Evidence of negative relationship between female fertility and feed efficiency in Nellore cattle^{1,2}

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ABSTRACT: The objective of this study was to evaluate phenotypic and genetic relationships between fertility traits and feed efficiency in male and female Nellore cattle. Data from 320 females born between 2004 and 2011 were used for phenotypic evaluation. These animals were evaluated for postweaning residual feed intake (RFI) and classified as negative (RFI < 0, mean = -0.294 ± 0.017 kg DM/d) or positive RFI (RFI > 0, mean = 0.305 ± 0.0189 kg DM/d). Of these, 118 prepuberal heifers were submitted to ultrasonography of the uterus and ovaries for monitoring the presence (or absence) of a corpus luteum and for the measurement of endometrial thickness. The following fertility traits were evaluated in all females: age at first calving, days to calving, first calving interval, calving success, stayability, and longevity. The variance components were estimated by the average information restricted maximum likelihood method under an animal model in 5-trait analysis of backfat and rump fat thickness, scrotal circumference, days to calving, and RFI. The total number of animals with records was 6,718, including 927 males with records of scrotal circumference and RFI and 264 females with records of days to

calving and RFI. Negative RFI females consumed 12.5% less DM daily than positive RFI females and had a lower rump fat thickness when evaluated postweaning. Among the fertility traits studied, only first calving interval differed ($P = 0.0858$) between RFI classes, with the interval of negative RFI females being 45 d shorter than that of positive RFI animals. The heritability estimates were 0.29, 0.34, 0.50, 0.12, and 0.16 for backfat and rump fat thickness, scrotal circumference, days to calving, and RFI, respectively. The genetic correlations between RFI and the other traits studied were unfavorable for selection and were of moderate magnitude with backfat thickness, rump fat thickness, and days to calving (0.53, 0.37, and -0.49 , respectively) and close to zero with scrotal circumference (0.07). Scrotal circumference (0.17 and 0.15) and days to calving (-0.10 and -0.22) were weakly and favorably correlated with backfat and rump fat thickness. There is evidence of moderate genetic antagonism between female fertility and feed efficiency, but with no evidence of a genetic correlation between male fertility and feed efficiency. There is also evidence of low genetic synergism between fat thickness and fertility.

Key words: beef cattle, days to calving, feed efficiency, genetic parameters, scrotal circumference

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INTRODUCTION

The efficiency of beef cattle production systems depends on the fertility rates of bulls and cows, the growth potential of young animals, and

the feed intake of cows and animals destined for slaughter. The inclusion of feed intake or associated traits as selection criteria in beef cattle breeding programs has major economic and environmental impacts on the production system (Herd and Arthur, 2009). Residual feed intake (RFI) is a feed efficiency measure that has proved to be promising in the identification of animals with lower maintenance requirements. However, the complexity of the metabolic mechanisms of nutrient partitioning (Castro Bulle et al., 2007) and the genetic correlations between traits may result in undesired genetic responses (Grion et al., 2014; Ceacero et al., 2016).

There are evidences of undesirable correlation between fertility and feed efficiency in some species such as mice, pig, and poultry (Pitchford, 2004). More recently, some authors (Arthur et al., 2005; Donoghue et al., 2011; Mu et al., 2016) also provided evidence that selection for RFI may result in negative effects on the fertility of cattle. However, Basarab et al. (2011) and Lawrence et al. (2011) found no differences in reproductive traits or offspring performance between high and low RFI females. Similarly, Kowalski et al. (2017) observed no relationship between RFI and testicular measurements of growing bulls. Within this context, the objective of the present study was to evaluate phenotypic and genetic relationships between fertility traits and feed efficiency in male and female Nellore cattle.

MATERIALS AND METHODS

Animals belonging to the Nellore herd of Instituto de Zootecnia, Centro APTA Bovinos de Corte, Sertãozinho, SP, Brazil, were used. The experimental procedures followed animal welfare guidelines and were conducted in accordance with State Law No. 11.977 of the State of São Paulo, Brazil.

