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Water requirements of beef production can be reduced by genetic selection

G.M. Pereira^a, A.A. Egito^{a,b}, R.C. Gomes^{a,b}, M.N. Ribas^c, R.A.A. Torres Junior^b, J.A. Fernandes Junior^d, G.R.O. Menezes^{b,*}

^a Animal Science Graduate Program, Federal University of Mato Grosso do Sul, Sen. Filinto Müller Av., 2443, 79070-900, Campo Grande, MS, Brazil

^b Embrapa Beef Cattle, Rádio Maia Av., 830, 70106-550 Campo Grande, MS, Brazil

^c Intergado Ltd, Rio Paranaguá St., 1463, 32280-300 Contagem, MG, Brazil

^d Grama Senepol, Santo Antonio da Grama Farm, Pirajuí, SP, Brazil

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ABSTRACT

Growing concerns regarding sustainability in agriculture include the availability of drinking water, which is putting pressure on livestock production, especially the beef sector, for more efficient practices. Thus, genetic parameters were estimated for traits related to water intake and water use efficiency in Senepol cattle. Senepol females ($n = 925$) and males ($n = 191$) were evaluated in performance tests carried out from 2014 to 2019. Daily dry matter intake (DMI) and water intake (WI) were recorded by electronic feed and water bunks (Intergado® Ltd.). Other traits assessed included average daily gain (ADG); mid-test metabolic BW ($BW^{0.75}$); residual water intake based on ADG (RWI_{ADG}), estimated as the residual of the linear regression equation of WI on ADG and $BW^{0.75}$; residual water intake based on DMI (RWI_{DMI}), estimated as the residual of the linear regression equation of WI on DMI and $BW^{0.75}$ (RWI_{DMI}); water conversion ratio ($= WI/ADG$); gross water efficiency ($GWE = ADG/WI$); residual feed intake estimated as the residual of the linear regression equation of DMI on ADG and $BW^{0.75}$ (RFI); feed conversion ratio ($= DMI/ADG$) and gross feed efficiency. Genetic (co)variances were estimated with bivariate analyses. The heritabilities for WI, RWI_{ADG} and RWI_{DMI} were 0.38, 0.36 and 0.33, respectively. Water conversion ratio, RWI_{ADG} and RWI_{DMI} showed positive genetic and phenotypic correlations with WI, whereas GWE was negatively correlated with WI, suggesting that traits related to water use efficiency may be useful to identify cattle with reduced WI. Water intake showed positive genetic ($r = 0.79$) and phenotypic ($r = 0.60$) correlations with DMI, suggesting the use of WI to estimate DMI in future studies. Both RWI_{ADG} and RWI_{DMI} were genetically correlated with RFI (0.67 and 0.57, respectively) and ADG (0.49 and 0.44, respectively), showing that RWI is positively associated with feed efficiency, but has an antagonistic relationship with growth. This antagonism, however, may be managed using selection indexes. Genetic improvement of water use efficiency in Senepol cattle is possible through selection and may reduce the water requirements of beef production systems.

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Implications

This study provides data that support actions for reducing the water footprint of the beef industry. Programs and cattlemen associations dedicated to the improvement of beef breeds may use the information provided here to optimize genetic selection strategies for reducing water and feed requirements. As climate change poses a risk to and increases the vulnerability of beef production systems, the genetic selection for increased efficiency may improve sustainability of the beef industry.

Introduction

Meeting the food demands of a constantly increasing human population based on a limiting land base will require greatly improved production efficiency (Berry and Crowley, 2013). Readily available, renewable and of low cost, water is considered to be a natural resource (Brew et al., 2011). However, facing an ever-growing demand for animal products in future decades, producers, scientists, agro-industries and consumers will have to join efforts in order to balance animal productivity and to reduce the risks posed by the increased water requirements of animals and by the scarcity of water itself (Palhares et al., 2017).

Furthermore, the global average water footprints estimated for beef are high, ranging from 15 415 to 15 497 l/kg of beef (Ran et al., 2016),

* Corresponding author.

E-mail address: gilberto.menezes@embrapa.br (G.R.O. Menezes).

