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Characterization of water intake and water efficiency in beef cattle[1,2]

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Abstract

In the future, water may not be as readily available due to increases in competition from a growing human population, wildlife, and other agricultural sectors, making selection for water efficiency of beef cattle increasingly important. Substantial selection emphasis has recently been placed on feed efficiency in an effort to reduce production costs, but no emphasis has been placed on making cattle more water efficient due to lack of data. Thus, the objective of this study was to calculate water efficiency metrics for cattle and evaluate their relationship to growth, feed intake (**FI**), and feed efficiency. Individual daily FI and water intake (**WI**) records were collected on 578 crossbred steers over a 70-d test period. Animals with low water intake ate less feed, had lower gains, and were more water efficient (as defined by water to gain ratio, **W/G**, and residual water intake, **RWI**). However, the amount of water consumed by animals had minimal phenotypic relationship with feed efficiency (residual feed intake [**RFI**], R^2 = 0.1050 and feed to gain ratio (**F/G**) ratio R^2 = 0.0726). Cattle that had low DMI consumed less water, had lower gains, had lower RFI, and had higher F/G. The level of feed consumed had minimal relationship with water efficiency. WI, W/G, RWI, and ADG had moderate heritability estimates of 0.39, 0.39, 0.37, and 0.37, respectively. High heritability estimates were observed for DMI and RFI (0.67 and 0.65, respectively). Feed to gain had a low heritability estimate of 0.16. WI had a strong positive genetic correlation with W/G (0.99) and RWI (0.88), thus selecting for decreased WI should also make cattle more water efficient. The genetic correlation between WI and ADG was 0.05; thus, selecting for low WI cattle should have little effect on growth. There is a low to moderate genetic correlation between WI and DMI (0.34). RWI has a positive genetic correlation with W/G ratio (0.89) and F/G ratio (0.42) and is negatively genetically correlated with RFI (–0.57). Water to gain and F/G had a strong positive genetic correlation (0.68). RFI has a positive genetic correlation with W/G ratio (0.37) and F/G (0.88). Minimal antagonisms seem to be present between WI and ADG, although it should be noted that standard errors were large and often not significantly different from zero due to the small sample size. However, care should be taken to ensure that unintended changes do not occur in DMI or other production traits and incorporation of WI into a selection index would likely prove to be the most effective method for selection.

Key words: beef cattle, water efficiency, water intake

Introduction

Freshwater is approximately 2.5% of all water resources (Thornton et al., 2009), but water has often been viewed as unlimited. More recently, water crises have been viewed as one of the top five likely global risks reported by the World Economic Forum (2017). It is predicted that in 2025, 64% of the world population will live in a water-deprived basin, compared with 38% in 2009 (Rosegrant et al., 2002). Effects of climate change on water availability could force the livestock sector to establish a new priority in production of animal products that require less water (Nardone et al., 2010).

Few studies have been conducted in beef cattle to examine how efficient cattle are at utilizing water. Currently, there are no heritability estimates in the scientific literature for water intake (**WI**) in beef cattle or other livestock animals. However, heritability estimates for WI have been reported in mice. Bachmanov et al. (2002) and Ramirez and Fuller (1976) reported heritability estimates for WI of 0.69 and 0.44, respectively. Phenotypic correlations between WI and body weight (BW) were moderate and positive (0.49; Bachmanov et al., 2002). WI also has a high, positive phenotypic correlation (0.65) with feed intake (**FI**) in mice (Bachmanov et al., 2002). However, beef cattle are ruminants, and it is unknown how heritability estimates of WI in ruminants will compare to those in monogastric species like mice.

Due to rising concerns about water availability in the future, it is important to understand the relationship between WI and other economically important traits like DMI and average daily gain (ADG). Thus, we must collect WI phenotypes, generate measures of water efficiency, and evaluate their relationships to other economically important production traits to determine if genetic antagonisms exist between these traits. In addition, understanding the genetic relationship between WI and DMI, ADG, and efficiency traits is important because other traits could potentially be used as indicator traits in selection for decreased WI. The objective of this study was to calculate water efficiency and evaluate the relationships between WI, water efficiency, DMI, feed efficiency, and ADG.

Materials and Methods

Study Design

An Insentec system (Hokofarm Group, The Netherlands) at the Willard Sparks feedlot located at Oklahoma State University was utilized to collect daily WI WI and FI on 578 crossbreed steers over a 3-year period from May 2014 to March 2017. Steers were fed in five feeding groups that consisted of three summer groups (group 1, n = 117, from May 2014 to August 2014; group 3, n = 118, from May 2015 to July 2015, and group 4, n = 105, from June 2016 to August 2016) and 2 winter groups (group 2, n = 115, from November 2014 to January 2015 and group 5, n = 123, from January 2017 to March 2017). This Insentec system consisted of one water bunk and six feed bunks per pen, and bunks were placed beneath a shade structure. Additional information on the facility structure and layout can be found in Ahlberg et al. (2018a, 2018b). Within each group, steers were blocked by weight (low and high) and randomly assigned to one of four pens, each containing approximately 30 steers per pen. FI and WI records were filtered to maintain data quality using the procedures outlined in Allwardt et al. (2017). Briefly, start and end weights were filtered for appropriateness (based on overall bunk volume and system settings) and each bunk visit was screened for length of visit, where very short visits (less than 5 s) and extremely long visits (greater than 3,600 s) were removed. Group 1–3 steers were managed using a slick bunk feed protocol and groups 4 and 5 had access to ad libitum feed during the 70-d test period. All animals had access to ad libitum water throughout the testing period.

Intakes were collected over a 70-d period following a 21-d acclimation to be in accordance with test length guidelines for DMI and weight gain published by the Beef Improvement Federation (BIF, 2016). During the testing period, BWs were collected every 14 d. All groups were fed the same growing diet throughout the 70-d test period that consisted of 15% cracked corn, 51.36% wet corn sweet bran, 28.44% prairie hay, and 5.20% supplement. Mean gross energy of composited samples was ~4,524.6 cal/g on a dry matter basis. Dry matter for the groups ranged from 70.04% to 74.02%. During the acclimation period cattle were implanted with Compudose (Elanco Animal Health, Greenfield, IN), an implant containing estradiol 17ß (E_2 ß), per facility protocol.

Two blood samples were collected on weigh days during the feeding period. Blood was drawn from the jugular vein of each animal and collected in 10 mL BD vacutainer tubes containing 1.5 mL of anticoagulant citrate dextrose (**ACD**). Whole blood was centrifuged to obtain white blood cells and DNA was extracted for each group using a phenol:chloroform:isoamyl alcohol extraction and ethanol precipitation. DNA samples were sent to GeneSeek (Lincoln, NE) for genotyping on the GeneSeek Genomic Profiler High-Density genotyping array (GGP HD150K). The GGP HD150K provides data on approximately 150,000 single nucleotide polymorphism (SNP) markers. Genotypes were filtered for quality control including for minor allele frequency less than 0.05, and SNP and animal call rate less than 0.90. All animal procedures were approved by the Institutional Animal Care and Use Committee at Oklahoma State University (protocol AG13-18) in accordance with Federation of Animal Science Societies (FASS, 2010) guidelines.

Phenotypic Data

ADG for each individual was calculated over the 70-d period by regressing the BW collected every 14 d over time to account for differences in rumen fill. Mid-test weight was obtained by taking the ADG for each individual from the regression analysis, multiplying by 35 d, and adding it to the intercept for each individual. Mid-metabolic weights (MMWT) were obtained by taking the mid-test weight to the 0.75 power.

Within each group, animals were assigned to either high, medium, or low WI and DMI groups using K-means clustering with $k = 3$. This methodology was chosen to more objectively establish intake groups and avoid arbitrarily ranking animals and assigning the top, middle, and bottom third of the data into each category. Cattle were objectively assigned to WI categories to determine if the level of water cattle consume has an effect on DMI, ADG, and feed and water efficiency.

