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Genetic parameters for performance, feed efficiency, and carcass traits in Senepol heifers

L.C. Novo [a], A. Gondo [b], R.C. Gomes [b], J.A. Fernandes Junior [c], M.N. Ribas [d], L.F. Brito [e], M.M.M. Laureano [a], C.V. Araújo [a], G.R.O. Menezes [b,*]

[a] Research and Study Center for Animal Breeding, Federal University of Mato Grosso, 1200 Alexandre Ferronato Av, Sinop, Mato Grosso 78555-000, Brazil
[b] EMBRAPA, Rádio Maia Av. 830, Campo Grande, Mato Grosso do Sul 79106-550, Brazil
[c] Fazenda Grama, Km 404 Mal. Rondon Road, Pirajuí, São Paulo 16600-000, Brazil
[d] INTERGADO LTDA, 1463 Rio Paranagua Street, Contagem, Minas Gerais 32280-300, Brazil
[e] Department of Animal Sciences, Purdue University, 270 S. Russell Street, West Lafayette, IN 47907, USA

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A B S T R A C T

Improving feed efficiency is a key breeding goal in the beef cattle industry. In this study, we estimated the genetic parameters for feed efficiency and carcass traits in Senepol cattle raised in tropical regions. Various indicators of feed efficiency [gain to feed ratio (G:F), feed conversion ratio (FCR), residual weight gain (RG), residual intake and body weight gain (RIG), and residual feed intake (RFI)] as well as growth [final BW, average daily gain (ADG), and DM intake (DMI)], and carcass [rib-eye area (REA), backfat thickness (BF), intramuscular fat score, and carcass conformation score] traits were included in the study. After data editing, records from 1 393 heifers obtained between 2009 and 2018 were used for the analyses. We fitted an animal model that included contemporary group (animals from the same farm that were evaluated in the same test season) as the fixed effect, and a linear effect of animal age at the beginning of the test as a covariate; in addition to random direct additive genetic and residual effects. The (co)variance components were estimated by Bayesian inference in uni- and bivariate analyses. Our results showed that feed efficiency indicators derived from residual variables such as RG, RIG, and RFI can be improved through genetic selection ($h^2 = 0.14 \pm 0.06$, 0.13 ± 0.06, and 0.20 ± 0.08, respectively). Variables calculated as ratios such as G:F and FCR were more influenced by environmental factors ($h^2 = 0.08 \pm 0.05$ and 0.09 ± 0.05), and were, therefore, less suitable for use in breeding programs. The traits with the greatest and impact on genetic progress in feed efficiency were ADG, REA, and BF. The traits with the greatest and least impact on growth and carcass traits were RG and RFI, respectively. Selection for feed efficiency will result in distinct overall effects on the growth and carcass traits of Senepol heifers. Direct selection for lower RFI may reduce DMI and increase carcass fatness at the finishing stage, but it might also result in reduced growth and muscle deposition. Residual BW gain is associated with the highest weight gain and zero impact on REA and BF, however, it is linked to higher feed consumption. Thus, the most suitable feed efficiency indicator was RIG, as it promoted the greatest decrease in feed intake concomitant with faster growth, with a similar impact on carcass traits when compared to the other feed efficiency indicators.

Implications

This study provides information to Senepol breeders to improve their competitiveness through genetic selection for feed efficiency, as feeding has a major impact on beef production costs. The currently available traits for identifying the most efficient animals are expected to respond differently to selection efforts. Performance and carcass attributes are related to feed efficiency traits, thus, the planning of Senepol breeding programs should consider adopting strategies that take this into account.

Introduction

Feed can represent up to 75% of the operating costs of beef cattle farms, a fact that often limits the producer's profitability considering the dependence of these costs on external factors such as climate and the international market (Coutinho Filho et al., 2006; Caldarelli et al., 2012). Within this context, grain prices are expected to increase by up to 32% until 2030 due to the effects of climate change effects; thus, the genetic selection for improved feed efficiency becomes a paramount

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

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tool for long-term sustainable beef cattle production (Scholtz et al., 2013; Magrin et al., 2014).

