrics can be computed in 2 steps, the first of which is a series of individual animal regressions, but this approach is statistically suboptimal. These metrics can alternatively be computed as restricted indices applied to the results of a multiple-trait analysis as was done here. This approach is much more statistically coherent. The RFI index is expressed in g/d of feed intake (therefore REV of DMI = 1) with the REV of ADG (-5.96 and -6.59 in heifers and cows, respectively) chosen such that selection for RFI is not expected to change ADG. Similarly, RADG is expressed in g/d of gain (therefore REV of ADG = 1) with the REV of ADDMI (-0.123 and -0.113 in heifers and cows, respectively) chosen such that selection for RADG is not expected to change ADDMI. Both restricted indices can be viewed as indicators of feed efficiency. The economically optimum weighting on ADDMI relative to ADG is likely to be intermediate between those implied by the RFI

and RADG-restricted indices (Thallman et al., 2018). The genetic correlations between these 2 weightings of the component traits were -0.86 in both cows and heifers, indicating that the ranking of individuals is not highly dependent on the REV applied to ADDMI and ADG.

Although the genetic correlations between the same traits as heifers and cows were 0.84 ± 0.09 and 0.73 ± 0.19 for ADDMI and ADG, respectively, the genetic correlations between feed efficiency indices as heifers and cows were considerably lower with larger standard errors (0.41 ± 0.36 and 0.31 ± 0.46 for RFI and RADG, respectively). This is because they are indices of antagonistically correlated traits. It is inherently more challenging to select for feed efficiency than either of the component traits and the genetic correlation between heifers and cows is considerably higher when the many genes that have proportionally similar effects on growth and intake are included than when only those genes that have proportionally dissimilar effects on growth and intake are considered.

Retallick et al. (2017) reported breed differences for feed intake in the growing heifers. Breed differences were not significant in mature cows, at least partially due to the lower power in this study due to the limited number of cows in which it was possible to measure ADDMI. Metabolic rate and BW gain are two of the primary drivers for feed intake. In sheep studies, we demonstrated that breed differences in metabolic rate could be accounted for by stage of maturity (Freetly et al., 2002), and the same equation form can be used to describe metabolic rate during aging in cattle (Freetly et al., 2003). Although metabolic rate differed by breed in the growing animal; in the sheep studies, there were no differences in mature ewes. If cattle follow the same model as sheep, breed differences in feed intake observed in growing animals and not in mature animals may be a function of breed difference in relative maturity and metabolic rate during the evaluation period. Although this study had limited power to test for breed effects in the mature cow, biological similarities in metabolic rate, ADG, and chemical composition of the gain across breeds in mature cows may also contribute to the absence of breed differences.

Conclusion

Feed intake and ADG are heritable and genetically correlated between heifers and cows. Selection for decreased feed intake and ADG in growing animals will probably have the same directional effects on mature cows. Breed differences in feed intake in growing animals do not imply breed differences in mature cows.

Acknowledgments

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Literature Cited

- Ahlberg, C. M., L. A. Kuehn, R. M. Thallman, S. D. Kachman, W. M. Snelling, and M. L. Spangler. 2016. Breed effects and genetic parameter estimates for calving difficulty and birth weight in a multibreed population. *J. Anim. Sci.* **94**:1857–1864. doi:10.2527/jas.2015-0161