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values much higher than those of other animal protein sources (Mekonnen and Hoekstra, 2012). Important to point out that water footprint comprises the water from plants for animal feed production (green water), surface or groundwater consumed as drinking water by the animals (blue water) and the water needed to dilute pollutants (gray water) (Hoekstra et al., 2011; Doreau et al., 2012; Ran et al., 2016). The world beef supply chain has been under pressure to reduce these values, with diet change movements gaining importance worldwide – e.g., vegetarianism and veganism. As pointed out by Nardone et al. (2010), an efficient use of water will be the major goal in order to permit the sustainability of animal agriculture.

An alternative approach to increase water use efficiency in cattle, to decrease the water footprint and to enhance sustainability in a climate change scenario is genetic improvement. Significant genetic advances in the productive and reproductive efficiency of beef cattle production have been achieved in the last decades (Abin et al., 2016; Schmidt et al., 2018; Teixeira et al., 2018; American Angus Association, 2020). However, to evaluate the feasibility of adopting a new trait as a selection criterion in a breeding program, it is necessary to quantify its genetic variability as well as its associations with already adopted traits.

To our best knowledge, only Menezes et al. (2018) and Ahlberg et al. (2019) estimated genetic parameters for traits related to water use in beef cattle, demonstrating the lack of knowledge on this subject. Menezes et al. (2018) published preliminary results of this present study for Senepol cattle, obtained with half of the data analyzed, while Ahlberg et al. (2019) worked with genotyped crossbred animals. Thus, genetic parameters for traits related to water use were estimated in Senepol cattle, a tropically adapted taurine breed, in order to evaluate the feasibility of genetic selection to reduce the water requirements of beef production.

Material and methods

Records from 1 116 purebred Senepol cattle (*Bos taurus taurus*), offspring of 87 bulls and 438 dams, were used. Phenotypic data were obtained from a compilation of nine commercial performance tests conducted on the Santo Antonio da Grama Farm, Pirajuí, SP, Brazil (21° 59' S; 49° 27' W), between 2014 and 2019. The pedigree data comprised 2 396 individuals and were provided by the Brazilian Association of Senepol Breeders and the Embrapa Geneplus Beef Cattle Breeding Program.

Water intake (WI, l/day), DM intake (DMI, kg/day) and average daily gain (ADG, kg/day) were obtained for females ($n = 925$, seven tests) and males ($n = 191$, two tests). Females and males started the tests with an average BW and age of 388 ± 57 kg and 501 ± 59 days and 473 ± 68 kg and 565 ± 55 days, respectively. In each of the nine tests, the animals were divided into two groups according to age (maximum range of 90 days in each group), totaling 18 test groups. Animals from each test group were housed in a collective pen.

Individual daily water and feed intake records were collected over a period of approximately 70 days using the Intergado® System (Intergado® Ltd., Contagem, Minas Gerais, Brazil) (Chizzotti et al., 2015; Oliveira et al., 2018). Daily water and feed intake data were excluded when the Intergado® System showed any malfunctioning. Prior to the tests, the animals were allowed to adapt to the diet and facilities for a minimum period of 14 days. The animals had *ad libitum* access to the total mixed ration and water. The feed composition of the diet offered was modified over the tests, but was equivalent in the content of total CP (15% for females and 16% for males) and total digestible nutrients (72% for females and 74% for males), on a DM basis.

The mean water and feed intake of all valid days during the test period provided WI and DMI, respectively. Weights at the beginning and end of the test were measured on fasted animals. The ADG was calculated by the difference between weight at the beginning and end of the test, divided by the number of days on test. The mid-test metabolic

BW ($BW^{0.75}$, kg) was calculated as $BW^{0.75} = [(BW \text{ at the beginning of the test} + BW \text{ at the end of the test})/2]^{0.75}$.

The water conversion ratio (WCR), gross water efficiency (GWE), feed conversion ratio (FCR) and gross feed efficiency (GFE) were calculated as the ratio between WI and ADG, ADG and WI, DMI and ADG, and ADG and DMI, respectively.

Residual feed intake (RFI) was estimated as the residual of the linear regression equation of DMI on ADG and $BW^{0.75}$ (Koch et al., 1963), fitting the regression model to each test group, separately. Two traits were used as alternatives to evaluate water use efficiency: residual water intake based on ADG (RWI_{ADG}), estimated as the residual of the linear regression equation of WI on ADG and $BW^{0.75}$, and residual water intake based on DMI (RWI_{DMI}), estimated as the residual of the linear regression equation of WI on DMI and $BW^{0.75}$ (Ahlberg et al., 2019).