Besides its effects on production costs, the selection for feed efficiency and lower feed intake is also related to lower methane emissions and may, therefore, be used as a component to reduce greenhouse gas emissions (Berry and Crowley, 2013). Commonly measured indicators of feed efficiency can have different impacts on growth and carcass traits. Although ratio traits are easier to calculate, the results obtained should be used with caution. When the two traits used to estimate the ratio variable are positively correlated (e.g. DM intake (DMI) and average daily gain (ADG)), selection for faster-growing animals may for instance, also increase feed intake (Crews Jr, 2005). On the other hand, traits measured as residuals, such as residual feed intake (RFI) and residual BW gain, are estimated by the regression of feed intake on the energy sinks involved in muscle and fat tissue deposition and body maintenance. Thus, the aim of using residuals traits is to prevent that observed genetic variances from being a consequence of the genetic correlations between these two factors (Berry and Crowley, 2013).

Selection for improved feed efficiency usually results in reduced feed intake with no or little loss in the growth rate and muscle deposition, however, this selection can have unfavorable effects on carcass fat accretion in beef cattle (Santana et al., 2012; Berry and Crowley, 2013). In the case of females, in 2019 accounted for 41% of all slaughtered animals in Brazil (IBGE, 2020), studies have shown that they present higher production costs when compared to males due to physiological factors and lower carcass yield which lead to a worse feed conversion ratio (FCR) (Coutinho Filho et al., 2006; Santos et al., 2017). However, the production costs may be reduced when beef heifers are selected for feed efficiency (Damiran et al., 2018).

To the best of our knowledge, there are no reports on the effects of genetic selection for improved feed efficiency on growth and carcass traits in Senepol heifers. Senepol is a taurine breed adapted to tropical climate conditions and has precocious development compared to non-adapted *Bos taurus taurus* and *Bos taurus indicus* breeds, respectively (Thrift et al., 2010).

Thus, the main objective of this study is to estimate genetic parameters for various feed efficiency traits and to investigate their potential for genetic selection and their impacts on performance and carcass traits in Senepol heifers.

Material and methods

Animals

We used records from 2 381 Senepol heifers participating in a commercial performance test conducted on the Santo Antonio da Grama Farm (Pirajuí, São Paulo, Brazil) from 2009 to 2017. The standard evaluation period lasted 70 days, in addition to 21 days of adaptation. The main criteria for participation in the performance test were a certificate indicating the purebred composition, age of 10 to 16 months, and a minimum weight of 250 kg. The animals were arranged on paddocks with *ad libitum* food and water. The feed composition of the diet offered was modified over the years, but was equivalent in the content of total CP (15%) and digestible nutrients (72%), sampled twice a week for complete chemical composition analysis. The basic diet formulation is shown in Table 1. The pedigree information was obtained from the database belonging to the Embrapa Beef Cattle Breeding Program—Geneplus and the Brazilian Association of Senepol Cattle Breeders—ABCB Senepol.

Data collection

From 2009 to 2012, the evaluation in the commercial test did not include feed efficiency information. From 2013 onward, the data of feed efficiency traits and weights were collected using the Intergado Electronic trough technology (Chizzotti et al., 2015; Oliveira et al., 2017).

Table 1
Basic chemical composition of the diets for the adaptation and performance test periods adopted in the evaluation of Senepol heifers.

Nutrient	Adaptation (21 days)	Performance test (~70 days)
CP (% DM)	16.20	14.65
Protein digestible in rumen (% DM)	11.20	10.80
Total digestible nutrients (% DM)	70.35	73.8
Non-fiber carbohydrates (% DM)	42.60	47.10
Effective NDF (% DM)	21.20	17.07
Ether extract (% DM)	3.20	4.54
Ca (% DM)	0.80	0.7
P (% DM)	0.35	0.30
Mg (% DM)	0.24	0.28
K (% DM)	1.00	0.80
Na (% DM)	0.21	0.19
S (% DM)	0.19	0.20
Zn (mg/kg DM)	100.00	90.00
Mn (mg/kg DM)	40.00	40.00
Cu (mg/kg DM)	20.00	18.50
I (mg/kg DM)	0.90	0.85
Co (mg/kg DM)	0.50	0.50
Se (mg/kg DM)	0.30	0.30
Chromium (mg/kg DM)	0.50	0.40
Biotin (IU/kg DM)	2.50	2.00
Vitamin A (IU/kg DM)	5 000.00	3 500.00
Vitamin D (IU/kg DM)	625.00	437.50
Vitamin E (IU/kg DM)	50.00	35.00
Sodium monoenzyme (mg/kg DM)	20.00	25.00