Efficiency measures

Appropriate methods for establishment or calculation of water efficiency have not been established in the scientific literature. Therefore, we have developed and utilized constructs similar to those developed for feed efficiency, realizing that, much like feed efficiency, these constructed phenotypes may not be the best measures of "efficiency" per se. We have utilized these traits to explore water efficiency and the relationships between the component traits, realizing there is not an industry standard for water-related traits. As we understand these traits and their relation to animal biology better in the future, these functions and calculations may change to reflect that knowledge.

Water efficiency measures, including water to gain ratio (**W/G**) and residual water intake (**RWI**) were calculated for each group. W/G was calculated as follows:

$$W/G = \frac{WI}{ADG}$$

where WI is the average daily water intake and ADG is the average daily gain over the 70-d test.

For each group, RWI was calculated as follows:

$$RWI = WI - eWI$$

where WI is defined as before and eWI is the expected WI calculated as follows:

$$eWI = \hat{b}_0 + \hat{b}_1 DMI + \hat{b}_2 MMWT$$

where $\hat{b}_0$ is the intercept, $\hat{b}_1$ is the regression coefficient for average daily DMI and $\hat{b}_2$ is the regression coefficient for MMWT. Regression coefficients (b_i) were estimated within each group and the coefficients are summarized in Supplementary Table S1. Dry matter intake (DMI) and MMWT were chosen because of their relatively strong relationship with WI and lower RWI would indicate animals that drink less water at the same relative size and level of DMI.

Feed efficiency measures, including feed to gain ratio (**F/G**) and residual feed intake (**RFI**) were calculated for each group. F/G (Koch et al., 1963) was calculated as follows:

$$F/G = \frac{DMI}{ADG}$$

where DMI is the average daily dry matter intake and ADG for the 70-d test.

For each group, RFI was calculated as follows (Koch et al., 1963):

$$RFI = DMI - eDMI$$

where DMI is the average daily dry matter intake and eDMI is the expected dry matter intake calculated as follows:

$$eDMI = \hat{b}_0 + \hat{b}_1 ADG + \hat{b}_2 MMWT + e$$

where $\hat{b}_0$ is the intercept, $\hat{b}_1$ is the regression coefficient for ADG, and $\hat{b}_2$ is the regression coefficient for (MMWT). Regression coefficients (b_i) were estimated for each group and the coefficients are summarized in Supplementary Table S1. Summary statistics for all traits are presented in Table 1.

Breed Composition

Although true breed composition of steers was unknown, cattle were visually evaluated before entering the trial period in an effort to exclude individuals that had *Bos indicus* ancestry because animals with *B. indicus* influence are known to consume less water, especially when temperatures are elevated (Winchester and Morris, 1956; Brew et al., 2011). Breed composition was later estimated utilizing each individual animal's genotypes within a multiple regression framework developed by Chiang et al. (2010). Genotypes were coded as the number of copies of allele B (using the Illumina A/B genotype calls) divided by 2 (Kuehn et al., 2011) to scale the number of copies of allele B to be between 0 and 1, which places them on the same scale as the breed allele frequency estimates. The following model was used to predict breed composition:

$$y = Xb + e$$

where y is a vector containing the scaled number of copies of allele B for an animal, X is a 36,403 by 16 matrix of frequencies for allele B (36,403 allele frequencies for 16 breeds) and b is a vector of regression coefficients that represents the percentage of each breed for each individual animal in y, and e is a vector of random residuals. This methodology requires robust estimates of allele frequencies in a large number of breeds, so breed specific allele frequencies used were those calculated in Kuehn et al. (2011). Estimates for the percent of each of the 16 breeds were then summed for each individual animal. If the value was less than 1, the difference from 1 was assigned as other to account for the fact that there are more than 16 breeds represented in the United States that were not represented in the available allele frequencies. Zeros were assigned for any small negative regression coefficients. Estimates that summed to greater than 1 were then scaled as follows:

$$\frac{1}{\sum \text{nonzero breed regression coefficients}} \times \text{each breed coefficient}$$

Figure 1 shows the mean percent of each breed observed in each group and across all groups. Because percentages for most breeds were low, estimates were grouped into biological types (British, Continental, *B. indicus*, and dairy) and the mean percentages of each biological type for each group are presented in Figure 2. Despite visual selection against animals that have *B. indicus* ancestry, a low level of *B. indicus* ancestry was present in three of the five groups.

Statistical Analysis

Summary statistics of phenotypic data for each group and level within group were calculated using SAS 9.4 System for Windows (SAS Institute, Inc., Cary, NC). Differences between low, medium,

Table 1. Summary statistics for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain ratio (W/G), and feed to gain ratio (F/G) for each group

Variable	Group	N	Mean	Minimum	Maximum	SD
WI, kg/d	1	117	40.50	21.20	65.80	8.01
	2	115	28.23	15.60	44.70	5.63
	3	118	36.37	24.10	61.40	6.75
	4	105	49.46	32.00	101.40	13.07
	5	123	34.92	25.50	50.90	4.84
DMI, kg/d	1	117	10.12	6.36	13.69	1.39
	2	115	10.23	6.04	14.07	1.62
	3	118	10.24	7.16	14.76	1.52
	4	105	10.53	7.76	12.74	0.92
	5	123	11.67	8.96	16.17	1.23
ADG, kg/d	1	117	1.39	0.62	2.24	0.29
	2	115	1.74	0.41	2.45	0.34
	3	118	1.46	0.53	2.32	0.31
	4	105	1.27	0.42	1.81	0.29
	5	123	1.84	1.10	2.55	0.29
RWI, kg/d	1	117	0.00	−13.49	18.85	6.42
	2	115	0.00	−7.38	17.56	3.91
	3	118	0.00	−10.39	23.75	5.38
	4	105	0.00	−20.87	46.16	10.93
	5	123	0.00	−5.49	9.08	2.64
RFI, kg/d	1	117	0.00	−2.61	2.68	0.95
	2	115	0.00	−2.27	2.19	0.88
	3	118	0.00	−3.18	2.16	1.11
	4	105	0.00	−1.63	1.61	0.64
	5	123	0.00	−3.51	2.40	0.76
WG, kg/d	1	117	29.83	18.33	55.99	6.30
	2	115	16.86	9.82	51.50	5.10
	3	118	25.78	15.54	54.84	6.51
	4	105	41.16	20.80	105.16	14.37
	5	123	19.31	13.32	28.29	2.99
FG, kg/d	1	117	7.48	4.50	14.00	1.36
	2	115	6.08	3.43	14.81	1.43
	3	118	7.25	4.83	18.04	1.71
	4	105	8.79	5.59	23.14	2.48
	5	123	6.48	4.58	10.70	1.01

and high WI and DMI levels were analyzed for WI, DMI, W/G, F/G, RWI, and RFI within each group and with data combined across groups. The following model was used for analyses of WI, DMI, ADG, W/G, F/G, RWI, and RFI measures for each individual group:

$$\text{Trait}_{ij} = \text{water intake level}_i + \text{SWT}_j + \text{B}_j + \text{C}_j + \text{I}_j + \text{D}_j + \text{e}_{ij}$$

where Trait_{ij} is the trait of interest (WI, DMI, ADG, RWI, RFI, W/G, and F/G) for the ith WI level and the *j*th individual, intake_level_i is the *i*th intake level (low, medium, or high for WI), SWT is the starting weight for the *j*th individual fitted as a covariate, B is the percent of British breed composition for the *j*th individual fitted as a covariate, C is the percent of continental breed composition for the *j*th individual fitted as a covariate, I is the percent *B. indicus* for the *j*th individual fitted as a covariate, D is the percent dairy breed composition for the *j*th individual fitted as a covariate, and *e* is the random residual.

