Evaluation of Post-weaning Efficiency in Nellore-Angus Crossbred Steers through Model Predicted Residual Consumption

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Abstract

The objective of this work was to evaluate efficiency traits of Nellore-Angus crossbred steers (n = 349) on feed. Steers were fed a grain-based diet beginning at approximately 12 months of age for an average of 140 days. Contemporary groups were born in the fall or spring of 2003 through 2007 in full-sibling embryo transfer families or half-sibling families all sired by the same bulls. Individual intake was measured and weights were recorded to permit calculation of average daily gain. Residual feed intake (RFI) was estimated as the residual of models employing regressions on metabolic mid-test weight and ADG. An additional efficiency metric was also constructed and evaluated: model predicted residual consumption (MPRC). Mixed linear models were used to analyze daily dry matter intake, average daily gain (ADG), metabolic mid-test weight, RFI, and MPRC. Large positive associations of DMI with MPRC and RFI were identified along with low positive associations between metabolic mid-weight with ADG and MPRC. Genome wide association analysis revealed 5 regions associated with DMI, but none for the other traits analyzed. Residual feed intake values varied greatly between the contemporary group value and the overall value for the steers, showing the calculation's dependency on the reference population. However, MPRC as based upon a standardized population, did not fluctuate. More selection phenotypes and strategies are needed for large-scale improvements in global beef cattle production sustainability. The stability of the MPRC metric could be beneficial for future feed efficiency research across multiple and diverse contemporary groups, and diverse production environments.

Keywords: *Bos indicus* crosses, feed efficiency, residual feed intake, post-weaning growth

1. Introduction

Many life cycle assessments have shown potential of reduced greenhouse gas emissions through improved production efficiency from various beef cattle production management strategies (Foley et al., 2011; Stackhouse-Lawson, Rotz, Oltjen, & Mitlöehner, 2012; Nguyen et al., 2013; Wang, Teague, Park, & Bevers, 2015); however, efficiency differences among individual animals is also an important sustainability consideration. Feed intake in cattle can be adjusted for weight and weight gain (Koch et al., 1963), and residuals from such a model would be theoretically independent of weight, ADG, and other modeled effects. For an individual, this deviation could represent an unbiased phenotype of efficiency, and is known as residual feed intake (**RFI**). Residual feed intake has been reported as moderately heritable (Koch et al., 1963; Arthur et al., 2001; Crews, 2005), and several have proposed that adequate variation exists in RFI for selection (Archer & Bergh, 2000; Herd & Bishop, 2000; Basarab et al., 2003). Nkrumah et al. (2006) proposed lower RFI reduced enteric methane production through more efficient nutrient utilization. However, concern may exist from some cattle breeders if selection for reduced RFI in steers caused undesirable decreased feed intake breeding values for heifer half-siblings, especially for extensive winter grazing scenarios. It also could be expected that contemporary group effects might be profound with RFI rankings. Especially in the limited sample sizes inherent in experimental agriculture, it is not difficult to imagine that an individual classified as 'efficient' in one contemporary group, could rank unfavorably and be 'inefficient' in another group. It is important to know if the rank in the contemporary group is a good representation of the rank in the population. The statistical adjustment of contemporary group for RFI is trusted to remove such effects.

Difficulties in interpretation of RFI results are emphasized when *Bos indicus* breeds such as the American

Brahman are included in a study with *Bos taurus* cattle (e.g., Elzo et al., 2009). In most scenarios, *Bos indicus* cattle have lower intake relative to expectation, and thus often have lower (more desirable) RFI relative to other breeds. However, this lower level of intake also results in relatively lower growth rates, such that cost of production (feed conversion ratio) is less desirable in these types despite their lower RFI. Evaluation of relative feed utilization efficiency might be better accomplished with another metric that could minimize the difficulties associated with RFI. Improving efficiency (reducing feed demand) and increasing productivity (beef produced per unit of energy consumed in the entire production system) are important components of improving measures of sustainable production; these considerations are particularly important in poverty-stricken and resource-limited regions, many of which rely on tropically adapted cattle populations. Metrics that allow identification of more efficient and productive *Bos indicus* cattle and their crosses may also become more important in temperate areas that may experience an increase in temperatures.