Weights at the beginning and end of the test were measured on fasted animals; however, this approach did not allow us to identify or trace abnormal patterns of growth. Final BW was collected at the end of the test period by simple weighing; ADG was determined by the difference between the final and initial weight, divided by the number of days on test (standard 70 effective days). All carcass traits were measured once at the end of the test on live animals, by a certified technician from the Ultrasound Guidelines Council, using the Bia Software from Designer Genes Technology (www.dgtbrasil.com.br/metodologia/). These traits were collected by ultrasonography in the region between the 12th and 13th ribs in the *Longissimus dorsi* muscle for rib eye area (REA) as cm^2 and backfat thickness (BF) as mm. In addition, the percentage of intramuscular fat (IMF) was determined in a longitudinal section of the same region following the same guidelines. Carcass conformation score (CCS) was obtained by the same technician through visual evaluation of live animals at the end of the test. The animals received a single score from 1 to 6, based on the visual evaluation proposed by Koury Filho et al. (2006): body structure (evaluation of body length and depth), muscle development (body volume and muscle convexity), and finishing precocity (proportion of body depth relative to leg height). Dry matter intake was determined by averaging daily feed intake collected with the Intergado Electronic troughs and measured as kg of natural matter, adjusted for DM, per day.

Data editing

The data sets used were collected between 2009 and 2018 from 2 381 heifers participating in several commercial performance test sessions. The tested animals were purebred with both sire and dam known. A pedigree file was created that contained 2 192 animals, including 392 bulls and 1 800 dams. Considering the acclimatization period prior to the test and the unknown information about the previous location of animals, including management and diet offered, the contemporary groups (CGs) were formed by grouping animals from the same performance test edition and farm of origin, creating 221 groups. Aiming to establish genetic connectedness among sires while demanding minimum progenies, data editing consisted of removing records of CGs with fewer than three animals, records of animals without BW data, and daughters of bulls with fewer than three progenies. Thus, 1 393 animals remained with an average age of 16.6 ± 1.96 months at the start of the performance test remained, as described in Table 2.

Feed efficiency traits

Gain to feed ratio (G:F) and FCR are reported as kg of gained weight/kg of DMI, and kg of DMI/kg of gained weight, respectively. Residual feed intake and residual BW gain (RG) were calculated as follows:

$$RFI = DMI_{observed} - DMI_{predicted}$$

$$RG = ADG_{observed} - ADG_{predicted}$$

The $DMI_{observed}$ represents the recorded consumption of DM and $ADG_{observed}$ represents the average daily component of the total weight gain observed during the test period. The $DMI_{predicted}$ and $ADG_{predicted}$ were calculated as proposed by Koch et al. (1963):

$$DMI_{predicted} = \mu + b_1 ADG + b_2 AMW^{0.75} + e$$

$$ADG_{predicted} = \mu + b_1 DMI + b_2 AMW^{0.75} + e$$

where μ is the model intercept that includes the performance test edition effect, $AMW^{0.75}$ is the average metabolic BW during the test period, and b_1 and b_2 are the regression coefficients of the first and second energy sinks considered. As not all commercial performance tests collect ultrasound traits and so to reflect commercial reality, we defined the RFI without including BF in the model used to obtain $DMI_{predicted}$. Along with the several performance test editions, the R^2 for $DMI_{predicted}$ and $ADG_{predicted}$ varied from 0.50 to 0.65. The residual intake and body weight gain (RIG) was calculated based on the method proposed by Berry and Crowley (2012), setting the adjusted RFI and RG to have a variance of 1 and then multiplying RFI by −1 before adding it to RG:

$$RIG = (-1 \times RFI) + RG$$

Statistical analysis

A mixed animal model was fitted considering CG as a fixed effect, the linear effect of age at testing as a covariate, and the additive genetic effect (random). This model can be represented in matrix form by the equation:

$$y = X\beta + Z\alpha + \varepsilon$$

where y is a vector of observations for each trait analyzed, X is an incidence matrix for the fixed effect levels, β is a vector of fixed effects for the CG classes and the linear effect of animal age at data collection as its covariate, Z is an incidence matrix of the direct additive genetic effects, α is a direct additive genetic effect vector, and ε is a vector of the residual terms with the same dimension as y.