For analyses of data combined across all groups, fixed effects of group and feed management were added to the model. Phenotypic correlations between all traits were estimated using SAS 9.4 System for Windows (SAS Institute, Inc.).

Genetic analyses were performed using single-step genomic BLUP (ssGBLUP; Aguilar et al., 2010; Christensen and Lund, 2010) methodology and genetic (co)variance parameters were estimated using an average information restricted maximum likelihood (AIREML) algorithm incorporated into the BLUPF90 software package (Misztal et al., 2014). However, in this study, we did not have any animals with pedigree, only genomic relationships established by genotypes, so this study was a simple GBLUP analysis and relationships were defined solely as a function of G^{-1}. The genomic relationship matrix was calculated as $G = ZZ'/k$ based on the method defined by VanRaden (2008), where *Z* is generated by subtracting *P* (allele frequencies, p_i, expressed as difference from 0.5) from *M* (matrix of marker alleles for each individual), and *k* is $2 \times \text{sum}(p_i \times (1 - p_i))$. Traits were fitted using the following bivariate linear animal models:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1b_1 \\ X_2b_2 \end{bmatrix} + \begin{bmatrix} Z_1u_1 \\ Z_2u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_i is a vector of phenotypes for trait 1 or 2 (WI, DMI, ADG, RWI, W/G, RFI, and F/G), b_i is a vector of fixed effects for trait 1 and 2 (group and feed management) and covariates (start weight, percent British, percent continental, percent *B. indicus*, and percent dairy), X_i is an incidence matrix for each element in b_i for trait 1 and 2, u_i is a vector of additive direct genetic

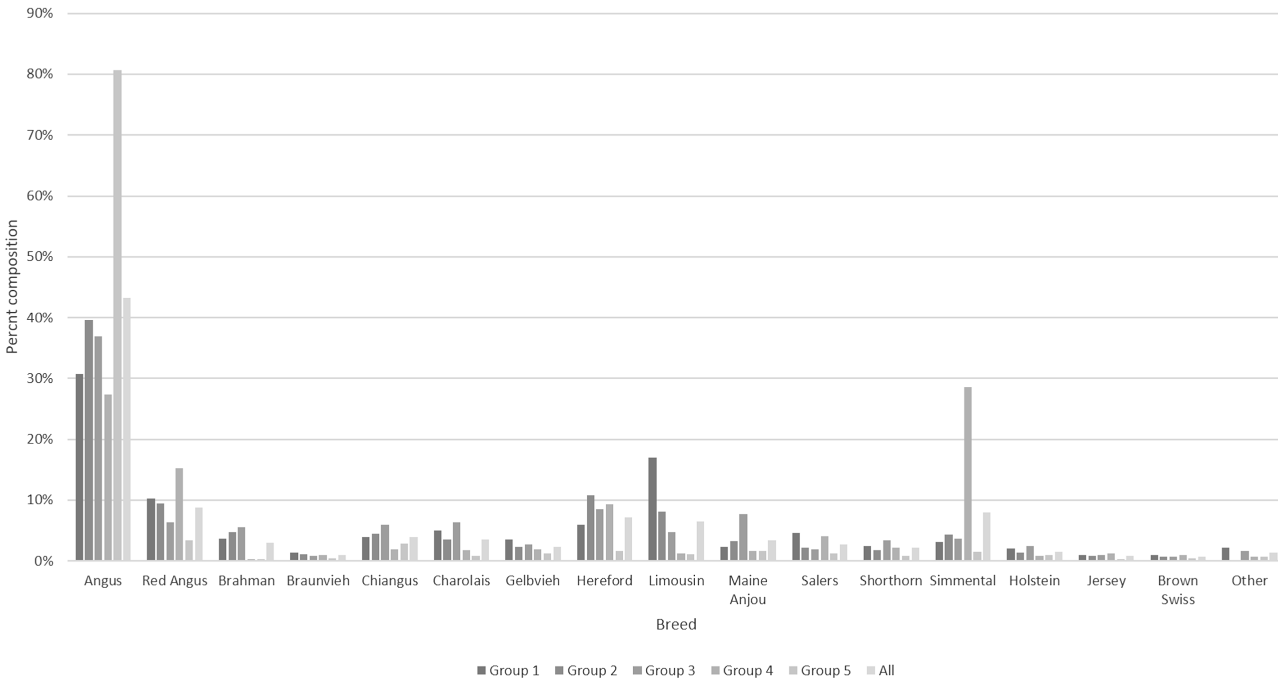

Figure 1. Mean breed composition estimated for each group and across all groups for 16 different breeds.

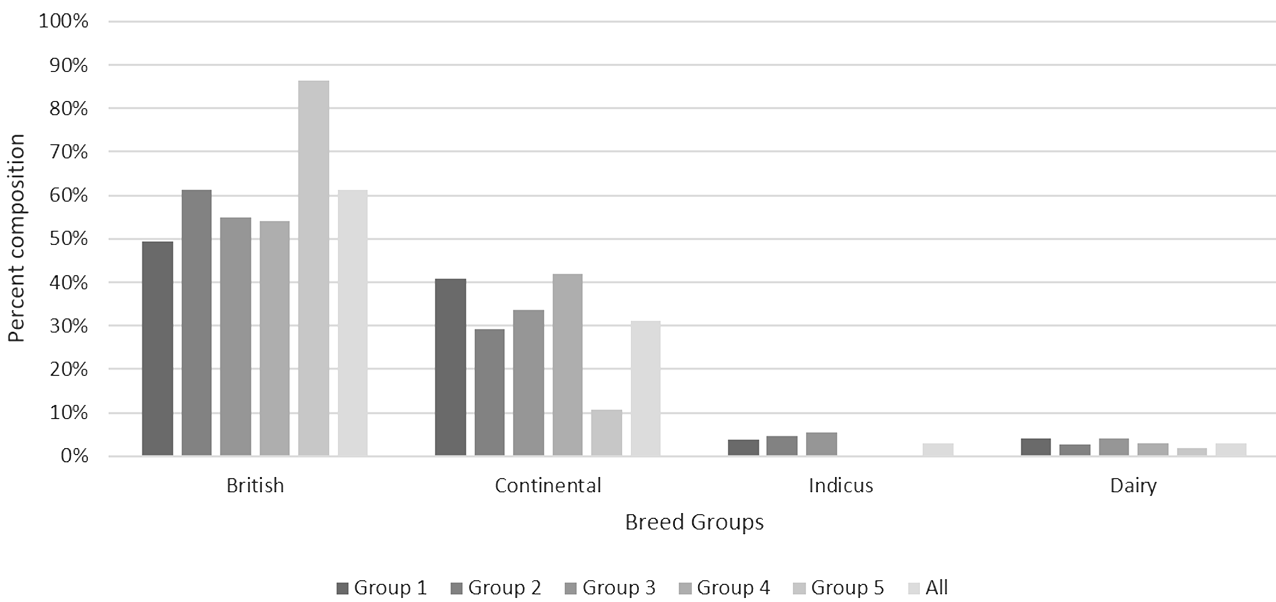

Figure 2. Mean breed composition when individual breeds were combined into their biological grouping within each group and across groups.

effects for traits 1 and 2, Z_i is an incidence matrix for u_i for traits 1 and 2, and e_i is a vector of random residuals for traits 1 and 2. Heritabilities and standard errors were averaged for each trait across all the bivariate runs for the trait of interest. The residual (co)variance structure used was:

$$\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} I\sigma^2_{e1} & I\sigma_{e1,e2} \\ I\sigma_{e2,e1} & I\sigma^2_{e2} \end{bmatrix}$$

where the matrix I represents an identity matrix with dimension equal to the number of records for each trait. The genetic (co) variance structure was:

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} G\sigma^2_{u1} & G\sigma_{u1,u2} \\ G\sigma_{u2,u1} & G\sigma^2_{u2} \end{bmatrix}$$

where the G matrix is the genomic relationship matrix. As an alternative to standard errors (where they are not provided by the software utilized), standard deviations were calculated for functions of (co)variances, thus calculations of phenotypic variance were derived by repeated sampling of parameter estimates from the asymptotic multivariate normal distribution, based on methodology presented by Meyer and Houle (2013). Standard errors were calculated for heritability, genetic correlations, and residual correlations using methodology outlined in Okamoto et al. (2019) and expanded upon in Tsuruta and Klei (2019).