A research population of F_2 Nellore-Angus was established in Central Texas in the mid-2000s to discover genomic regions associated with multiple beef production and efficiency traits. Phenotypes related to post-weaning growth and feed efficiency were recorded for steers from that population. The objectives of this project were to: (1) assess an efficiency metric based on a standardized nutrition model, especially in comparison to RFI and its components, (2) characterize family performance for feed efficiency traits, (3) assess correspondence of efficiency traits with carcass and animal temperament, and (4) assess association of SNP with the efficiency phenotypes.

2. Materials and Methods

2.1 Animals

All procedures involving animals were approved by the Texas A&M University Institutional Animal Care and Use Committee. The animals in the overall project population were described previously in detail (Riley et al., 2013; Hulsman Hanna et al., 2014). In brief, those with records in this research were steers sired by 4 F_1 Nellore-Angus bulls from 14 full-sibling F_2 Nellore-Angus families produced by embryo transfer and 4 half-sibling families (from half *Bos indicus-Bos taurus* dams). These steers (n = 349) were born in either fall (embryo transfer calves only) or spring from 2003 to 2007.

After weaning, calves grazed pastures for approximately 130 days. Warm season pastures included coastal bermudagrass (*Cynodon dactylon*), Eastern gamagrass (*Tripsacum dactyloides*), and Kleingrass (*Panicum coloratum*). Steers were supplemented with coastal bermudagrass hay or sorghum-sudangrass (*Sorghum bicolor*) hay in the winter. After this growing period, calves were placed in pens and fed a grain-based diet (Table 1), and individual feed intake was evaluated using a Calan gate system (American Calan, Inc., Northwood, NH) beginning at 11 to 13 months of age. These facilities were either soil surfaced pens with bunks under a shade structure (Year 1) or concrete surfaced pens with shade over 50% of the pen area. Feed was offered *ad libitum*, and refused feed was collected and weighed at 7-day intervals, with fresh feed offered if there was substantial buildup of refused feed. The diet was periodically checked for DM content, which averaged 90%. A few steers refused to eat from the Calan gate bunks, and their records were excluded from analyses. Steer weights were recorded every 28 days while on feed. Steers were fed to achieve a 12th-rib back-fat thickness of 0.9 cm based upon visual appraisal. The average time on feed was 140 days and ranged from 128 to 151.

Table 1. Ration formulation[1]

Ingredient	%
Ground milo	20.00
Ground corn	31.25
Cottonseed meal	9.00
Cottonseed hulls	25.00
Molasses	10.00
Premix[2]	3.00
Ammonium chloride	0.25
R-1500[3]	1.50

[1] Expressed as a percent on an as-fed basis

[2] Composition of premix: ground limestone, 60%; trace mineralized salt, 16.7% (NaCl, 98%; Zn, 0.35%; Mn, 0.28%; Fe, 0.175%, Cu, 0.035%, I, 0.007%, Co, 0.007%); mono-dicalcium phosphate, 13%; potassium chloride 6.7%; Vitamin premix, 3.3% (vitamin A, 2,200,000 IU/kg; vitamin D, 1,100,000 IU/kg, vitamin E, 2,200 IU/kg); Zinc oxide, 0.33%.

[3] R-1500 contains 1.65 g monensin sodium (Rumensin™) per kg.

2.2 Traits Evaluated

Observed dry matter intake (**DMI**) was regressed on ADG and mean metabolic BW ($BW^{0.75}$) to yield residual feed intake (**RFI**) values within contemporary groups for a 140-day feeding period. Using the NRC (1996) beef cattle model, daily feed intake of each steer was predicted based on observed weight gain and standardized input for animal type, age, sex, condition, and breed. This model-predicted intake was subtracted from observed DMI and the difference defined as **model predicted residual consumption** (**MPRC**). Similar to RFI, those animals that consumed less than predicted (and thus, were more efficient) had negative values of MPRC. Unlike RFI, this measure used the same standard model to predict intake across all contemporary groups, rather than estimating a unique regression model within each group.

2.3 Genotypes

The BovineSNP50v.1 assay (Illumina Inc., San Diego, CA) was obtained for all project animals and was previously described in detail by Tolleson et al. (2017). The quality-edited set of SNP markers used in genome-wide association analyses was 34,980.