The contemporary groups were defined as test group and farm of origin of the animal. Records outside the range of three SDs from the mean of the contemporary groups were eliminated. Only animals with valid records for all traits were kept in the data analysis. Animals of contemporary groups with fewer than three individuals were also discarded. Descriptive statistics of the traits studied are provided in Table 1.

The (co)variance components were obtained by Gibbs sampling in bivariate analyses using the GIBBS2F90 and POSTGIBBF90 programs (Misztal et al., 2002). The bivariate approach was chosen due to difficulty of estimating a positive definite matrix, given the high number (11) of traits and limited size of the database (1 116 animals with records). An animal model was used that included direct additive genetic and residual effects as random effects and the contemporary group as fixed effects, in addition to the linear effect of age of the animal nested in the respective contemporary groups as a covariate.

The model used for bivariate analysis between each pair of traits was:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_1 and y_2 are vectors of phenotypic measurements for traits 1 and 2; b_1 and b_2 are vectors of the previously described fixed effects; a_1 and a_2 are vectors of random direct additive genetic effects and e_1 and e_2 are vectors of random residuals. X_1 and X_2 are design matrices of fixed effects, and Z_1 and Z_2 are design matrices relating traits to random additive genetic effects.

Table 1
Descriptive statistics of all traits studied in Senepol cattle.

Traits ³	Females ¹	Males ²
	Mean \pm SD	Mean \pm SD
WI (l)	24.80 \pm 4.05	37.11 \pm 4.75
WCR (l/kg)	32.35 \pm 10.41	33.86 \pm 10.41
GWE (kg/l)	0.03 \pm 0.01	0.03 \pm 0.01
RWI_{ADG} (l)	$5.31 \times 10^{-18} \pm 2.99$	$5.24 \times 10^{-6} \pm 3.74$
RWI_{DMI} (l)	$-3.24 \times 10^{-6} \pm 2.82$	$2.09 \times 10^{-5} \pm 3.55$
DMI (kg)	7.60 \pm 1.16	9.96 \pm 2.08
FCR (kg/kg)	9.96 \pm 3.12	8.96 \pm 2.65
GFE (kg/kg)	0.11 \pm 0.03	0.12 \pm 0.03
RFI (kg)	$-3.24 \times 10^{-6} \pm 0.73$	$1.48 \times 10^{-17} \pm 0.76$
ADG (kg/d)	0.82 \pm 0.22	1.17 \pm 0.30
$BW^{0.75}$ (kg)	92.25 \pm 9.59	108.42 \pm 11.33

¹ 925 individuals with records from 97 contemporary groups.

² 191 individuals with records from 13 contemporary groups.

³ WI = average daily water intake; DMI = average daily DM intake; ADG = average daily weight gain; WCR = water conversion ratio; GWE = gross water efficiency; RWI_{ADG} = residual water intake based on ADG; RWI_{DMI} = residual water intake based on DMI; FCR = feed conversion ratio; GFE = gross feed efficiency; RFI = residual feed intake; $BW^{0.75}$ = mid-test metabolic BW.

For all analyses, a chain length of 300 000 cycles was adopted, discarding the first 50 000 cycles as burn-in and using a thinning interval of 10 cycles. Thus, 25 000 samples were effectively used for final inferences. The convergence of the Gibbs sampling algorithm was verified using the BOA package available in the R software (Plummer et al., 2006). Heritabilities and genetic correlations were obtained based on the mean of the marginal posterior (co)variances estimated. For each trait, heritability was obtained by averaging across all bivariate analyses using SDs from each analysis as weights. The standard deviation for each heritability estimate was obtained through a simple average across all bivariate analyses.

Results

Measuring individual water intake in cattle is difficult leading to rare and small data sets available to be analyzed. This limitation has impact on the confidence of the results obtained, especially for genetic covariance components that demand stronger data structure to be accurately estimated. Posterior standard deviations for all genetic and phenotypic parameters estimates are presented in order to provide information for a conscious interpretation of the results.

(Co)variance components

The phenotypic standard deviation estimates for all traits are reported in Table 2. Given the statistical model adopted in the analyses, direct additive genetic SD estimates can be calculated in a straightforward way by multiplying heritability and phenotypic SD estimates. All traits reached the stationary phase of the Gibbs chain, indicating that the sampling processes for estimating (co)variance components were appropriate. With the outputs of all bivariate analyses, a direct additive genetic full (co)variance matrix was built, confirming to be a definite positive matrix.