Genetic parameters and (co)variance components were estimated by Bayesian inference using the GIBBS1F90 and Postgibbsf90 software (Misztal et al., 2002). A total of 300 000 cycles were processed, with a burn-in of 30 000 and values saved every 10 cycles, resulting in a chain of 27 000 cycles analyzed. The Geweke Criterion applied for convergence diagnosis (Geweke, 1992), which compares the convergence of the Markov chain start and end averages, using the "Coda" package (Plummer et al., 2006). Heritability and variance component estimates were obtained from univariate analyses, while covariance components and genetic correlations were obtained from bivariate analyses.

Results

Heritability estimates

Table 3 shows the *posteriori* means of heritability for the traits analyzed. In general, the mean heritability estimates ranged from medium to high (from 0.13 to 0.48), except for G:F and FCR, which were 0.08 ± 0.05 and 0.09 ± 0.05, respectively. Traits related to weight and carcass composition (e.g., BW, REA, BF, IMF, and CCS) had the highest mean heritability (0.41 ± 0.07). The feed efficiency indicators and ADG had moderate heritability estimates (>0.12).

Genetic correlations

Tables 4 and 5 show the genetic correlations among all traits investigated. Generally, the SD of the genetic correlations were high; thus, the results should be interpreted with caution. Body weight was highly correlated with growth and carcass quality traits (e.g., ADG, REA, BF, and CCS). Dry matter intake showed a moderate to a high positive genetic association (>0.40) with carcass, growth, and finishing traits. The estimated correlations of feed efficiency indicators were quite variable. There was a high genetic correlation of G:F with ADG (0.84 ± 0.11) and moderate genetic correlation with CCS (0.40 ± 0.31), but

Table 2
Descriptive statistics of growth, carcass, and feed efficiency traits in Senepol cattle.

Trait[1]	N	Mean	SD	Minimum	Maximum
Age (months)	1 393	16.66	1.96	10.85	21.67
BW (kg)	1 393	447.94	63.29	253.10	626.00
ADG (kg/day)	1 393	0.83	0.25	0.21	1.56
DMI (kg/day)	1 393	7.72	1.28	3.62	12.32
REA (cm^2)	1 393	69.19	11.21	35.45	102.24
BF (mm)	1 393	6.85	2.92	1.02	15.11
IMF (% of fat)	1 393	3.36	1.17	0.57	7.33
CCS (grade;1–6)	1 393	4.20	1.20	1.00	6.00
G:F (kg of weight/kg of DM)	1 393	0.11	0.03	0.04	0.21
FCR (kg of DM/kg of weight)	1 393	10.22	3.75	4.77	26.09
RG (kg/day)	1 393	−0.0022	0.17	−0.55	0.55
RIG (SD unit)	1 393	−0.0039	1.58	−4.39	4.74
RFI (kg of DM/day)	1 393	−0.0038	0.73	−2.60	2.52

[1] ADG = average daily gain, DMI = dry matter, REA = rib eye area, BF = backfat thickness, IMF = intramuscular fat, CCS = carcass conformation score, G:F = gain to feed ratio, FCR = feed conversion ratio, RG = residual BW gain, RIG = residual intake and BW gain, RFI = residual feed intake.

Table 3
Heritability and phenotypic variance estimates for growth, carcass, and feed efficiency traits in Senepol cattle.

Trait[1]	h^2 [5]	SD	σ_p^2 [2]	HPD_I[3]	HPD_S[4]
BW	0.48	0.08	1 774.90	0.33	0.64
ADG	0.20	0.07	0.03	0.08	0.34
DMI	0.32	0.08	0.96	0.18	0.47
REA	0.43	0.09	76.98	0.26	0.60
BF	0.45	0.08	4.36	0.32	0.63
IMF	0.37	0.08	0.90	0.21	0.54
CCS	0.31	0.08	0.97	0.17	0.46
G:F	0.08	0.05	0.00	0.00	0.17
FCR	0.09	0.05	7.19	0.01	0.20
RG	0.14	0.06	0.03	0.03	0.25
RIG	0.13	0.06	2.43	0.02	0.25
RFI	0.20	0.08	0.48	0.06	0.36

[1] ADG = average daily gain, DMI = DM intake, REA = rib eye area, BF = backfat thickness, IMF = intramuscular fat, CCS = carcass conformation score, G:F = gain to feed ratio, FCR = feed conversion ratio, RG = residual BW gain, RIG = residual intake and BW gain, RFI = residual feed intake.
[2] σ_p^2 = phenotypic variance.
[3] HPD_I = 95% highest posterior density interval—lower limit.
[4] HPD_S = 95% highest posterior density interval—upper limit.
[5] h^2 = heritabilily.