2.4 Statistical Analyses

Preliminary analyses were used to construct final models for each trait. Investigated fixed effects included steer birth year, birth season, feedlot pen (a block effect), age of dam (nursing dam for embryo transfer calves), and age in days as a covariate. Random effects investigated included additive direct and maternal additive effects. Single-trait analyses were conducted with ASReml (Gilmour, Gogel, Cullis, & Thompson, 2009). Additional analyses were conducted to deliberately assess the effect of family as designed; those additional analyses did not include modeled random genetic effects other than the residual variance.

Genome-wide association analyses were conducted using JMP Genomics (SAS Inst., Inc., Cary, NC). These consisted of fixed regressions on genotypic values (number of copies of the minor allele at each locus) and inclusion of the genomic relationship matrix (Yu et al., 2006) to model the covariances among animals. The false discovery rate (FDR) was controlled per methodology of Benjamini & Hochberg (1995). Map coordinates of associated SNP were obtained from the bovine reference assembly UMD-3.1 (Zimin et al., 2009), and the nearest gene to each SNP was identified using the R package MAP2NCBI (Hulsman Hanna & Riley, 2014).

The relationship between RFI and MPRC was illustrated by calculating simple correlation and Spearman's rank correlation between the two traits and through comparison of individuals' classification for each respective trait. Analysis of RFI and its components was done by comparing contemporary group RFI and classification to an overall RFI and classification. Group and overall classification was also compared for MPRC.

3. Results

3.1 Descriptive Statistics and Family Differences

Summary statistics for the evaluated steer traits are presented in Table 2. For all traits, likelihood ratio tests indicated that the only random term supported was additive genetic effects. From preliminary analyses, contemporary groups were designated as combinations of year and season of birth. This effect ($P < 0.001$ all traits) included 9 levels, and ranged from 13 to 63 steers per group. Age of dam was not a significant source of variation for these traits. Linear regressions of trait on steer age in days ($P < 0.04$) indicated that older steers had heavier metabolic mid-weight, lower ADG, and higher (worse) MPRC (0.05 ± 0.008 kg, -0.07 ± 0.03 kg/d, and 0.007 ± 0.003, respectively), but steer age was not influential ($P > 0.29$) for DMI or RFI. Estimates of additive and residual variances were 3.64 and 3.16 kg^2, 0.003 and 0.007 kg^2, 0.15 and 0.35 kg^2, 0.14 and 0.67 $units^2$, and 0.07 and 0.67 $units^2$ for metabolic mid-weight, ADG, DMI, MPRC, and RFI, respectively.

Table 2. Descriptive statistics of evaluated traits (n = 349 steers)[1]

	Mean	SD	Minimum	Maximum
MMWT, kg	74.70	6.34	58	92
ADG, kg	1.13	0.29	0.4	1.98
DMI, kg	9.18	1.57	4.83	14.28
RFI	0.00	0.83	-3.10	2.72
MPRC	-0.17	1.37	-3.93	3.53

[1]MMWT = metabolic mid-weight
ADG = average daily gain
DMI = dry matter intake
RFI = residual feed intake
MPRC = model predicted residual consumption

Table 3. Family means for efficiency traits[1]

Sire	Family	MMWT	ADG	DMI	MPRC
297J	70	34.1[ab]	0.51[ab]	4.49[a]	0.49
	71	35.1[a]	0.51[ab]	4.20[ab]	-0.23
	95	35.3[a]	0.53[a]	4.39[a]	-0.09
432H	72	32.6[c]	0.45[ab]	3.93[ab]	0.09
	73	32.6[abc]	0.47[ab]	4.27[ab]	0.67
	82	34.0[ab]	0.47[ab]	4.24[ab]	0.43
	96	35.4[a]	0.53[a]	4.53[a]	0.24
437J	74	31.8[abc]	0.39[ab]	4.17[ab]	1.20
	75	32.7[bc]	0.52[ab]	4.39[ab]	0.33
	81	34.5[a]	0.53[a]	4.41[a]	0.13
	83	35.0[a]	0.48[ab]	4.42[ab]	0.63
	97	34.5[a]	0.51[ab]	4.29[ab]	0.08
551G	76	30.3[c]	0.44[ab]	3.76[ab]	-0.05
	77	34.6[a]	0.52[a]	4.35[ab]	0.04
	80	32.8[bc]	0.45[ab]	3.75[b]	-0.28
	84	31.6[c]	0.40[b]	3.56[b]	-0.09
	98	33.7[ab]	0.53[ab]	4.32[ab]	0.04
Avg SE		0.65	0.04	0.26	0.25
Min SE		0.40	0.03	0.21	0.15
Max SE		1.22	0.06	0.40	0.46