Results and Discussion

WI Levels

Summary statistics for each group and trait are presented in Table 1. Differences in WI for low, medium, and high WI groups are presented in Table 2. There is a significant difference in WI between low, medium, and high levels within all groups and across groups. For all groups except for group 1, there is a smaller increase from low to medium WI levels (10.36, 5.44, 7.23, 10.50, and 5.45 kg for groups 1, 2, 3, 4, and 5, respectively) than from medium to high levels (9.40, 7.27, 9.18, 18.55, and 6.96 kg for groups 1, 2, 3, 4, and 5, respectively). Pairwise comparisons between low, medium, and high WI are significantly different when all groups are combined. Breed did not have a significant effect on WI in any group (Supplementary Table S2). There was no significant reduction in WI when comparing low, medium, and high groups for *B. indicus* breeds, likely because of the very small amount of this germplasm present in our population.

There is a significant difference in DMI between low, medium, and high WI levels within all groups and when all data is combined, except between group 3 medium and high ($P = 0.2096$). Higher WI was associated with higher DMI. Larger increases in DMI are observed as cattle go from medium to high WI (1.09, 2.07, 0.43, 0.45, and 1.26 kg for groups 1, 2, 3, 4, and 5, respectively) as compared with moving from low to medium intake (0.84, 1.13, 1.09, 0.45, and 0.96 kg for groups 1, 2, 3, 4, and 5, respectively). Cattle consumed progressively more feed from the low to the high WI group ($P < 0.0001$). For most mammals, water is consumed during or shortly before or after feeding events, and in rats, food-related drinking accounts for approximately 70% of their daily WI (Kraly, 1983), which could explain these results.

Animals that drank more water had significantly higher ADG within all groups and across all groups except for group 4 (Table 2; $P > 0.05$). Low WI cattle have decreased gains compared to high WI cattle, and this could affect days on feed and increase feed costs. As illustrated in Table 2, cattle with higher WI have higher DMI; thus, we would expect cattle with higher WI to have higher gains as a result of increased DMI. Langemeier et al. (1992) reported that improvements in ADG will reduce cost of gain, thus increasing profitability. Mark et al. (2000) found that ADG is more important for lighter weight placements because they are on feed for a longer period of time.

Residual WI is significantly different ($P < 0.0003$) between WI levels within each group and across all groups. Low WI animals have more favorable RWI than animals that have medium or high WI. Low WI animals consume less water and utilize water more efficiently relative to their DMI and body size. Water quantity and quality is currently not limiting in beef production

Table 2. LSMEANS for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain ratio (W/G), and feed to gain ratio (F/G) for each group at low, medium, and high water intake levels[a]

Trait	Group 1	Group 2	Group 3	Group 4	Group 5	All
WI, kg/d						
Low	34.86^{b}	23.39^{b}	29.44^{b}	39.81^{b}	31.23^{b}	32.79^{b}
Medium	45.22^{c}	28.83^{c}	36.67^{c}	50.31^{c}	36.68^{c}	39.77^{c}
High	54.62^{d}	36.10^{d}	45.85^{d}	68.86^{d}	43.64^{d}	50.91^{d}
DMI, kg/d						
Low	9.64^{b}	9.31^{b}	9.42^{b}	10.20^{b}	11.00^{b}	10.01^{b}
Medium	10.48^{c}	10.44^{c}	10.51^{c}	10.65^{c}	11.96^{c}	10.90^{c}
High	11.57^{d}	11.42^{d}	10.94^{c}	11.10^{d}	13.22^{d}	11.68^{d}
ADG, kg/d						
Low	1.29^{b}	1.51^{b}	1.31^{b}	1.23^{b}	1.70^{b}	1.41^{b}
Medium	1.47^{c}	1.80^{c}	1.49^{c}	1.27^{b}	1.92^{c}	1.61^{c}
High	1.68^{d}	2.00^{d}	1.64^{d}	1.35^{b}	2.14^{d}	1.77^{d}
RWI, kg/d						
Low	−3.99^{b}	−2.55^{b}	−4.91^{b}	−6.72^{b}	−1.50^{b}	−3.98^{b}
Medium	3.46^{c}	0.06^{c}	−0.29^{c}	−0.03^{c}	0.82^{c}	0.85^{c}
High	9.14^{d}	5.00^{d}	7.61^{d}	15.08^{d}	3.74^{d}	8.69^{d}
RFI, kg/d						
Low	−0.19^{b}	−0.22^{b}	−0.38^{b}	−0.25^{b}	−0.40^{b}	−0.28^{b}
Medium	0.17^{bc}	−0.00^{b}	0.18^{c}	0.07^{c}	0.13^{c}	0.13^{c}
High	0.61^{c}	0.49^{c}	0.16^{bc}	0.44^{d}	1.02^{d}	0.52^{d}
W/G, kg/d						
Low	28.10^{b}	17.12^{b}	24.12^{b}	36.16^{b}	18.76^{b}	25.57^{b}
Medium	31.75^{bcd}	16.37^{b}	25.47^{bc}	40.94^{b}	19.30^{b}	26.74^{b}
High	32.88^{d}	17.86^{b}	28.55^{c}	52.76^{c}	20.53^{b}	31.23^{c}
F/G, kg/d						
Low	7.74^{b}	6.59^{b}	7.60^{b}	9.09^{b}	6.61^{b}	7.57^{b}
Medium	7.28^{bc}	5.91^{c}	7.24^{b}	8.71^{b}	6.29^{b}	7.06^{cd}
High	6.94^{c}	5.60^{cd}	6.73^{b}	8.28^{b}	6.13^{b}	6.72^{d}

[a]Individuals divided into low, medium, and high water intake levels based on k-mean clustering of individual average daily water intake, Group 1: low $n = 66$, medium $n = 38$, high $n = 13$, Group 2: low $n = 44$, medium $n = 48$ high $n = 23$, Group 3: low $n = 36$ medium $n = 56$, high $n = 26$, Group 4: low $n = 49$, medium $n = 34$, high $n = 22$, Group 5: low $n = 56$, medium $n = 54$, high $n = 12$.
[bcd]Differences in superscripts within each column and variable indicate significant differences between groups ($P < 0.05$).

for many areas of the country. However, for producers that run cow-calf operations in dry climates or in areas where water quality is poor, water quantity and quality can be limiting. For many producers, dugouts and ponds only have a limited supply of water and drought can greatly reduce or eliminate these supplies entirely, rendering that pasture unfit for grazing. During drought, even wells can run dry and producers may not be able to provide water to their animals. One option is to haul water, which requires a good estimate of the herd's water requirements (Winchester and Morris, 1956; NRC, 2000; Arias and Mader, 2011; Ahlberg et al. 2018b). In these situations, it would be beneficial to have cattle that have both low water consumption and are efficient at utilizing available water resources.

RFI is more similar between WI levels than DMI. However, low WI animals are the most feed efficient (have lower RFI values) except for group 1 and 2, which were numerically more efficient, but not statistically different. Cattle with low and medium WI levels in group 2 had similar RFI values which were lower than high WI cattle (P = 0.2619). Only high and low WI classes had different RFI in group 1 (P = 0.0039). Animals that are feed efficient and have low WI and/or high water efficiency are desirable. The relationship between feed efficiency or water consumption and production traits must also be assessed using genetic correlations to identify whether there are any genetic antagonisms present.