Table 4
Genetic correlations, SD and phenotypic correlations among growth, carcass, and feed efficiency traits in Senepol cattle.

Trait[1]	BW	ADG	DMI	REA	BF	IMF	CCS
Genetic correlations							
G:F	0.07 ± 0.27	0.84 ± 0.11	0.28 ± 0.41	−0.34 ± 0.28	0.09 ± 0.25	−0.58 ± 0.26	0.40 ± 0.31
FCR	−0.21 ± 0.27	−0.83 ± 0.13	−0.30 ± 0.32	0.11 ± 0.27	0.09 ± 0.25	0.46 ± 0.29	−0.38 ± 0.28
RG	0.30 ± 0.21	0.84 ± 0.08	0.33 ± 0.28	−0.08 ± 0.24	0.03 ± 0.22	−0.51 ± 0.23	0.50 ± 0.25
RIG	0.20 ± 0.22	0.20 ± 0.27	−0.34 ± 0.24	−0.23 ± 0.27	0.16 ± 0.23	−0.21 ± 0.26	0.40 ± 0.23
RFI	−0.07 ± 0.21	0.46 ± 0.23	0.71 ± 0.13	0.19 ± 0.24	−0.23 ± 0.21	−0.17 ± 0.22	−0.21 ± 0.22
BW	–	0.52 ± 0.17	0.66 ± 0.12	0.66 ± 0.09	0.47 ± 0.11	−0.20 ± 0.16	0.74 ± 0.08
ADG	–	–	0.83 ± 0.13	0.15 ± 0.21	0.05 ± 0.19	−0.50 ± 0.21	0.53 ± 0.20
DMI	–	–	–	0.51 ± 0.16	0.18 ± 0.16	−0.33 ± 0.17	0.43 ± 0.16
Phenotypic correlations							
G:F	0.03	0.83	−0.22	−0.04	0.02	0.04	−0.07
FCR	−0.05	−0.80	0.14	−0.01	−0.07	−0.10	0.00
RG	0.07	0.64	−0.02	−0.03	−0.06	−0.12	0.06
RIG	0.05	0.36	−0.36	0.00	0.00	−0.05	0.07
RFI	0.00	0.02	0.58	−0.01	−0.05	−0.04	−0.05
BW	–	0.32	0.56	0.74	0.63	0.20	0.54
ADG	–	–	0.33	0.17	0.18	0.14	0.10
DMI	–	–	–	0.35	0.27	0.16	0.29

[1] ADG = average daily gain, DMI = DM intake, REA = rib eye area, BF = backfat thickness, IMF = intramuscular fat, CCS = carcass conformation score, G:F = gain to feed, FCR = feed conversion ratio, RG = residual BW gain, RIG = residual intake and BW gain, RFI = residual feed intake.

non-significant with BW (0.07 ± 0.27) and BF (0.09 ± 0.25). Gain to feed ratio was also negatively correlated with REA (−0.34 ± 0.28) and IMF (−0.58 ± 0.26). Opposite results were observed between carcass traits and FCR, which was expected given the inverse nature of this trait in relation to G:F.

For RFI, as expected, a null correlation was observed with BW (−0.07 ± 0.21). Favorable yet non-significant values were found for BF (−0.23 ± 0.21), IMF (−0.17 ± 0.22), and CCS (−0.21 ± 0.22), indicating that animals with lower RFI might have increased fat deposition and better carcass conformation, although more data are needed for a definite conclusion. The opposite was observed for ADG (0.46 ± 0.23) and REA (0.19 ± 0.24), which corresponds to the observed decrease in DMI (0.71 ± 0.13).

The use of alternative measures such as RG and RIG yielded a more positive genetic correlation with growth-related traits compared to RFI, as demonstrated by the genetic correlations with BW [(0.30 ± 0.21) for RG and (0.20 ± 0.22) for RIG] and ADG [(0.84 ± 0.08) for RG and (0.20 ± 0.27) for RIG]. However, carcass finishing was negatively genetically correlated with IMF deposition [(−0.51 ± 0.23) for RG and (−0.21 ± 0.26) for RIG]. For RG, the genetic correlation with REA was approximately zero, showing an advantage over RIG, which decreases carcass quality due to lower muscularity. However, the opposite effect was observed for BF in which the use of RIG favors the deposition of subcutaneous fat compared to RG. Overall, RG had more favorable genetic associations, although selection for RG can indirectly increase DMI (0.33 ± 0.24).