Phenotypic Evaluation

The data used refer to 320 Nellore females born between 2004 and 2011, which were evaluated for RFI after weaning in performance tests (age at the beginning and end of the test: 308 ± 45 and 384 ± 47 d). The performance tests consisted of an adaptation period of at least 21 d and collection of individual intake data for 77 ± 11 d.

The females were housed in individual pens. The DMI of each animal was obtained as the difference between the individual amount of feed offered and daily leftovers. Samples of leftovers corresponding

to each interval of 28 d were prepared for each animal, predried by forced ventilation at 55 °C for 72 h, ground in a mill to pass through a 2-mm sieve, and dried for 8 h at 105 °C for the determination of DM. The females were weighed every 14 d after fasting for 12 h (2005 and 2006) and every 28 d from 2009 to 2011 after fasting for 12 h. Therefore, each female was weighed at least 4 times.

The ADG of each animal was estimated by the linear regression coefficient of weights as a function of days in test: $y = \alpha + \beta \times \text{DIT} + \varepsilon$, where y = weight of the animal; α = intercept of the regression equation representing the initial weight; β = linear regression coefficient representing the average daily weight gain; DIT = days in test, and ε = random error. The metabolic midtest weight was calculated as follows: $\text{MW} = [\alpha + \beta \times (\text{DIT}/2)]^{0.75}$, where MW = metabolic midtest weight and α , β , and DIT as described earlier.

For each test, RFI was calculated as the residue of the regression equation of DMI on ADG and metabolic midtest weight: $\text{DMI} = \beta_0 + \beta_W \times \text{MW} + \beta_G \times \text{ADG} + \varepsilon$, where β_0 = intercept of the regression; β_W = linear regression coefficient of MW; MW = metabolic midtest weight; β_G = linear regression coefficient of ADG; and ε = residue of the equation, that is, RFI. The females were classified as negative RFI (<0 , high efficiency) or positive RFI (>0 , low efficiency).

The carcass traits (longissimus muscle area and backfat and rump fat thickness) were measured at the end of the performance test by ultrasound using an 18-cm linear probe (3.5-MHz transducer; Aquila System; Pie Medical Equipment B.V., Maastricht, The Netherlands), as described by Pinheiro et al. (2012).

Prepubertal heifers. Of the 320 females evaluated, 118 prepubertal heifers were submitted to ultrasonography (6.0-MHz transducer; Aquila System; Pie Medical Equipment B.V., Maastricht, The Netherlands) of the uterus and ovaries for monitoring the presence (or absence) of a corpus luteum and for the measurement of endometrial thickness. At least 7 scans per heifer were obtained at an interval of about 21 d, from 329 to 790 d of age.

Regarding the presence of the first corpus luteum indicating first ovulation, value 1 was assigned to heifers that had a corpus luteum and value 0 to those that did not. For heifers that had a corpus luteum, age and weight were considered in the analyses. Endometrial thickness was measured by placing the probe to obtain longitudinal images. Three images per heifer were saved and the image

showing the best quality of visualization and position was used for the measurement.

Females. Females evaluated for RFI were exposed at a mean age of 23 mo, except for those born in 2005 that were exposed at a mean age of 13.8 mo. The natural mating period lasted 90 d, with single-sire (2 or 3 yr old) breeding groups containing 20 to 30 females/group, including heifers and multiparous cows of the same herd. Further details about the reproductive management adopted in the herd have been described by [Mercadante et al. \(2002\)](#). The postcalving traits studied were age at first calving, first calving interval, days to calving (considering all breeding seasons in which the female participated), calving success, stayability, and longevity.

First calving interval was calculated as the difference between the second and the first calving date, and females that did not calve were not included. Days to calving were obtained for all females that calved as the difference between the calving date and the date of the beginning of that breeding season. Records resulting from abortions and those of cows submitted to fixed-time artificial insemination were discarded. In the case of cows that calved after the beginning of the breeding season, the date of the beginning of the breeding season was adjusted by adding 4 d to the calving date and cows that did not calve were penalized by adding 21 to the largest days to calving value within the breeding year and herd ([Mercadante et al., 2002, 2005](#)).