No differences in W/G were detected among low, medium, and high WI classes for cattle fed during the winter time (groups 2 and 5). For the summer groups, significant differences in W/G between low and high WI levels were noted (P = 0.0096, P = 0.0141, and P < 0.0001 for groups 1, 3, and 4, respectively), where cattle that have low WI utilize less water per pound of gain. There may be differences in the summer that are not present in the winter due to the fact that cattle have higher WI during the summer months as a strategy to reduce heat load and regulate body temperature (Beede and Collier, 1986), as water has a role in maintaining thermal equilibrium (Arias and Mader, 2011). For this reason, cattle may require more water in the summer to achieve a certain level of weight gain than they do when not exposed to environmental stressors. This is similar to the results for RWI, where low WI cattle were more efficient than high WI cattle. For group 4 and across all groups, animals with high WI levels required more water to gain one pound than animals with medium WI (P = 0.0012 and P < 0.0001, respectively).

Feed to gain for cattle from groups 3, 4, and 5 was not related to the amount of water that the animals consumed (P > 0.05). Group 1 and 2 cattle did exhibit differences in F/G with low WI animals having poorer F/G ratios (P = 0.0464 and P = 0.0126, respectively) than high WI cattle. Group 2 cattle with low WI also have poorer F/G ratio (P = 0.0266) than medium WI cattle. In this study, we noted conflicting relationships between feed efficiency metrics and WI levels depending on whether efficiency was defined as F/G or RFI. Elzo et al. (2010) reported that RFI decreased (cattle became more feed efficient) as the level of Brahman increased, but gain to feed ratio decreased (less efficient). This relationship is consistent with our results, even though the overall level of *B. indicus* influence was low.

Phenotypic Correlations

Pearson and Spearman correlations between all traits are presented in Table 3. The phenotypic correlation between FI and WI in mice (0.65, Bachmanov et al., 2002) is higher than in the current study. Cattle and mice have different physiology primarily due to the fact that cattle are ruminants and mice are monogastrics. There is also a drastic difference in body size, which leads to differences in maintenance requirements (Demment and Van Soest, 1985). The large positive correlation between FI and WI in mice may be due to their mutual dependency on body size, but it might involve another unknown mechanism that is linked to FI and WI (Bachmanov et al., 2002). Regardless of the cause, the direction of the relationship is the same in beef cattle, although smaller in magnitude. Figure 3A shows the linear relationship between WI and DMI (R^2 = 0.141). For every 1 kg increase in DMI, WI increases by an average of 2.705 kg. However, much of the variation in WI appears to be independent of DMI. Regression coefficients within each group are summarized in Supplementary Table S3.

Spearman correlations between WI and RFI and F/G ratio were higher than Pearson correlations, indicating that there is less reranking among animals for feed efficiency traits when there are changes in WI. Animals with low WI tend to also have low RFI (R^2 = 0.102; Figure 3B), but substantial variation also exists. Figure 3C illustrates the weak linear relationship between WI and F/G ratio (R^2 = 0.073), and within-group coefficients are summarized in Supplementary Table S3. The most efficient animals (low F/G ratio) have a wide range in WI. While the linear relationship between WI and DMI is low to moderate, relationships between WI and RFI and F/G are much weaker.

WI has strong, positive Pearson correlations with water efficiency measures. The Spearman correlation between WI and RWI is lower than the corresponding Pearson correlation; however, the Spearman correlation between WI and W/G is slightly higher than the Pearson. Pearson and Spearman correlations between WI and W/G suggest that there is slightly more reranking of animals for RWI than W/G ratio at similar WI levels. Cattle with higher WI are less water efficient, as illustrated by the moderate linear relationships depicted in Figure 3D and E. No previous phenotypic correlations between WI and water efficiency measures have been reported, but these

Table 3. Pearson (below the diagonal) and Spearman (above the diagonal) phenotypic correlations for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI) water to gain ratio (W/G), and feed to gain ratio (F/G)[a]

	WI	DMI	ADG	RWI	RFI	W/G	F/G
WI		0.389***	−0.109**	0.451***	0.266***	0.711***	0.383***
DMI	0.366***		0.501***	0.027	0.583***	−0.084*	0.058
ADG	−0.094*	0.530***		0.127**	0.002	−0.734***	−0.892***
RWI	0.602***	−0.000	0.051		−0.017	0.221***	−0.102*
RFI	0.258***	0.595***	0.001	−0.032		0.168***	0.383***
W/G	0.698***	−0.088*	−0.694***	0.383***	0.149**		0.811***
F/G	0.276***	−0.012	−0.779***	−0.04	0.295***	0.808***	

[a]Units for all traits are in kg/d.
Correlations are significantly different from zero at *P < 0.05, **P < 0.01, ***P < 0.0001.

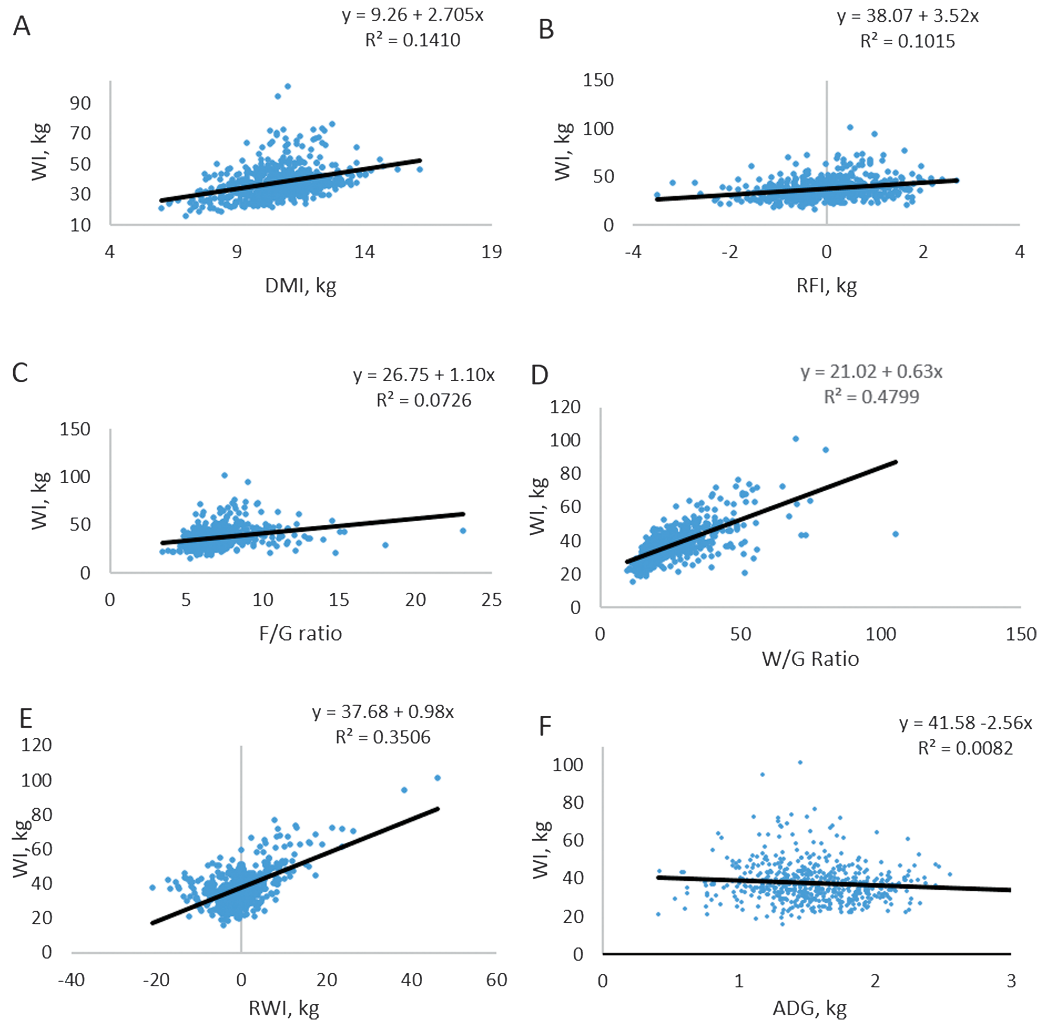

Figure 3. Plots depicting relationships between water intake and various feed and water efficiency traits. (A) Dry matter intake (DMI) and water intake (WI), (B) residual feed intake (RFI) and water intake (WI), (C) feed to gain (F/G) and water intake (WI), (D) water to gain (W/G) and water intake (WI), (E) residual water intake (RWI) and water intake (WI), (F) average daily gain (ADG), and water intake (WI). Within-group regression coefficients are summarized in Supplementary Table S3.