Discussion

Heritability estimates

The high average heritability estimates for the growth and carcass traits indicate that these traits can be improved through genetic selection. The heritability estimates obtained are within the ranges reported in the literature (Pereira et al., 2006; Santana et al., 2014; Yokoo et al., 2015; Ceacero et al., 2016; Torres-Vázquez et al., 2018). The heritabilities obtained for growth- and carcass-related traits (e.g., BW and REA) are consistent with those reported for both *Bos taurus taurus* and *Bos taurus indicus* breeds ($h^2 > 0.40$), although the estimated heritability for ADG (0.20 ± 0.07) is lower than those reported for taurine [>0.30 for males and 0.53 for heifers (Berry and Crowley, 2012; Torres-Vázquez et al., 2018; Freetly et al., 2020)] and zebuine breeds [(>0.34 (Barwick et al., 2009; Santana et al., 2014; Ceacero et al., 2016)]; however, they are close to values estimated for tropically adapted breeds [<0.32 for Caracu and Tropical Composite breeds (Pereira et al., 2006; Barwick et al., 2009)].

The observed differences are due to population characteristics [breeds (e.g., Caracu, Nellore), genetic diversity, and selection intensity], statistical models used, sample size, and differences in trait measurement protocols. Furthermore, the capability of tropically adapted animals to adjust their metabolism under different circumstances (improved resilience), and consequently be less affected by the environment, is reflected by the small phenotypic SD found here (Table 2). Additionally, the higher genetic variances reflect the lack of artificial genetic selection in Senepol cattle.

Barwick et al. (2009), studying Brahman and Tropical Composite cattle populations, reported higher additive genetic variances in the composite populations, with a greater contribution of the adapted breeds compared to Brahman. Similar effects could explain the higher heritability estimates observed for growth and carcass traits in Senepol cattle, as the additive genetic variances obtained were higher than those reported in the literature, especially for REA and BF (Barwick et al., 2009; Martínez et al., 2016).

While most studies use data from performance tests applied to males, when females are tested either the population is small ($n <$ 2000) or the tests are performed using a pasture-based diet with an uncontrolled environment, factors that influence the phenotypic variances and SD, especially for feed efficiency traits (Pereira et al., 2006; Del Claro et al., 2012). In our study, although the number of animals included in the analyses was limited, the controlled test environment and the grain-based diet resulted in slightly higher heritabilities than those reported in the literature for females.

A wide range of heritability estimates for ADG has been reported in the literature, ranging from 0.13 to 0.55 (Pereira et al., 2006; Barwick et al., 2009; Marques et al., 2013; Santana et al., 2014; Martínez et al., 2016). According to Pereira et al. (2006), such variation may be due to

Table 5
Genetic correlations and their respective SD (above diagonal) and phenotypic correlations (below diagonal) between feed efficiency traits in Senepol cattle.

Trait[1]	G:F	FCR	RG	RIG	RFI
G:F	–	−0.95 ± 0.06	0.98 ± 0.02	0.63 ± 0.27	0.00 ± 0.38
FCR	−0.91	–	−0.95 ± 0.07	−0.65 ± 0.36	0.05 ± 0.42
RG	0.65	−0.55	–	0.66 ± 0.17	−0.04 ± 0.33
RIG	0.57	−0.47	0.81	–	−0.79 ± 0.20
RFI	−0.31	0.24	−0.35	−0.82	–

[1] G:F = gain to feed, FCR = feed conversion ratio, RG = residual BW gain, RIG = residual intake and BW gain, RFI = residual feed intake.

environmental factors (e.g., production systems). For instance, the heritability estimate observed in this study is higher than those reported for populations that received feed supplementation in addition to pasture, due to a better-controlled environment.

Our findings suggest that RG, RIG, and RFI seem to be better indicators of feed efficiency to be used for genetic selection purposes, while a greater environmental influence is observed for G:F and FCR had a lower heritability estimates. Thus, G:F and FCR might not be the best traits for genetic selection that aimed at improving feed efficiency. The RFI heritability observed here agrees with the literature data ranging from 0.14 to 0.66. In two meta-analyses, Berry and Crowley (2013) estimated a mean heritability for RFI of 0.33 ± 0.013 and Del Claro et al. (2012) reported a weighted average of 0.25 ± 0.01.