Heritability

The heritability estimates for all traits ranged from 0.07 to 0.41 (Table 2). In general, these estimates exhibited high SDs and wide 95% highest posterior density intervals, likely due to the limited amount of available data. The highest heritability estimate was obtained for $BW^{0.75}$ and the lowest for FCR. The heritabilities varied widely among the traits related to water use efficiency, with estimates higher than 0.30 for WI, RWI_{ADG} and RWI_{DMI} , while the heritability for WCR and GWE was <0.10. Regarding feed efficiency traits, heritability estimates

of <0.15 were found, whereas the heritability for DMI was 0.28. A low heritability of 0.10 was obtained for ADG.

Genetic and phenotypic correlations

Genetic and phenotypic correlations among traits related to water use are presented in Table 3. For all pairs of traits, the genetic correlations were higher than the phenotypic ones, including posterior SDs. In general, moderate to high genetic correlations were found, with the lowest value of -0.44 between WI and GWE and the highest value of 0.98 between RWI_{ADG} and RWI_{DMI} . On the other hand, the phenotypic correlations were slightly lower, with the lowest value of 0.27 between WI and WCR and the highest value of -0.92 between GWE and WCR. Strong genetic and phenotypic associations were obtained between DMI and the novel traits (RWI_{ADG} and RWI_{DMI} , >0.80), which were higher than the correlations estimated between DMI and the traditional traits (WCR and GWE, <0.57). Genetic and phenotypic correlations higher than 0.90 and with low posterior SD were observed between RWI_{ADG} and RWI_{DMI} , as well as between WCR and GWE. Moderate genetic and phenotypic correlations were estimated between the novel and traditional traits, adopted to evaluate water use efficiency, ranging from 0.35 to 0.71.

Table 4 shows the genetic and phenotypic correlation estimates between traits related to water use efficiency and those related to growth and feed intake. Overall, high SDs were obtained for the genetic correlations, likely due to the limited amount of available data. Strong genetic (0.79) and phenotypic (0.60) associations were detected between WI and DMI, showing low posterior SD what indicates accurate estimates. The two growth-related traits (ADG and $BW^{0.75}$) showed positive correlations with WI, ranging from 0.33 to 0.75. The two traditional traits used to evaluate water use efficiency (WCR and GWE) exhibited moderate to high genetic and phenotypic correlations with FCR and GFE. The genetic correlation estimates of RWI_{ADG} and RWI_{DMI} with RFI were 0.64 and 0.51, respectively; however, the phenotypic correlations were lower (0.34 and -0.06). Lastly, ADG showed positive genetic correlations of 0.49 and 0.44 with RWI_{ADG} and RWI_{DMI} , respectively, while the phenotypic correlations were close to zero.

Discussion

The present study reports the parameter estimates for water use efficiency and contributes to the understanding of the impacts of water requirements reduction on traits of economic interest. The moderate heritability and high phenotypic variance of WI initially indicate the possibility of genetic selection to reduce the water requirements of beef cattle production and confirm previous findings reported for mice (Ramirez and Fuller, 1976; Bachmanov et al., 2002) and cattle (Ahlberg et al., 2019). The strong associations with growth, feed intake and BW make sense from a physiological point of view, as water participates in digestive and metabolic processes and is a major component of fluids and tissues, especially muscle tissue (National Academies of Sciences, Engineering, and Medicine (NASEM), 2016). In general, the findings indicate that selection for lower water intake is possible but may result in individuals with a low BW and reduced performance if not combined with other selection criteria.

Regarding the strong association between water intake and feed intake is the possibility of applying the former to estimate the latter. The determination of feed intake is not only an expensive task, particularly in pasture-based systems, but is also of substantial scientific interest and is important for applied genetic improvement in an attempt to select animals with better feed efficiency. Given the phenotypic (0.60) and genetic (0.80) correlations between DMI and WI, water intake explains an important proportion of the phenotypic (36%) and genetic (64%) variation in feed intake. Assuming constant selection intensity for DMI and WI as well as their genetic correlation and heritability estimates, the expected selection response for DMI when indirectly

Table 2
Phenotypic SD and heritability estimates of all traits studied in Senepol cattle.