[1]MMWT = metabolic mid-weight

ADG = average daily gain

DMI = dry matter intake

MPRC = model predicted residual consumption

[a-c]Within a column: means that do not share a common superscript differ after Bonferroni correction for multiple comparisons ($P < 0.000325$).

Differences among families for metabolic mid-weight, ADG, and DMI are shown in Table 3. Although family was a significant effect ($P < 0.05$) in analysis of MPRC, there were no significant differences after correction for multiple comparisons. Family was not an influential component ($P = 0.14$) of RFI in these data. Families sired by 297J had higher values for metabolic mid-weight, ADG, and DMI. The other 3 bulls sired at least one family with a significantly lower metabolic mid-weight. Differences in ADG and DMI mostly involved families sired by 551G, especially family 84, which had lower ($P < 0.0003$) ADG than 4 other families, 1 each from each sire (including another from 551G). Families 80 and 84 (sired by 551G) had lower ($P < 0.0003$) DMI than 4 families that were sired by the other 3 bulls. Family differences, in the absence of modeled genetic effects, could be indicative of the genetic variation in such traits; previously family effects were noted as large for this experimental population, especially for udder traits (Tolleson et al., 2017) and carcass traits (Riley et al., 2019), but to a lesser degree for other traits.

3.2 Correlations Involving RFI and MPRC

The traits of this study were in many cases strongly related to each other. There were large positive associations of DMI with MPRC and RFI, and low positive associations between metabolic mid-weight with ADG and MPRC, as indicated by the unadjusted correlation coefficients presented in Table 4. As expected, residual correlations of ADG and DMI with RFI were not different from 0. However, correlations (residual and simple) for MPRC with ADG were negative.

Table 4. Simple (above diagonal) and residual (below diagonal) correlation coefficients of efficiency traits[1, 2, 3]

	MMWT	ADG	DMI	MPRC	RFI
MMWT		**0.22**	**0.54**	**0.11**	0
ADG	**0.54**		**0.52**	**-0.48**	0
DMI	**0.66**	**0.76**		**0.47**	**0.53**
MPRC	**0.11**	-0.08	**0.56**		**0.61**
RFI	0	0	**0.57**	**0.96**	

[1]MMWT = metabolic mid-weight

ADG = average daily gain

DMI = dry matter intake

RFI = residual feed intake

MPRC = model predicted residual consumption

[2]Coefficients in bold-faced font differ from 0 ($P < 0.05$).

[3]Residuals were from models that included steer age as a fixed linear covariate, contemporary group as a fixed effect, and animal as a random effect.

Residual feed intake and MPRC have the same base calculation, (observed DMI minus predicted DMI), but they differ regarding how the predicted DMI value is estimated. For RFI, the predicted value is based on a regression of data collected from a given cohort, while for MPRC the predicted value is based on observed performance using a standard model. Considering the similarity in how the two measurements are calculated it is not surprising that analysis revealed a strong positive correlation coefficient of MPRC and RFI. The two measures also had a significant Spearman's rank correlation coefficient (0.62) indicating that steers should rank similarly for MPRC and RFI. This relationship is seen in the Nellore-Angus steers in this study. When comparing RFI vs. MPRC classification within contemporary groups relative to animals that were 1.5 SD away from the mean as low and high (as opposed to the commonly used 0.5 SD), 319 of the steers' rank categories were the same, however 30 differed. This indicates that the average contemporary group value could have major effects on its own efficiency group ranking.