traits exhibit the same strong phenotypic correlations that are found between DMI and feed efficiency measures (Archer et al., 2002; Bouquet et al., 2010).

As depicted in Figure 3F, the amount of water consumed by animals has little relationship with ADG. The relationship between WI and ADG is substantially different from the relationship between DMI and ADG, which have a strong, positive correlation (Arthur et al., 2001; Nkrumah et al., 2007).

DMI has strong, positive Pearson and Spearman correlations with ADG and RFI. Cattle that have higher DMI will have greater ADG, but will also be less efficient at utilizing feed, as illustrated by higher RFI values. Similar phenotypic correlations between DMI and ADG have previously been reported by Arthur et al. (2001), Basarab et al. (2003), and Nkrumah et al. (2007). Nkrumah et al. (2007) and Arthur et al. (2001) reported a higher phenotypic correlation of 0.770 and 0.720, respectively, between DMI and RFI.

Phenotypic correlations between DMI and F/G ratio were not different from zero. Positive, moderate phenotypic correlations between DMI and F/G ratio have been reported by Koots et al. (1994), Liu et al. (2000), Arthur et al. (2001), and Nkrumah et al. (2007). Cattle that consume less will also generally require less feed per pound of gain. DMI had a weak, negative Pearson and Spearman correlation with W/G ratio but was uncorrelated to RWI (Pearson $P = 0.999$ and Spearman $P = 0.520$). No correlations between DMI and water efficiency measures currently exist within the scientific literature.

No previous estimates of phenotypic correlations between ADG and W/G have been reported in the literature. However, Berry and Crowley (2013) reviewed 39 scientific articles and reported that phenotypic correlations between ADG and F/G in the scientific literature ranged from −0.910 to 0.650, with an average of −0.520. Strong correlations exist between ratio traits and their component traits (Berry and Crowley, 2013). ADG is not phenotypically correlated with RFI (Pearson, $P = 0.988$ and Spearman, $P = 0.958$), as would be expected. Pearson correlations between ADG and RWI were not different from zero ($P = 0.223$), but did exhibit a weak, positive Spearman correlation. RFI and RWI are phenotypically independent of their regressors when calculated using least squares regression (Berry and Crowley, 2013). However, RFI and RWI are not necessarily genetically independent of their regressors (Kennedy et al., 1993; Berry and Crowley, 2013). ADG would not be expected to be phenotypically correlated with RFI but could be correlated with RWI, as it was not included in its calculation.

Water efficiency measures have weak linear relationships with each other and to feed efficiency traits, with the exception of F/G and W/G, as illustrated in Figure 4. A strong linear relationship between W/G and F/G could be attributed to gain driving both of these values. Cattle that are considered water efficient as defined by low RWI are generally also considered water efficient as classified by W/G (Figure 4A). Feed efficiency traits (F/G and RFI) have low, positive Pearson and Spearman correlations, and their relationship is illustrated in Figure 4B. Phenotypic correlations between RFI and F/G were reviewed by Berry and Crowley (2013) and ranged from –0.620 to 0.760 (average of 0.390), which is very similar to the values in this study. Comparable to the water efficiency measures, cattle that have low RFI also have a low F/G ratio. RWI and RFI are uncorrelated (Pearson P = 0.438 and Spearman P = 0.684), as illustrated in Figure 4C. Similar to the relationship between RWI and RFI, RWI and F/G are uncorrelated as defined by the Pearson correlation (P =0.341), while the Spearman correlation is low, but significantly different from zero.

Genetic Parameters

Variance components and heritability estimates for each trait are presented in Table 4. WI, RWI, and W/G had moderate heritability estimates of 0.39, 0.37, and 0.39, respectively. There are currently no other estimates of heritability for WI, RWI, or W/G in livestock. However, heritabilities for WI have been reported in mice. Bachmanov et al. (2002) utilized 28 different strands of mice, collecting individual WI over a 4-d period, to generate a heritability estimate of 0.69. Ramirez and Fuller (1976) utilized heterogeneous mice, fully inbred mice, and partially inbred mice that had individual WIs collected over 38 d. Heritability was estimated to be 0.44 (Ramirez and Fuller, 1976). Both heritability estimates in mice are higher than our heritability estimate for WI in beef cattle. Beef cattle are much larger in size and are ruminants, whereas mice are monogastric. Differences in how these species metabolize water could explain why higher heritabilities were observed in mice. Ahlberg et al. (2018a) established that WI in cattle requires 35–42 d of data for accurate measurement of WI phenotypes. Although ruminants are undoubtedly quite different from monogastrics, Bachmanov et al. (2002) only collected data over 4-d, and the short test duration could have affected the heritability estimate. Differences could also be attributed to using inbred lines of mice or due to effects of seasonal variation in weather, since mice are housed in a controlled environment and cattle tend to be exposed to different weather conditions. The fact that WI is a moderately heritable trait means that the amount of water consumed by beef cattle can be changed though selection. Selecting for water efficiency while accounting for important output traits would be ideal. However, using ratio traits (such as RWI or W/G) for genetic selection presents challenges when trying to predict the changes in component traits for future generations (Arthur et al., 2001). Using the component traits of RFI or RWI (namely DMI, WI, and ADG) to form a selection index to select for improved feed or water efficiency would be a more useful and appropriate option.

ADG has a moderate heritability, which indicates that ADG would respond well to selection if cattle are selected for increased gain. According to a review by Berry and Crowley (2013), ADG heritability estimates ranges from 0.06 to 0.65. Brown et al. (1988), Archer et al. (1997), Herd and Bishop (2000), Schenkel et al. (2004), and Akanno et al. (2018), reported similar heritability estimates for ADG (0.36, 0.41, 0.38, 0.35, and 0.37 respectively).