Traits ²	Phenotypic SD	$h^2 \pm PSD^3$	h^2 HPD _{95%} ¹
WI (l)	3.839	0.37 ± 0.10	0.20–0.56
WCR (l/kg)	8.251	0.09 ± 0.05	0.00–0.11
GWE (kg/l)	0.007	0.09 ± 0.05	0.00–0.12
RWI_{ADG} (l)	3.162	0.35 ± 0.09	0.16–0.51
RWI_{DMI} (l)	2.985	0.32 ± 0.10	0.13–0.47
DMI (kg)	0.963	0.28 ± 0.09	0.12–0.45
FCR (kg/kg)	2.294	0.07 ± 0.05	0.00–0.09
GFE (kg/kg)	0.023	0.07 ± 0.05	0.00–0.10
RFI (kg)	0.701	0.13 ± 0.07	0.00–0.21
ADG (kg/d)	0.200	0.11 ± 0.06	0.00–0.19
$BW^{0.75}$ (kg)	7.715	0.40 ± 0.10	0.22–0.59

¹ 95% Highest Posterior Density Interval for h^2 .

² WI = average daily water intake; DMI = average daily DM intake; ADG = average daily weight gain; WCR = water conversion ratio; GWE = gross water efficiency; RWI_{ADG} = residual water intake based on ADG; RWI_{DMI} = residual water intake based on DMI; FCR = feed conversion ratio; GFE = gross feed efficiency; RFI = residual feed intake; $BW^{0.75}$ = mid-test metabolic BW.

³ Posterior SD.

Table 3

Genetic (above diagonal) and phenotypic (below diagonal) correlations with respective posterior SDs estimates between traits measuring water use efficiency in Senepol cattle.

Traits ¹	WI	RWI _{ADG}	RWI _{DMI}	WCR	GWE
WI		0.86 ± 0.06	0.83 ± 0.08	0.57 ± 0.32	-0.44 ± 0.33
RWI _{ADG}	0.83 ± 0.01		0.98 ± 0.02	0.66 ± 0.28	-0.59 ± 0.26
RWI _{DMI}	0.80 ± 0.01	0.91 ± 0.01		0.71 ± 0.26	-0.59 ± 0.26
WCR	0.27 ± 0.03	0.52 ± 0.03	0.35 ± 0.03		-0.95 ± 0.12
GWE	-0.30 ± 0.03	-0.56 ± 0.02	-0.37 ± 0.03	-0.92 ± 0.01	

¹ WI = average daily water intake; RWI_{ADG} = residual water intake based on average daily weight gain; RWI_{DMI} = residual water intake based on average daily DM intake; WCR = water conversion ratio; GWE = gross water efficiency.

selecting through WI, in one generation, is 4% bigger than directly using DMI. Indeed, this is a conservative approach, since selection intensity for WI is expected to be approximately four times higher than for DMI as one Intergado® System's automatic water drinker, for a same period of time, can evaluate 35 animals while an electronic feed bin only eight. Considering its lower cost of measurement and the possibility of evaluating a larger population, this trait can be used to estimate feed intake and, consequently, measures of feed efficiency. However, one must first know the correlations between feed efficiency measures estimated based on water intake and those determined by the direct measurement of feed intake.

Although there are studies on factors that affect the water intake by animals (e.g. Brew et al., 2011; Ahlberg et al., 2018), genetic approaches to increase water use efficiency are rare – for cattle, only Ahlberg et al. (2019). Within this context, an important contribution of the present study is that it compared different traits in order to support the definition of selection criteria in breeding programs for greater water use efficiency. The traits evaluated here are derived from measures traditionally used to represent the efficiency of feed utilization, such as FCR, GFE and RFI (Koch et al., 1963).

The first observation regarding the differences between water efficiency measures is related to heritability. Moderate heritabilities were observed for RWI (0.33 to 0.36), while the heritabilities for WCR and GWE were low (0.09). These estimates would initially impair the use of the latter when selecting for greater water use efficiency and would favor the use of measures of RWI. However, it should be pointed out that, contrary to the literature (Berry and Crowley, 2013), the heritabilities for ADG, FCR and GFE were also low. Within this context, it is possible that the low heritabilities observed for WCR and GWE are due to the difficulty in distinguishing genetic variance from residual variance in the database used. Thus, the conclusion that these traits are weakly heritable and are therefore not recommended for selection should be made with caution.