- Archer, J. A., A. Reverter, R. M. Herd, D. J. Johnston, and P. F. Arthur. 2002. Genetic variation in feed intake and efficiency of mature beef cows and relationships with postweaning measurements. In 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France: World Congress.
- Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. *J. Anim. Sci.* **79**:2805–2811. doi:10.2527/2001.79112805x
- Berry, D. P., B. Horan, M. O'Donovan, F. Buckley, E. Kennedy, M. McEvoy, and P. Dillon. 2007. Genetics of grass dry matter intake, energy balance, and digestibility in grazing Irish dairy cows. *J. Dairy Sci.* **90**:4835–4845. doi:10.3168/jds.2007-0116
- Black, T. E., K. M. Bischoff, V. R. Mercadante, G. H. Marquezini, N. Dilorenzo, C. C. Chase, Jr., S. W. Coleman, T. D. Maddock, and G. C. Lamb. 2013. Relationships among performance, residual feed intake, and temperament assessed in growing beef heifers and subsequently as 3-year-old, lactating beef cows. *J. Anim. Sci.* **91**:2254–2263. doi:10.2527/jas.2012-5242
- Buttchereit, N., E. Stamer, W. Junge, and G. Thaller. 2011. Short communication: Genetic relationships among daily energy balance, feed intake, body condition score, and fat to protein ratio of milk in dairy cows. *J. Dairy Sci.* **94**:1586–1591. doi:10.3168/jds.2010-3396
- Eisen, E. J. 1977. Restricted selection index: An approach to selecting for feed efficiency. *J. Anim. Sci.* **44**:958–972. doi:10.2527/jas1977.446958x
- Elzo, M. A., D. G. Riley, G. R. Hansen, D. D. Johnson, R. O. Myer, S. W. Coleman, C. C. Chase, J. G. Wasdin, and J. D. Driver. 2009. Effect of breed composition on phenotypic residual feed intake and growth in Angus, Brahman, and Angus × Brahman crossbred cattle. *J. Anim. Sci.* **87**:3877–3886. doi:10.2527/jas.2008-1553
- Fan, L. Q., D. R. Bailey, and N. H. Shannon. 1995. Genetic parameter estimation of postweaning gain, feed intake, and feed efficiency for Hereford and Angus bulls fed two different diets. *J. Anim. Sci.* **73**:365–372. doi:10.2527/1995.732365x
- FASS. 1999. *Guide for the care and use of agricultural animals in research and teaching*. 2nd ed. Fed. Anim. Sci. Soc., Savoy, IL.
- Freetly, H. C., and J. A. Nienaber. 1998. Efficiency of energy and nitrogen loss and gain in mature cows. *J. Anim. Sci.* **76**:896–905. doi:10.2527/1998.763896x
- Freetly, H. C., J. A. Nienaber, and T. Brown-Brandl. 2002. Relationships among heat production, body weight, and age in Finnsheep and Rambouillet ewes. *J. Anim. Sci.* **80**:825–832. doi:10.2527/2002.803825x
- Freetly, H. C., J. A. Nienaber, and T. M. Brown-Brandl. 2003. Relationship between aging and nutritionally controlled growth rate on heat production of heifers. *J. Anim. Sci.* **81**:1847–1852. doi:10.2527/2003.8171847x
- Herd, R. M., and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. *Livest. Prod. Sci.* **63**:111–119. doi:10.1016/S0301-6226(99)00122-0
- Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* **22**:486–494. doi:10.2134/jas1963.22486x
- Li, B., W. F. Fikse, J. Lassen, M. H. Lidauer, P. Løvendahl, P. Mäntysaari, and B. Berglund. 2016. Genetic parameters for dry matter intake in primiparous Holstein, Nordic Red, and Jersey cows in the first half of lactation. *J. Dairy Sci.* **99**:7232–7239. doi:10.3168/jds.2015-10669
- Lin, C. Y. 1980. Relative efficiency of selection methods for improvement of feed efficiency. *J. Dairy Sci.* **63**:491–494. doi:10.3168/jds.S0022-0302(80)82960-2
- Manafiazar, L., Goonewardene, F. Miglior, D. H. Crews, Jr., J. A. Basarab, E. Okine, Z. Wang. 2016. Genetic and phenotypic correlations among feed efficiency, production and selection conformation traits in dairy cows. 2016. *Animal* **10**:381–389. doi:10.1017/S1751731115002281
- Mao, F., L. Chen, M. Vinsky, E. Okine, Z. Wang, J. Basarab, D. H. Crews, Jr., and C. Li. 2013. Phenotypic and genetic relationships of feed efficiency with growth performance, ultrasound, and carcass merit traits in Angus and Charolais steers. *J. Anim. Sci.* **91**:2067–2076. doi:10.2527/jas.2012-5470
- Mujibi, F. D., J. D. Nkrumah, O. N. Durunna, J. R. Grant, J. Mah, Z. Wang, J. Basarab, G. Plastow, D. H. Crews, Jr., and S. S. Moore. 2011. Associations of marker panel scores with feed intake and efficiency traits in beef cattle using preselected single nucleotide polymorphisms. *J. Anim. Sci.* **89**:3362–3371. doi:10.2527/jas.2010-3362
- Nkrumah, J. D., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, D. H. Crews, Jr., and S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and measures of efficiency with growth and carcass merit of beef cattle. *J. Anim. Sci.* **85**:2711–2720. doi:10.2527/jas.2006-767
- Nkrumah, J. D., E. L. Sherman, C. Li, E. Marques, D. H. Crews, Jr., R. Bartusiak, B. Murdoch, Z. Wang, J. A. Basarab, and S. S. Moore. 2007. Primary genome scan to identify putative quantitative trait loci for feedlot growth rate, feed intake, and feed efficiency of beef cattle. *J. Anim. Sci.* **85**:3170–3181. doi:10.2527/jas.2007-0234
- Retallick, K. J., J. M. Bormann, R. L. Weaver, M. D. MacNeil, H. L. Bradford, H. C. Freetly, K. E. Hales, D. W. Moser, W. M. Snelling, R. M. Thallman, et al. 2017. Genetic variance and covariance and breed differences for feed intake and average daily gain to improve feed efficiency in growing cattle. *J. Anim. Sci.* **95**:1444–1450. doi:10.2527/jas.2016.1260
- Rolfe, K. M., W. M. Snelling, M. K. Nielsen, H. C. Freetly, C. L. Ferrell, and T. G. Jenkins. 2011. Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection. *J. Anim. Sci.* **89**:3452–3459. doi:10.2527/jas.2011-3961
- Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth and body composition traits of young beef bulls. *Can. J. Anim. Sci.* **84**:177–184. doi:10.4141/A03-085
- Tetens, J., G. Thaller, and N. Krattenmacher. 2014. Genetic and genomic dissection of dry matter intake at different lactation stages in primiparous Holstein cows. *J. Dairy Sci.* **97**:520–531. doi:10.3168/jds.2013-7301
- Thallman, R. M., L. A. Kuehn, W. M. Snelling, K. J. Retallick, J. M. Bormann, H. C. Freetly, K. E. Hales, G. L. Bennett, R. L. Weaver, D. W. Moser, et al. 2018. Reducing the period of data collection for intake and gain to improve response to selection for feed efficiency in beef cattle. *J. Anim. Sci.* **96**:854–866. doi:10.1093/jas/skx077
- Veerkamp, R. F., and R. Thompson. 1999. A covariance function for feed intake, live weight, and milk yield estimated using a random regression model. *J. Dairy Sci.* **82**:1565–1573. doi:10.3168/jds.S0022-0302(99)75384-1