The important difference between MPRC and RFI is the ability to more readily compare across contemporary groups/cohorts. Residual feed intake is dependent upon those contemporary groupings. To illustrate RFI's dependency on the contemporary group an animal is in, an overall RFI (pooled RFI) was calculated and compared to the steer's contemporary group RFI (group RFI). Comparison revealed no animals pooled RFI value matched its group RFI value. Shifting from a negative group RFI value to a positive pooled value did not occur, however 37 animals that had a positive group RFI value had a negative pooled RFI value. Thirty-three steers had over a 2-fold change in RFI from group to pooled. Group classification was compared to pooled classification as well, revealing 53 steers were reclassified. When the same comparison was done with group MPRC classification and pooled MPRC classification, 70 steers had different classifications between the two, the MPRC value itself however, did not change.

Table 5. Simple (first row within an efficiency trait) and residual (second row) correlation coefficients with temperament traits of yearling steers[1, 2, 3]

Trait	Aggressiveness	Nervousness	Flightiness	Gregariousness	Overall
MMWT	0.03	**-0.22**	**-0.19**	**-0.21**	**-0.20**
	0.01	**-0.16**	**-0.11**	**-0.15**	**-0.16**
ADG	-0.09	**-0.14**	**-0.14**	-0.02	**-0.17**
	-0.02	-0.09	-0.10	**-0.13**	**-0.16**
DMI	-0.01	**-0.16**	**-0.15**	-0.08	**-0.19**
	0.03	-0.10	-0.08	-0.12	-0.09
MPRC	0.08	0.02	0.02	-0.02	0.01
	0.07	-0.01	0.01	0	0.08
RFI	0.02	0.05	0.04	0.05	0.1
	0.04	0.03	0.03	0.03	0.09

[1]Coefficients in bold-faced font differed from 0 ($P < 0.05$).

[2]Residuals for efficiency traits were from models that included steer age as a fixed linear covariate, contemporary group as a fixed effect, and animal as a random effect.

[3]Residuals for temperament traits from models of Riley et al. (2016). Those traits scored on a 1-to-9 scale

included aggressiveness—the willingness of the animal to hit an evaluator; nervousness—visual indications to include trembling, vocalization, and other activities (urination, etc.); flightiness—indicated by running, jumping, or climbing behavior; gregariousness—willingness and comfort associated with being isolated from other animals; and overall temperament— distinct evaluator assessment based upon all information observed.

Table 5 provides correlations between efficiency traits and temperament scores. Similar to other reports, we saw slightly negative correlations between steer temperament and metabolic mid-weight, ADG, and DMI. Both simple and residual correlations involving temperament with MPRC and with RFI were not significant.

3.3 Genome-wide Associations

Table 6 provides genes with suggestive associations with DMI. Although a strict control of FDR = 0.05 produced no detected associations of genomic regions with ADG, RFI, or MPRC, a more relaxed control of FDR (0.17) resulted in associations with DMI that included a single SNP on BTA 9 and 4 SNP in a region of BTA 11 (67.1 to 75.7 Mb).

Table 6. Genomic markers with suggestive association ($P = 0.17$) with daily dry matter intake (DMI) and closest genes

BTA	Mb	Name	Candidate gene	Boundary
9	1.29	ARS BFGL NGS 115046	SPARC related modular calcium binding 2 (*SMOC2*)	within
11	67.11	Hapmap30504 BTA 126653	rho GTPase activating protein 25 (*ARHGAP25*)	within
11	69.84	BTA 28849 no rs	Yippee-like 5 (*YPEL5*)	69.70
11	72.64	Hapmap29423 BTA 126740	microtubule associated protein RP/EB family member 3 (*MAPRE3*)	within
11	75.69	ARS BFGL NGS 12720	kelch like family member 29 (*KLHL29*)	75.62

[1]BTA = *Bos taurus* autosome; Mb = megabase location UMD-3.1 bovine assembly.
[2]Boundary indicates the Mb location of the nearest gene boundary to the marker. Entry in this column of "within" means that the marker was located within the published gene boundaries.