The second observation regarding the differences in water use efficiency measures is related to the method used to calculate RWI. Regardless of whether feed intake (RWI_{DMI}) or ADG (RWI_{ADG}) was used as the independent variable in multiple regression analysis, the two RWI measures had similar heritability coefficients. Likewise, the genetic and phenotypic correlations with other traits of interest were similar in terms of both magnitude and direction. Finally, the genetic and phenotypic correlation coefficients between the two measures were high (0.98 and 0.91, respectively). In general, these results show that either method can be used to calculate RWI.

The proposal of using RWI as a measure of water use efficiency is recent, and current knowledge is based on the publications of Fischer and Faverdin (2016) and Ahlberg et al. (2019). Although applied to dairy cattle, the approach of Fischer and Faverdin (2016) resembles that defined here as RWI_{ADG}. The authors calculated RWI as the residual of the regression of water intake on live weight and cumulative milk yield, a production measure like ADG. In contrast, Ahlberg et al. (2019) considered RWI to the residual of regression of water intake on live weight and DMI, represented in this study by RWI_{DMI}. The importance of comparing the two approaches for the calculation of RWI is not only related to the need of evaluating their possible impacts on other traits, but mainly to the fact that the first approach is potentially less costly since it does not require the measurement of feed intake and may therefore be applicable to larger populations. As previously pointed out, one Intergado® System's electronic water drinkers allows measuring WI for 35 animals, while its electronic feed bin can evaluate only eight for DMI. Besides, WI could be measured on grass-fed production systems, while DMI needs to be in the feedlot.

An additional comment on the water use efficiency traits evaluated should be made regarding the associations with traits of economic interest, such as ADG. The RWI measures, for example, showed moderate but antagonistic correlations with ADG. WCR and GWE also exhibited moderate genetic correlations with this trait, but these correlations

Table 4

Genetic and phenotypic correlations estimates with respective posterior SDs between traits measuring water use efficiency and those measuring growth and feed efficiency intake in Senepol cattle.

Traits ¹	WI	RWI _{ADG}	RWI _{DMI}	WCR	GWE
Genetic correlations					
ADG	0.75 ± 0.20	0.49 ± 0.32	0.44 ± 0.35	-0.27 ± 0.49	0.45 ± 0.34
BW ^{0.75}	0.55 ± 0.16	0.02 ± 0.23	0.00 ± 0.24	0.21 ± 0.47	-0.03 ± 0.45
DMI	0.79 ± 0.12	0.37 ± 0.23	0.32 ± 0.26	-0.02 ± 0.42	0.14 ± 0.39
FCR	-0.03 ± 0.38	-0.11 ± 0.38	-0.14 ± 0.39	0.69 ± 0.33	-0.69 ± 0.44
GFE	0.27 ± 0.36	0.31 ± 0.38	0.40 ± 0.37	-0.53 ± 0.49	0.64 ± 0.29
RFI	0.66 ± 0.20	0.64 ± 0.24	0.51 ± 0.29	0.03 ± 0.50	0.05 ± 0.47
Phenotypic correlations					
ADG	0.33 ± 0.03	-0.05 ± 0.04	0.11 ± 0.04	-0.75 ± 0.02	0.78 ± 0.01
BW ^{0.75}	0.55 ± 0.03	0.05 ± 0.04	0.05 ± 0.04	0.06 ± 0.04	-0.06 ± 0.03
DMI	0.60 ± 0.02	0.26 ± 0.04	0.02 ± 0.04	-0.03 ± 0.04	0.02 ± 0.04
FCR	-0.02 ± 0.04	0.18 ± 0.04	-0.11 ± 0.04	0.86 ± 0.01	-0.79 ± 0.01
GFE	0.03 ± 0.04	-0.17 ± 0.04	0.14 ± 0.04	-0.80 ± 0.01	0.83 ± 0.01
RFI	0.30 ± 0.03	0.34 ± 0.03	-0.06 ± 0.04	0.19 ± 0.03	-0.21 ± 0.03

¹ WI = average daily water intake; DMI = average daily DM intake; ADG = average daily weight gain; WCR = water conversion ratio; GWE = gross water efficiency; RWI_{ADG} = residual water intake based on ADG; RWI_{DMI} = residual water intake based on DMI; FCR = feed conversion ratio; GFE = gross feed efficiency; RFI = residual feed intake; BW^{0.75} = mid-test metabolic BW.

were favorable. An explanation for the moderate genetic correlations of the RWI measures with ADG is unclear. RWI_{ADG} , mainly because its estimation uses ADG, should be independent of the growth rate, as was the case of $BW^{0.75}$. However, this independency is expected only in a phenotypic level, being possible the existence of a genetic component not accounted in computing RWI_{ADG} . Kennedy et al. (1993) pointed out that RFI could not be genetically independent from ADG, despite being phenotypically. As RWI_{ADG} is computed similarly to RFI, the same argument could be used to explain the results here. What can be concluded from these relationships so far is that WCR and GWE suggest the possibility of increasing water use efficiency simultaneously to animal performance. However, there is important concern regarding the possible negative impacts of the use of RWI on the growth rate.