DMI and RFI had high heritability estimates of 0.67 and 0.65, respectively. Berry and Crowley (2013) reported heritability estimates for DMI that range from 0.06 to 0.70 from 38 different studies. The heritability estimates for RFI in this study were on

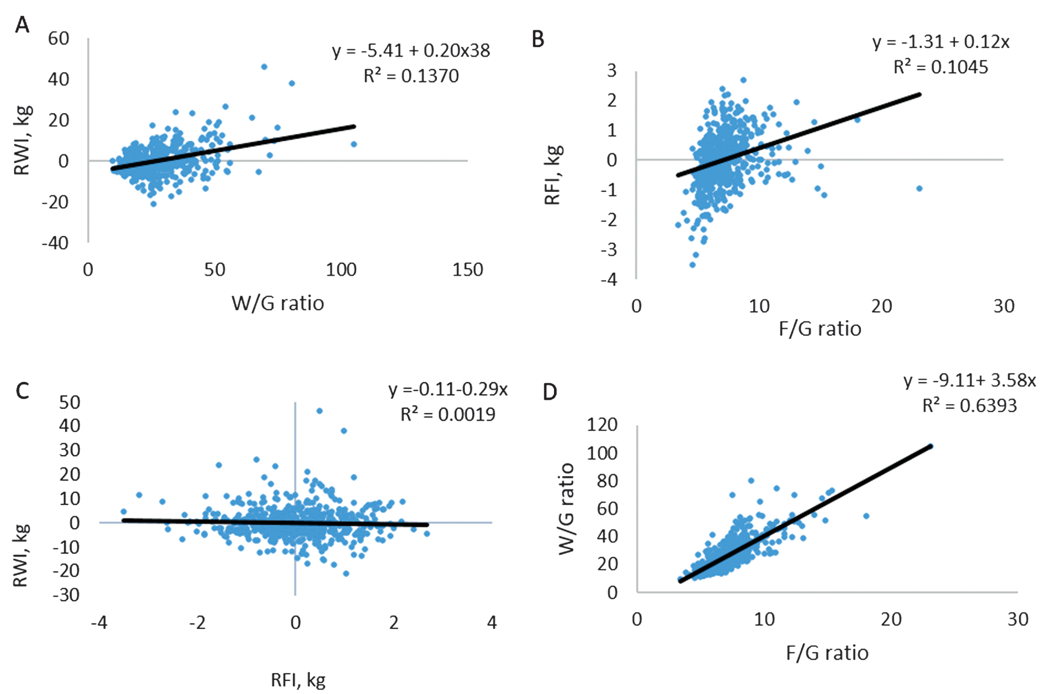

Figure 4. Plots depicting relationships between various feed and water efficiency traits. (A) Individual water to gain (W/G) plot against individual residual water intake (RWI), (B) individual residual feed intake (RFI) plot against individual feed to gain ratio (F/G), (C) individual residual feed intake (RFI) plot against individual residual water intake (RWI), (D) individual feed to gain ratio (F/G) plot against individual water to gain ratio (W/G).

Table 4. Variance component and heritability estimates for average daily water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain ratio (W/G), and feed to gain ratio (F/G)

Trait	Genetic variance[a]	Residual variance[a]	Phenotype variance[b]	Heritability[a]
WI, kg/d	23.32 (8.76)	36.75 (8.07)	60.07 (3.75)	0.39 (0.07)
DMI, kg/d	0.94 (0.26)	0.46 (0.20)	1.40 (0.09)	0.67 (0.04)
ADG, kg/d	0.04 (0.01)	0.06 (0.01)	0.10 (0.01)	0.37 (0.05)
RWI, kg/d	14.83 (6.21)	25.67 (5.73)	40.50 (2.53)	0.37 (0.22)
RFI, kg/d	0.49 (0.14)	0.26 (0.12)	0.75 (0.05)	0.65 (0.06)
W/G, kg/d	22.95 (8.26)	36.38 (7.60)	59.33 (3.68)	0.39 (0.05)
F/G, kg/d	0.42 (0.34)	2.11 (0.33)	2.53 (0.15)	0.16 (0.15)

[a]Standard errors, reported in parenthesis, were generated by AIREML.
[b]Standard deviations are reported in parenthesis because phenotypic variance was calculated from genetic and residual variance.

Table 5. Genetic (above the diagonal) and residual (below the diagonal) correlations[a] between water intake, (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain ratio (W/G), and feed to gain ratio (F/G)

	WI	DMI	ADG	RWI	RFI	W/G	F/G
WI		0.34 (0.27)	0.05 (0.05)	0.88 (0.33)	0.33 (0.11)	0.99 (0.57)	0.90 (0.85)
DMI	0.66 (0.03)		0.68 (0.01)	−0.10 (0.10)	0.68 (0.02)	−0.13 (0.31)	0.08 (0.04)
ADG	0.55 (0.01)	0.60 (0.04)		−0.17 (0.16)	−0.031 (0.01)	−0.57 (0.31)	−0.63 (0.44)
RWI	0.79 (0.16)	0.18 (0.01)	0.21(0.06)		−0.57 (0.17)	0.89 (0.35)	0.42 (0.71)
RFI	0.34 (0.02)	0.77 (0.08)	0.01 (0.001)	−0.03 (0.01)		0.37 (0.25)	0.88 (0.29)
W/G	0.07 (0.06)	−0.17 (0.04)	−0.57 (0.12)	0.40 (0.13)	0.05 (0.02)		0.68 (0.43)
F/G	−0.47 (0.02)	−0.44 (0.02)	−0.85 (0.02)	−0.18 (0.07)	0.001 (0.0001)	0.80 (0.25)	

[a]Standard errors are reported in parentheses.

the upper end of this range. Koch et al. (1963) reported similar heritability estimates for DMI using Angus, Hereford, and Shorthorn cattle. Archer et al. (1997) utilized a population of Angus, Hereford, Polled Hereford, and Shorthorn animals and reported a similar heritability to the current study (0.62). Breed composition in Archer et al. (1997) was similar to the current study, as British breeds (Angus, Hereford, Shorthorn, and Red Angus) comprised over 60% of the breed germplasm in the current study (and usually not less than 50% of each group; Figure 2). Feed to gain had lower heritability than the other FI and efficiency traits (0.16). However, it is within the range of heritability estimates (0.07–0.46) reported by Berry and Crowley (2013). Similar heritability estimates were reported by Brown et al. (1988), Korver et al. (1991), Gengler et al. (1995), Herd and Bishop (2000), Hoque et al. (2006), Okanishi et al. (2008), and Elzo et al. (2010). Heritability estimates tended to be on the higher end of literature estimates, likely due to small sample size (and the large standard errors associated) and could also have been higher due to the fact that crossbred cattle were included in the analysis. Because breeds were grouped into biological types rather than specific breeds due to population size within each breed, heritability estimates could be slightly biased due to incomplete partitioning of some individual breed effects.

Genetic correlations for each trait are reported in Table 5. WI exhibited positive genetic correlations with most of the traits in this study, although of different magnitudes. ADG has a very low genetic correlation with WI, but the estimate had a very large standard deviation. DMI and RFI had a moderate genetic correlation with WI, while RWI, W/G, and F/G had a high genetic correlation with WI. The F/G estimates are outside of the accepted parameter space. This may be due to the fact that F/G is a ratio trait, so it has statistical properties that make these values hard to utilize within this framework and due to the low number of observations in the current study. Although standard errors were high in some instances, the current study indicates that there will be minimal effect on ADG if selection emphasis is placed on WI. However, genetic correlations are difficult to estimate with high precision using only approximately 500 animals and meta analyses including data from multiple studies should be considered to more precisely estimate the genetic parameters and correlations. Our results suggest that cow/calf producers could select for lower WI in the cowherd without hindering ADG in calves that would be sold. Whether producers are selling calves at weaning or retaining ownership though the finishing phase, calves with high growth potential are desirable in terminal marketplaces. Cattle sold at weaning or after backgrounding are priced on weight, thus heavier calves often generate more revenue.

Selecting animals for lower WI could also result in animals that are more feed efficient due to positive genetic correlations with RFI and F/G. Although WI and F/G have a high genetic correlation, this estimate also has a large standard deviation which would be considered not different from zero. The high genetic correlation between WI and W/G and F/G could be attributed to the fact that water makes up a large percentage of body mass.

Due to the strong, positive correlation with WI and water efficiency measures, selection to improve water efficiency would also decrease WI. During times when water is limited, having cattle that are efficient at utilizing water would be beneficial. If a priority is placed on WI along with relevant output traits related to productivity, producers could select cattle that maintain productivity when water resources are limited.