Some researchers have proposed the inclusion of ultrasound measurements in the estimate of DMI and thus of RFI (Berry and Crowley, 2013). However, this inclusion may have little or no impact on the heritability estimation of RFI, further explaining only 0–7% of the variation in DMI (Berry and Crowley, 2013; Ceacero et al., 2016). Thus, the estimation of RFI and DMI without considering carcass traits in this study possibly had no negative impact on their heritabilities.

Moreover, a comprehensive meta-analysis conducted by Del Claro et al. (2012) indicated that approximately 67% of RFI heritability estimates were affected by sex, country, and breed. The effect of sex could not be assessed in our study because only female records were included in the analyses. Although our data are from a performance test and grain-based diet, the heritability estimated for RFI is closer to the pooled heritability of 0.12 ± 0.06 reported by Del Claro et al. (2012) for females than to the 0.34 ± 0.06 reported for males. Females are physiologically less feed efficient showing higher lipogenesis than males (Mckenna et al., 2018). This might partially explain the slightly lower heritability estimates observed for feed efficiency traits in the present study compared to the literature (Crews Jr, 2005; Berry and Crowley, 2012 and 2013; Santana et al., 2012; Ceacero et al., 2016).

The heritabilities for G:F (0.08) and FCR (0.09) were low and within the lower bound of estimates reported in the literature (0.06 to 0.46), but below the average of 0.23 for FCR (Berry and Crowley, 2013;Santana et al., 2014 ; Ceacero et al., 2016). The low to moderate estimates observed in this study might be explained by the effects of diet quality on the expression of the genetic potential of the animals. The heritability results indicate that feed efficiency traits estimated by regressions using RG, RIG, and RFI are more heritable than those estimated using ratios such as G:F and FCR, although they are all directly or indirectly associated with the estimates of ADG and DMI.

Genetic correlations

The SD of the genetic correlations obtained in our study were mostly high, possibly due to the limited number of animals. Hence, the results should be interpreted with caution. In general, direct selection based on the feed efficiency indicators evaluated is expected to result in a decrease in both feed intake and ADG. However, REA might deteriorate, with a consequent effect on the carcass value of animals ($r_g = 0.34 \pm 0.28$ for G:F, -0.23 ± 0.27 for RIG and 0.19 ± 0.24 for RFI). Residual weight gain is a trait that prioritizes animal weight gain. It seems that direct selection for RG will not affect gains in carcass muscularity compared to the other indicators ($r_g = -0.08 \pm 0.24$), but may increase DMI ($r_g = 0.33 \pm 0.28$). Conversely, selection for RFI will result in a decrease in DMI ($r_g = 0.71 \pm 0.13$), but with a significant reduction in ADG ($r_g = 0.46 \pm 0.23$), which may not be advantageous at the end of the production stage. Similar but lower correlations between RFI and ADG were reported for Nellore [$r_g = 0.33 \pm 0.06$ (Ceacero et al., 2016)] and Angus breeds [$r_g = 0.34 \pm 0.14$ (Torres-Vázquez et al., 2018)], while the genetic correlation with DMI, is within the range reported in the literature [$r_g = 0.68$ to0.95 (Santana et al., 2014; Ceacero et al., 2016; Torres-Vázquez et al., 2018)].

The RIG as proposed by Berry and Crowley (2012) has a lower effect on ADG and favorable effect on DMI ($r_g = 0.20 \pm 0.27$ and -0.34 ± 0.24, respectively) compared to other efficiency traits in which genetic selection for RIG might result in weight gain associated with reduced DMI. Similar results have been reported for Nellore cattle (Santana et al., 2014; Ceacero et al., 2016). The effect of feed efficiency indicators on carcass traits reflected the decrease in feed intake, as muscle deposition is energetically more demanding than the depositions of adipose tissue (Herd et al., 2004). Thus, when reducing DMI, the body adapts by decreasing protein turnover and increased calpastatin activity, which inhibits protein degradation. This was demonstrated by the unfavorable genetic correlations between indicators of feed efficiency (e.g., G:F, FCR, RIG, and RFI) and REA. The reduction in carcass fat deposition in more feed efficient animals widely reported in the literature (Crews Jr, 2005; Berry and Crowley, 2013; Ceacero et al., 2016) does not appear to occur in Senepol cattle according to our results ($r_g = -0.23 \pm 0.21$ for RFI and BF). The reduction in the total amount of ingested metabolizable energy, it is expected that subcutaneous fat deposition, with the most significant proportion of energy being used for tissue deposition (Basarab et al., 2003).