The calving success records were obtained directly from the calving data and were equal to 1 (calved) or 0 (did not calve). Cases of abortion were considered 0 and stillbirths and calvings outside the birth season as 1 because calving success is independent of the calving date ([Mercadante et al., 2005](#)).

For stayability, value 1 was assigned to females that participated in at least 4 breeding seasons and had at least 3 calves and value 0 to those that did not meet either requisite. Stayability was calculated only for females born until 2008 because animals born in subsequent years did not have the same opportunity to calve and to remain sufficient time in the herd.

Longevity was calculated by subtracting the date of the last record of the cow in the breeding season files, which could be the date of the beginning of the breeding season, date of the end of the breeding season, calving date or weaning date, from the date of birth of the cow.

Statistical analysis. The data were analyzed with the MIXED procedure of the SAS program (SAS Institute, Inc., Cary, NC) for traits with a normal distribution (RFI, DMI, endometrial thickness, age at corpus luteum, weight at corpus luteum, age at first calving, first calving interval, days to calving, and longevity) or the GENMOD procedure of SAS for traits with a binomial distribution (presence of corpus luteum, calving success, and stayability) using a PROBIT link function.

The models included the fixed effects of RFI class and year of birth for all traits. For the ultrasound-measured carcass traits, the effect of animal age was included in the model as covariate (linear effect). For endometrial thickness, the fixed effect of the presence of corpus luteum (0 or 1) and interactions was added. For first calving interval, the year of first calving instead of year of birth was included in the model, and the fixed effect of calf sex and age at first calving as covariate were added. For days to calving and calving success, the model included the fixed effects of presence of calf in the previous season (0 or 1), in addition to age of cow at the beginning of the breeding season as a covariate (linear and quadratic effects).

Genetic Evaluation

The database from the Nellore herd of Centro APTA Bovinos de Corte, Sertãozinho, São Paulo, Brazil (21°10'S; 47°57'W) was used. Phenotypic and genetic correlations between the fertility traits and RFI were calculated. The variance components were estimated by the REML method using the AIREMLF90 program ([Misztal et al., 2014](#)) in a 5-trait analysis of backfat and rump fat thickness, scrotal circumference, days to calving, and RFI. As an alternative of SE, the SD of phenotypic and genetic parameters was calculated by repeated sampling of parameters estimates from their asymptotic multivariate normal distribution, as presented by [Houle and Meyer \(2015\)](#). Records of 6,718 animals, with at least one record for one of the 5 traits, were used, including 927 males with records of scrotal circumference and RFI and 264 females with records of days to calving and RFI. The relationship matrix contained 6,858 animals.

Backfat and rump fat thickness was obtained in males and females born from 1996 to 2015, at 375 ± 26 d of age in males and at 577 ± 38 d in females. Scrotal circumference was measured at 372 ± 26 d of age in animals born from 1990 to 2016. Days to calving was obtained in females submitted to single-sire

natural mating for 90 d from 1978 to 2015. Females that did not calve were penalized by adding 21 to the largest days to calving value within year of breeding and herd as described by Mercadante et al. (2002). The RFI of males and females was obtained in 26 performance tests (individual pens or paddocks with automatic feeders) lasting 85 ± 16 d after adaptation for at least 21 d. The animals born from 2004 to 2016 started the test at 285 ± 35 d of age with a body weight of 242 ± 48 kg. The mean DMI, ADG, and metabolic midtest weight obtained during the test were 7.20 ± 1.53 kg DM/d, 1.04 ± 0.24 kg/d, and 69.4 ± 9.81 kg, respectively. Details on obtaining RFI records have been described by Grion et al. (2014) and Ceacero et al. (2016).