Complementary to the analysis of the correlations with growth rate, it is also important to evaluate the associations of water efficiency with feed efficiency. In general, all water use efficiency measures showed a moderate and positive correlation with the measures of feed efficiency, but in a specific manner. For example, the two RWI measures were better correlated with RFI than with FCR or GFE. This finding can be explained by the similarity of the method used for their calculation and by the use of BW for the estimation. Furthermore, WCR and GWE were better correlated with their homologs (FCR and GFE).

The positive associations between feed use efficiency and water use efficiency may represent an opportunity to reduce the water footprint of beef production. The water footprint comprises evapotranspiration water from plants for animal feed production (green water), surface or groundwater consumed as drinking water by the animals (blue water), and the water needed to dilute pollutants (gray water) (Hoekstra et al., 2011; Doreau et al., 2012; Ran et al., 2016). The water footprint of beef production is estimated at 15 415 to 15 497 l/kg beef produced (Mekonnen and Hoekstra, 2012; Ran et al., 2016). Our results show that selection for improved efficiency on water use will reduce blue water footprint (drinking water) and, due to the positive genetic correlation between water efficiency and feed efficiency (RFI), this selection can also lead to reduced green water footprint, since these animals will have lower feed requirements (Gomes et al., 2012). Assuming constant selection intensity for RFI and RWI_{ADG} as well as their genetic correlation and heritability estimates, the expected selection response for RFI when indirectly selecting through RWI_{ADG} , in one generation, is 72% bigger than directly using RFI.

Finally, it is important to mention that, although accounting for a smaller part of the water footprint, a reduction of the blue water footprint might be strategic for adapting beef production systems to climate change scenarios. The intensification of production systems will increase water requirements, especially because of the genetic improvement of herds (Winchester and Morris, 1956; Phillips, 1960; Beatty et al., 2006; Brew et al., 2011), increasing weight gain rates, BW and, consequently, water intake by the animal. Since blue water is sensitive to water scarcity (Beckett and Oltjen, 1993; Hoekstra et al., 2011), selection for improved water use efficiency might be a strategy to reduce the risks and to enhance the sustainability of beef production systems.

Ethics approval

The study was conducted following animal welfare guidelines in accordance with the Brazilian Legislation on Animal Handling. All animal procedures were approved by the Ethics and Animal Handling Committee of Embrapa Beef Cattle, Campo Grande, MS, Brazil (Protocol No. 007/2016).

Data and model availability statement

GIBBS2F90 and POSTGIBBF90 programs are available for free download and use for research purposes at the website of the Animal Breeding and Genetics Group from the University of Georgia, USA (<http://nce.ads.uga.edu/html/projects/programs/>). The data sets analyzed in the

current study are available upon reasonable request from their owners (Santo Antonio da Grama Farm, Brazilian Association of Senepol Breeders, and Geneplus Embrapa Beef Cattle Breeding Program).

Author ORCIDs

Gilberto Romeiro de Oliveira Menezes – ORCID number: 0000-0002-2221-1525.

Author contributions

Gabriel de Moraes Pereira: Investigation, formal analysis, writing – original draft, writing – review & editing and funding acquisition; Andrea Alves do Egito: Investigation, writing – original draft and visualization; Rodrigo da Costa Gomes: Conceptualization, methodology, investigation and writing – original draft; Marcelo Neves Ribas: Conceptualization, methodology, resources and data curation; Roberto Augusto de Almeida Torres Junior: Methodology, formal analysis and writing – original draft; José Antônio Fernandes Junior: Resources, data curation, supervision and project administration; Gilberto Romeiro de Oliveira Menezes: Conceptualization, methodology, writing – original draft, writing – review & editing and project administration.

Declaration of interest

None.

Uncited references

Demment and Van Soest, 1985
Thornton et al., 2009

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