The SNP on BTA 9 with suggestive association with DMI was located within the gene SPARC related modular calcium binding 2 (*SMOC2*; Vannahme, Gösling, Paulsson, Maurer, & Hartmann, 2003), which is a regulator of cell-matrix interactions (Maier, Paulsson, & Hartmann, 2008). The protein product of this gene has been demonstrated to be involved in differentiation in a variety of tissues and structures in mammals, including lung (Wilk, Herbert, Shoemaker, Gottlieb, & Karamohamed, 2007), blood vessels (Rocnik, Liu, Sato, Walsh, & Vaziri, 2006), teeth (AlFawaz et al., 2013; Kim et al., 2016), endometrium (Araujo et al., 2017), cardiac tissue (in which it was differentially methylated; Laugier et al., 2017), kidney, (Gerarduzzi et al., 2017), eye (Al-Dabbagh et al., 2017), cartilage (Wilson et al., 2016), cranial structure in dogs (Marchant et al., 2017), and brain tissue (Roy et al., 2013).

The region located from 67 to 76 Mb on BTA 11 had 4 SNP with suggestive association with DMI. Two of those were within genes, rho GTPase activating protein 25 (*ARHGAP25*; Cs épányi-Kömi et al., 2012) and microtubule associated protein RP/EB family member 3 *(MAPRE3)*. The former (*ARHGAP25*) has a regulatory role in neutrophil phagocytosis (Cs épányi-Kömi, Sirokmány, Geiszt, & Ligeti, 2012) as well as in mobilization of hematopoietic stem and progenitor cells (Wang et al., 2016). The protein produced by *MAPRE3* is an end binding protein and consistent with its name is involved in the assembly of basic molecular structures (Su & Qi, 2001; Komarova et al., 2009). This gene (*MAPRE3*) was differentially expressed in lymphatic ileal tissue of scrapie infested lambs relative to controls (Austb ø et al., 2008), and levels of its protein were elevated in mice olfactory bulbs with respect to a particular odor (Li et al., 2010). Another SNP with suggestive association in this region was near Yippee-like 5 (*YPEL5*) that has documented roles with cell division processes (Hosono et al., 2010). The last of these 4 SNP was near kelch like family member 29 (*KLHL29*, Jin et al., 2017).

4. Discussion

4.1 Relationships Involving Efficiency Traits

The residual correlation coefficients in Table 4 confirm the strong positive relationship of DMI with RFI and with MPRC. These are not genetic correlations, but it is reasonable to think that those would also be large and positive, similar to those reported in Nellore cattle by Matos Ceacero et al. (2016) and in *Bos taurus* crossbred cattle by Rolfe et al. (2011). This relationship suggests that selection for reduced RFI would also reduce breeding values for DMI, which may be detrimental for growing steers on *ad libitum* feed, but would almost certainly be

undesirable for their half-sisters as they become producing cows (C. A. Ferrell, personal communication). Decreased DMI could lead to energy and protein requirement deficiencies, and in turn decreased cow and offspring productivity (Funston, Summers, & Roberts, 2012). If satiety in grazing cattle is related to maintenance requirement, then reduced DMI might be indicative of reduced maintenance requirements (manifested as improved efficiency if intake were fixed). It seems appropriate to avoid any management or selection program that could potentially reduce the feed intake (and/or appetite) of beef cows grazing marginal and/or climate-variable resources. If DMI reduction is voluntary and is accompanied by lowered nutritional requirements without reduced production, this could improve production efficiency. Cusack et al. (2021) stated in their sustainability review of global beef production that no one type or breed of cattle showed clear advantages globally; however, the adaptation aspect and production levels of low RFI cattle when utilized in more challenging and variable environments need to be investigated before the most useful strategies can be determined, especially to aid in poverty reduction.

Reclassification of animals when comparing the smaller contemporary groups to the overall group is not surprising; the key difference between MPRC and RFI is that the MPRC value remains stable across comparison because it is based upon a single reference population. Residual feed intake however is a less stable value because it is dependent on the population in consideration (contemporary vs overall in this study). The stability of the MPRC measurement may be advantageous for doing comparisons across different groups, studies, and populations, and, potentially across highly variable production environments.