For backfat thickness, rump fat thickness, and scrotal circumference, the model included the direct additive genetic effect of the animal and residual effect as random effects, the fixed effects of contemporary group (year $\times$ herd $\times$ sex; $i = 1, \dots, 80$ for fat thickness and year $\times$ herd; $i = 1, \dots, 81$ for scrotal circumference) and month of birth ($i = 1, \dots, 4$), and the

covariates age of dam (linear and quadratic effects) and linear effect of age of animal at measurement. For days to calving, the model included the additive genetic effect of the animal, permanent environmental effect of the animal and residual effect as random effects, the fixed effects of contemporary group (year of breeding $\times$ herd; $i = 1, \dots, 110$) and presence (or absence) of calf in the previous season ($i = 0$ or 1), and the covariate age of female at the beginning of breeding (5.61 ± 3.23 yr, linear and quadratic effects). For RFI, the model included the direct additive genetic effect of the animal and residual effect as random effects, the fixed effects of contemporary group (year of birth $\times$ facility; $i = 1, \dots, 26$) and month of birth ($i = 1, \dots, 3$), and the covariates age of cow (linear and quadratic effects) and age of animal at the beginning of the test (linear effect).

RESULTS

The total range detected was 2.47 kg/d for RFI of females and 7.16 kg/d for DMI (Table 1),

Table 1. Descriptive statistics of the variables used for the phenotypic and genetic evaluations

Trait	n^1	CG ²	Mean	SD	Minimum	Maximum
Postweaning performance test						
RFI, ³ kg DM/d	320	6	-0.024	0.372	-1.18	1.29
Intake, kg DM/d	320	6	6.39	1.09	2.15	9.31
Average daily gain, kg/d	320	6	0.873	0.192	0.176	1.355
Final weight on test, kg/d	320	6	283	53	133	414
Longissimus area, cm ²	315	6	48.1	7.10	30.9	68.8
Backfat thickness, mm	315	6	2.47	1.56	0	9.00
Rump fat thickness, mm	315	6	5.84	2.29	1.5	13.5
Final age on test, d	320	6	381	44	267	503
Phenotypic evaluation						
Presence of corpus luteum, %	118	2	73.7	44.2	0	100
Endometrial thickness, mm	118	2	11.6	1.05	9.0	14.6
Age at corpus luteum, d	87	2	636	104	425	790
Weight at corpus luteum, kg	87	2	381	34	316	463
Age at first calving, d	231	6	1106	157	722	1,524
First calving interval, d	145	7	511	181	320	1,121
Days to calving, ⁴ d	290/894	6	351	40	272	415
Calving success, ⁴ %	320/1,073	6	58.0	49.4	0	100
Stayability, %	163	3	33.1	47.2	0	100
Longevity, yr	320	6	4.76	2.41	1.07	11.2
Genetic evaluation						
Backfat thickness, ⁴ mm	3,090	80	1.77	1.35	0	10.5
Rump fat thickness, ⁴ mm	2,625	66	4.96	2.30	0	19.2
Scrotal circumference, cm	3,206	81	23.0	2.75	14.0	32.5
Days to calving, ⁴ d	2,831/13,446	110	344	36.0	263	428
RFI, kg DM/d	1,301	26	0.00	0.609	-2.37	4.84

¹ n = number of animals.

²CG = contemporary group. Number of CGs.

³RFI = residual feed intake.

⁴Number of animals/number of observations.

demonstrating wide variation in the feed intake of females of the herd. In genetic analysis involving all animals studied, the range in RFI measured was 7.21 kg DM/d.

Eighty-seven (73.7%) of the 118 heifers evaluated by ultrasonography had a corpus luteum. There was 2-yr variation in age at first calving and in calving interval. If heritable, the large variation suggests potential for genetic improvement. Days to calving is limited by the breeding season, which partially controls its variation. Nevertheless, the range of 143 d detected (including the additional 21 d for females that did not calve) shows the potential use of this trait for the evaluation of female reproductive efficiency.

Negative RFI females consumed 12.5% less feed daily than positive RFI animals ($P < 0.01$) when evaluated postweaning. More efficient females (negative RFI) also had greater rump fat thickness than less efficient females (positive RFI). No significant differences in the reproductive tract measures were observed between RFI classes (Table 2).

Among the reproductive traits evaluated in prepubertal heifers and subsequently in all females (Table 2), only first calving interval differed between RFI classes ($P = 0.0858$). The interval was 45 d shorter in negative RFI females compared with positive RFI females.