DMI exhibited weak, negative genetic correlations with RWI and W/G and a weak, positive correlation with F/G, though standard errors indicate these estimates are not different from zero. It is likely that these estimates will be more accurate when a larger number of phenotypes and data are available for analysis. The current study reports a similar genetic correlation between DMI and F/G as noted by Mao et al. (2013; −0.020).

Selecting for decreased F/G ratio may reduce the amount of feed required for growth but could also lead to increases in mature BW due to its relationship with ADG, which raises the cost of maintenance in breeding programs (Arthur et al., 2001). Like F/G, selecting to decrease W/G could decrease the amount of water needed for growth but could have the same effect on mature BW and maintenance cost. Much like selection for DMI and ADG, it is likely that selection for WI and ADG using indices would be a more effective method to avoid these increases in cost, as opposed to direct selection on W/G. DMI has a strong, positive correlation with ADG and RFI. Previous studies (Arthur et al., 2001; Mujibi et al., 2010) reported similar genetic correlations between DMI and RFI (0.690 and 0.680, respectively). A review by Berry and Crowley (2013) reported genetic correlations ranging from −0.340 to 0.850 with the average correlation being 0.720, which is similar to DMI and RFI in the current study. Incorporating measures of growth and metabolic body size help capture the variation among animals in energy utilization for growth and maintenance (Nkrumah et al., 2007). Strong, positive genetic correlations of 0.450, 0.540, and 0.530 between ADG and DMI were also reported by Liu et al. (2000), Arthur et al. (2001), and Mujibi et al. (2010), respectively.

ADG exhibited negative genetic correlations with feed and water efficiency traits. The strong genetic correlations between ADG and F/G have raised concerns about selection on F/G ratio to improve efficiency in the overall production system, as it can lead to direct increases in mature BW and maintenance costs in the cowherd (Barlow, 1984; Archer et al., 1997). The weak negative genetic correlation between ADG and RFI was similar to correlations reported by Herd and Bishop (2000) and Arthur et al. (2001). However, Jensen et al. (1992) reported a genetic correlation between ADG and RFI of 0.320. Due to the nature of RFI calculation, the phenotypic correlation between ADG and RFI is expected to be zero, even if they are not necessarily genetically independent (Kennedy et al., 1993; Berry and Crowley, 2013). Due to the extremely low correlation between RFI and ADG in this study, selecting to improve RFI should not inhibit production of efficient steers in the feedlot or mature cows that efficiently utilize feed for maintenance (Arthur et al., 2001). A selection index including gain and DMI should be utilized to overcome the unfavorable correlation between the two traits.

Selecting to improve water efficiency by selecting cattle that have lower RWI is predicted to result in a slight decrease in growth. One potential solution would be to include ADG in the calculation of RWI, which should make them phenotypically independent, and possibly reduce the genetic correlation between the traits. While this is an option, it would be most effective to select for these traits using a selection index. Both W/G and RFI and F/G and RWI have moderate, positive genetic correlations. Cattle selected for improved F/G ratio would result in cattle that are more water efficient (reduced RWI). The same relationship holds true when cattle are selected for decreased RFI. Water efficiency measures were highly genetically correlated and feed efficiency measures were also highly genetically correlated. Nkrumah et al. (2007) observed a similar relationship between RFI and F/G ratio, noting that cattle with high RFI also have high F/G ratio. RFI can contain a large amount of statistical error as well as true differences in feed efficiency (Berry and Crowley, 2013). This same problem can be true for F/G, which can lead to the large variation reported in the genetic relationship between RFI and F/G (Berry and Crowley, 2013). This same property is expected to be true for RWI phenotypes as well.

As RWI increases, W/G also increases. Cattle that are selected for improved water efficiency using RWI will also have improved (lower) W/G ratios. Interestingly, RWI and RFI exhibit a strong, negative genetic correlation. Feed costs comprise a high percentage of input cost in cattle production (Herd et al., 2004), resulting in the desire to select animals that are more feed efficient. Due to the antagonistic relationship between RFI and RWI, selecting for both RWI and RFI would be somewhat challenging. Even though water does not currently tend to be an expensive resource in and of itself, it is not always abundant and can have economic impact through reduction in stocking density or culling of cattle, thus importance may be more related to thresholds of availability or quality of water. It is likely that the best possible avenue for selection on these traits is to include all of the component traits (WI, DMI, and ADG) in a selection index with other economically relevant traits so that selection pressure is applied to all traits simultaneously based on their importance to the breeding objective and aggregate merit becomes the selection criterion.

Breed Effects

Breed effects for all traits are presented in Table 6. Cattle with greater continental and *B. indicus* influence tend to have lower WI than cattle with British or dairy influence. Winchester and Morris (1956) also showed that *B. indicus* cattle consume less water than taurine cattle, especially as temperatures increase. Cattle that have some percentage of *B. indicus* influence also have lower W/G ratio and RWI than *Bos taurus* cattle. However, estimates for Continental cattle indicate slightly higher RWI than all other biological types, but lower W/G ratios than British and dairy influenced cattle. Cattle of continental breeds are known for higher post weaning gain than British breeds (Williams et al., 2010). The additional growth that is associated with continental breeds could contribute to the advantage continental influence cattle have in W/G ratio over British influence cattle.

Cattle with a larger percentage of continental influence consumed the least feed, and cattle with significant dairy percentage consumed the most. Retallick et al. (2017) showed that British breeds (Angus, Hereford, Shorthorn, and Red Angus) tended to have larger DMI breed effects than continental breeds. Cattle with a larger percentage of British influence tended to result in higher F/G ratio as compared to the rest of the biological types. Unlike F/G ratio, where dairy has the most favorable relative effect, cattle with significant dairy percentage have the most unfavorable RFI. Cattle with a high percentage of continental ancestry have the smallest effect, suggesting they would have the lowest RFI values. Cattle with higher percentages of Continental and *B. indicus* influence had lower estimates for ADG than cattle with higher percentages of dairy or British ancestry. Williams et al. (2010) found that both dairy breeds and continental breeds of cattle have the highest breed

Table 6. Direct breed effects as deviations from British breeds for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain ratio (W/G), and feed to gain ratio (F/G)

Trait	British	Continental	*Bos indicus*	Dairy
WI, kg/d	0.00	−3.31	−11.38	6.26
DMI, kg/d	0.00	−1.10	1.67	4.41
ADG, kg/d	0.00	−0.11	−0.01	0.28
RWI, kg/d	0.00	0.08	−15.93	−5.41
RFI, kg/d	0.00	−0.95	1.06	1.18
W/G, kg/d	0.00	−0.30	−13.33	0.73
F/G, kg/d	0.00	−0.30	−0.77	−1.70

effects for ADG with British and *B. indicus* having the lowest. It should be noted that these estimates are based on very small breed fractions in the case of the *B. indicus* and dairy populations because the study was focused on taurine beef cattle, and it would be beneficial to replicate these analyses in cattle of different biological types.

Conclusion

While other measures may ultimately define efficient water utilization in the future, in this study, we presented the first constructs relating to water efficiency and the first genetic relationships between likely component traits that will assist with development of water efficiency metrics in the future. WI, RWI, W/G, and ADG are moderately heritable, DMI and RFI are highly heritable, and F/G is lowly heritable in this study. WI has no genetic correlation with ADG, moderate genetic correlations with DMI and RFI, and strong genetic correlations with RWI, W/G, and F/G. Water efficiency measures are highly genetically correlated and feed efficiency measures are also highly genetically correlated to each other. Favorable genetic correlations exist between RWI and WI, W/G and F/G, but antagonisms exist between RWI and RFI, as well as between RWI and DMI. Genetic antagonisms, particularly between feed and water efficiency, can be solved by including WI in a selection index with DMI, ADG, and other economically important traits. Further work is warranted to elucidate the genetic relationships between WI and other economically important traits for both terminal and maternal systems.

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

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