Based on these results, there appear to be very limited opportunities to use these efficiency traits as predictor traits for beef traits later in the value chain, or vice versa in similar *Bos indicus* crossbred. Although there were some significant correlation coefficients (estimated using either unadjusted trait values or residuals from appropriate models) of these traits with temperament scores (Riley et al., 2016), most were not large (Table 5). This suggests that temperament was not strongly associated with such traits in this population, and this was consistent with reported low genetic correlations of similar traits with flight speed as a temperament trait (Rolfe et al., 2011). However, many researchers have reported strong associations of good temperament with good performance in growing cattle (e.g., Nkrumah et al., 2007; Cafè et al., 2011). There were strong positive correlations between DMI, ADG, and RFI with traits such as carcass weight and ribeye area, but otherwise these efficiency traits were weakly correlated ($|r| < 0.2$) with quality traits, sensory panel palatability assessments, and panel assessed flavor and aromatics measured on steaks or carcass sides with or without electrical stimulation (data not shown).

4.2 Genome-wide Associations

There have been many genome-wide association studies of efficiency traits in many cattle populations. Several have reported associations of regions of BTA 11 with DMI or RFI (Márquez, Enns, Grosz, Alexander, & MacNeil, 2009; Sherman, Nkrumah, Li, Bartusiak, Murdoch, & Moore, 2009; Bolormaa et al., 2011; Lu et al., 2013; Seabury et al., 2017). Rolf et al. (2012) reported loci associated with average feed intake in Angus cattle on BTA 11 very near the suggestive loci from the present study (78.3 Mb) as well as an association of a locus on BTA 9 (105.9 Mb) with RFI. Abo-Ismail et al. (2018) developed a custom panel of SNP for use with feed efficiency trait improvement. They considered 3 SNP loci on BTA 9 (Rolf et al., 2012; Abo-Ismail et al., 2014) and 10 loci on BTA 11 (Rolf et al., 2012; Yao et al., 2013; Abo-Ismail et al., 2014). Three loci of the 10 loci from BTA 11 were included in that panel (4.7, 3.6, and 28.8 Mb). Genome-wide association studies of these traits in Nellore cattle have reported no DMI or RFI associations on BTA 9 or 11 (de Oliveira et al., 2014; Santana et al., 2014) and associations on both chromosomes with DMI (Olivieri et al., 2016). There has been noted minimal across-population overlap of detected SNP with association for these traits (Saatchi et al., 2014). New methods have been developed to look at multiple feed efficiency GWAS studies to identify similarities. Pathway based meta-analysis, using 201 significant SNP markers from 10 different studies, identified a significant pathway related to residual feed intake: valine leucine and isoleucine degradation. That significant pathway included 3 markers, from 3 different genes, that could be important to residual feed intake (Duarte et al., 2019). Other approaches, such as system biology approaches, may be beneficial to identifying genes that influence feed efficiency (Alexandre et al., 2019).

5. Conclusion

Evaluation of feed efficiency traits such as DMI, RFI, and MPRC in these Nellore-Angus steers revealed family differences for ADG and DMI, but not for MPRC or RFI. Although RFI and MPRC had similar correlations with DMI, MPRC had substantial negative correlation with ADG and slightly positive correlation with weight, whereas RFI will have 0 correlation with these traits by its calculation. The significant correlations between feed

efficiency and temperament evaluations seen here were weak, suggesting that temperament differences were not associated with performance traits evaluated in this population. Correlation between RFI and MPRC was 0.61. Use of MPRC as a standardized metric should be investigated relative to RFI because it may facilitate improved across-cohort comparisons and may be useful across diverse production settings as it is computed from a stable reference population, and does not fluctuate between cohort groups. Genome-wide analysis revealed no associations with ADG, RFI, or MPRC, but 5 SNPs were associated with DMI adding to the growing list of SNPs associated with feed efficiency traits. Because MPRC was correlated with both DMI (positively) and ADG (negatively) it is likely more closely associated with economic indicators of production efficiency, but these same benefits may present selection issues similar to the use of RFI. Further use of MPRC may facilitate improved comparisons across studies, and its evaluation across diverse production environments is encouraged.

Acknowledgements

Declaration of Interest

The authors declare that there are no conflicts of interest.

Ethics statement

All procedures were in compliance with the Guide for the Care and Use of Agricultural Animals in Research and Teaching (FASS, 2010) and approved by the Texas A&M University Animal Care and Use Committee

Software and data repository resources

The authors declare that the data of this research are not deposited in any official repository.

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