The heritability estimates for backfat and rump fat thickness were of medium to high magnitude (Table 3). The heritability for scrotal circumference was also high. On the other hand, the heritabilities for days to calving and RFI were of moderate to low magnitude. The genetic correlations between RFI and the other traits studied were unfavorable for selection and were of moderate magnitude with backfat thickness, rump fat thickness, and days to calving (0.53, 0.37, and -0.49 , respectively) and close to zero with scrotal circumference (0.07). Scrotal circumference (0.17 and 0.15) and days to calving (-0.10 and -0.22) were weakly and favorably correlated with backfat and rump fat thickness. All phenotypic correlations were less than 0.10, except for the correlation between fat thicknesses (0.60) and between these traits and scrotal circumference (0.22 and 0.27). The repeatability estimate of days to calving was 0.17 ± 0.002 .

DISCUSSION

Reproductive and feed efficiency traits are the main traits of economic importance for production systems because the cow herd consumes most of the feed resources of the system (Pitchford, 2004). The combined study of these traits is recommended because the genetic improvement achieved by selection for higher feed efficiency may be annulled by

Table 2. Fertility traits of Nellore heifers classified as negative and positive residual feed intake

Trait	<i>n</i> ¹	Negative RFI ²	<i>n</i>	Positive RFI	<i>P</i>
Postweaning performance test					
RFI, kg DM/d	175	-0.294 ± 0.017	145	0.305 ± 0.0189	<0.0001
Feed intake, kg DM/d	175	6.02 ± 0.067	145	6.88 ± 0.074	<0.0001
Average daily gain, kg/d	175	0.862 ± 0.012	145	0.870 ± 0.013	0.6288
Final weight on test, kg	175	286 ± 3.43	145	283 ± 3.65	0.6283
Longissimus area, cm ²	166	48.4 ± 0.425	149	47.7 ± 0.448	0.2057
Backfat thickness, mm	166	2.46 ± 0.0851	149	2.45 ± 0.090	0.9478
Rump fat thickness, mm	166	5.60 ± 0.133	149	6.07 ± 0.141	0.0159
Final age on test, d	175	382 ± 3.11	145	382 ± 3.31	0.9067
Phenotypic evaluation					
Presence of corpus luteum, %	59	74.6 ± 17.8	59	72.9 ± 17.5	0.8315
Endometrial thickness, mm	59	11.6 ± 0.148	59	11.5 ± 0.144	0.5787
Age at corpus luteum, d	44	646 ± 15.4	43	629 ± 15.6	0.4458
Weight at corpus luteum, kg	44	382 ± 5.16	43	379 ± 5.21	0.6130
Age at first calving, d	130	$1,138 \pm 8.35$	101	$1,135 \pm 9.76$	0.8123
First calving interval, d	71	463 ± 21.9	74	508 ± 21.5	0.0858
Days to calving, d	162	350 ± 1.89	128	350 ± 2.09	0.8902
Calving success, %	175	56.8 ± 5.68	145	57.9 ± 6.05	0.7332
Stayability, %	93	32.4 ± 13.6	70	32.7 ± 16.0	0.9875
Longevity, yr	175	4.71 ± 0.165	145	4.82 ± 0.182	0.6600

¹*n* = number of animals.

²RFI = residual feed intake.

Table 3. Estimates of heritability (diagonal), phenotypic correlation (below the diagonal), and genetic correlation (above the diagonal) and associated SD (in parentheses) obtained for backfat and rump fat thickness, scrotal circumference, days to calving, and residual feed intake

Trait ¹	BF	RF	SC	DC	RFI
BF	0.29 (0.004)	0.80 (0.005)	0.17 (0.01)	-0.10 (0.01)	0.53 (0.009)
RF	0.60 (0.006)	0.34 (0.043)	0.15 (0.012)	-0.22 (0.011)	0.37 (0.011)
SC	0.22 (0.006)	0.27 (0.005)	0.50 (0.005)	-0.06 (0.012)	0.07 (0.012)
DC	-0.06 (0.002)	-0.08 (0.004)	—	0.12 (0.002)	-0.49 (0.009)
RFI	0.05 (0.008)	0.03 (0.004)	-0.02 (0.006)	0.05 (0.009)	0.16 (0.014)

¹BF = backfat thickness; RF = rump fat thickness; SC = scrotal circumference; DC = days to calving; RFI = residual feed intake.

undesirable correlated responses in reproductive traits.