The lower carcass fat deposition in more feed-efficient animals as reported in the literature (Santana et al., 2012 and 2014; Ceacero et al., 2016) is a mechanism to improve the utilization and to reduce the requirement of ingestible metabolizable energy. Sun et al. (2019) reported the differential regulation of gene expression linked to muscle, adipose tissue, and rumen tissue deposition in more feed-efficient animals, as well as the same mechanisms in the latter two at the epithelial level. This may improve nutrient absorption since the rumen is responsible for the absorption of volatile fatty acids, a secondary and metabolizable energy source in ruminants (Sun et al., 2019). However, in this work, the reduction in the fat deposition was observed only intramuscularly, as represented by IMF, with little or no effect on BF. Even though the animals used had an average age of 16.66 ± 1.96 months, which is considered by Guimarães et al. (2017) an early age for the expression of subcutaneous fat deposition in Senepol males, the females studied here had an average BF of 6.85 ± 2.92 mm, conflicting with the author's 3.31 ± 0.37 at a similar age.

Within this context, the effect of RFI on BF cannot be attributed to the age of the animals at evaluation since they already expressed considerable subcutaneous fat. In this case, the results might be explained by the fact that this study was solely based on female weight gain tests, in contrast to most studies that evaluate the feed efficiency in feedlot males. Sex-specific differential expression of genes related to lipid metabolism has been reported (Mckenna et al., 2018). Males have higher fatty acid oxidation and produce alternative substrates for better utilization of the ingested energy, while feed efficient females tend to reduce the breakdown of fatty acids to promote energy storage due to the higher concentration of metabolites indicating a state of malnutrition. These results may explain not only the low genetic influence of feed efficiency traits on BF but also the favorable correlation of RFI with IMF because the reduced DMI for lower-RFI animals can lead to a malnutrition condition, hence higher energy storage in efficient females.

Based on our findings, the inclusion of RIG in selection indexes for Senepol heifers is recommended with due care. This trait can be included concomitantly or as an alternative to RFI in selection programs, associated with growth and carcass traits to prevent carcass losses. Feed efficiency traits themselves are not recommended for a single trait-based selection as they may promote losses on growth rates and carcass quality.

Conclusion

Residual intake and body weight gain is the most suitable indicator to genetically improve feed efficiency in Senepol cattle, because of its moderate heritability is expected to reduce feed intake concomitantly with an increase in weight gain. In addition, RIG has a similar effect on carcass traits when compared to other feed efficiency indicators and may be included in selection indexes of Senepol breeding programs.

Ethics approval

The study was conducted in accordance with animal welfare guidelines according to Brazilian Law on Animal Handling. All animal procedures were approved by the Ethics and Animal Handling Committee of the Embrapa Beef Cattle, Campo Grande, MS, Brazil (Protocol Number 007/2016).

Data and model availability statement

The software used are available for download and use for research purposes at the website of the Animal Breeding and Genetics Group from 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 Embrapa Geneplus Beef Cattle Breeding Program).

Author ORCIDs

R.C. Gomes - ORCID: 0000-0001-8410-7216; L.F. Brito - ORCID: 0000-0002-5819-0922; M.M.M. Laureano - ORCID: 0000-0002-1702-6413; C.V. Araújo - ORCID: 0000-0001-9378-7348.

Author contributions

Larissa Carolina Novo: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft preparation, Writing—review & editing, Funding acquisition; Andrea Gondo: Formal analysis, Investigation, Methodology, Validation, Writing—review & editing; Rodrigo da Costa Gomes: Formal analysis, Methodology, Investigation, Writing—review & editing; José Antônio Fernandes Junior: Conceptualization, Resources, Data curation, Investigation, Project administration; Marcelo Neves Ribas: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Data curation, Project administration; Writing—review & editing; Luiz Fernando Brito: Conceptualization, Visualization, Writing—original draft preparation, Writing—review & editing; Monyka Marianna Massolini Laureano: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft preparation, Writing—review & editing; Cláudio Vieira Araújo: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft preparation, Writing—review & editing; Gilberto Romeiro de Oliveira Menezes: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing—original draft preparation, Writing—review & editing, Supervision, Project administration.

Declaration of interest

None.

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