Phenotypic Evaluation

The coefficient of variation was 5.8% for RFI in females, expressed in relation to mean DMI. This variation agrees with the 4.46% obtained in evaluations of growing females (Basarab et al., 2011), but was lower than the variation observed for growing males (7.13% and 8.76%) (Hafla et al., 2012; Fontoura et al., 2016) in studies investigating the phenotypic relationship between feed efficiency and fertility.

The detection of the corpus luteum in part of the heifers submitted to ultrasonographic evaluation of the reproductive tract provided evidence of ovulation and the onset of puberty. The mean age at puberty (636 ± 104 d) in 73.7% of the heifers evaluated is considered high when compared with *Bos taurus* females. Donoghue et al. (2011) detected the presence of a corpus luteum (by ultrasonography of the reproductive tract) at 436 d of age in 83% of Angus heifers, whereas Basarab et al. (2011) observed that 72.5% of crossbred *B. taurus* heifers reached puberty (based on serum progesterone concentration) at 388 d of age. The age at first calving of $1,106 \pm 157$ d was similar to that reported by Terakado et al. (2015) for a large database of Nellore females. However, the rate of calving success (58%) was lower than the 75% reported by Mercadante et al. (2003), who studied previous years of the herds analyzed in the present study. This result is probably because of the attempt to maintain females previously evaluated for RFI in the herd. The pregnancy rate was also lower than the 73% reported by Terakado et al. (2015).

Two RFI classes of females, most efficient (negative RFI) and least efficient (positive RFI), were compared. Despite lower DMI and lower rump fat thickness, most and least efficient heifers did not differ in terms of the presence of a corpus luteum,

endometrial thickness, or age and weight at corpus luteum. In addition, age at first calving was also similar in most and least efficient females, that is, there seems to be no effect of feed efficiency on the growth or maturation of the uterus and ovaries. However, Donoghue et al. (2011) observed greater rump fat thickness in cycling females compared with noncycling females at yearling and at 1.5 yr of age. Furthermore, more efficient females (negative RFI) almost always had lower rump fat thickness (Arthur et al., 2005; Donoghue et al., 2011; Jones et al., 2018; Laurence et al., 2016). In contrast to the present study, Shaffer et al. (2011) reported that *B. taurus* heifers classified as positive RFI reached puberty 13 d earlier than those classified as negative RFI, but there was no interference with pregnancy or calving rates in the first breeding. Donoghue et al. (2011) showed that Angus heifers selected for low RFI calved later during the birth season than heifers selected for high RFI, but this delay had no impact on conception or birth rates in the following breeding season. Basarab et al. (2011) were unable to identify differences among heifers classified based on classical RFI (regression of DMI on ADG and metabolic weight), but observed that more efficient heifers (classified based on classical RFI including fat thickness) were older and heavier at puberty than less efficient heifers. Taken together, these findings point to a phenotypic relationship between feed efficiency, subcutaneous fat thickness, and age at puberty in heifers.

In the present study, the interval between the first and second calving tended to be shorter in the most efficient females (negative RFI). Donoghue et al. (2011) observed the opposite trend, that is, negative RFI females delayed the date of conception in the first breeding season, which resulted in an advanced calving date that was maintained in the subsequent calving. However, Jones et al. (2018) found no differences in pregnancy rates in the first breeding between heifers genetically divergent for RFI (obtained based on the predicted breeding

value of the parent) 9 wk or 6 wk after mating. Laurence et al. (2016) also observed no difference in days to calving in the second breeding.

With respect to the fertility traits that evaluate the whole period that females remain in the herd including all records of days to calving and calving success, a similar performance of most and least efficient females was observed for stayability (with 1 being attributed to females that participated in at least 4 breeding seasons and calved at least 3 calves) and longevity. There are relatively few reports in the literature that investigated the reproductive performance of most and least efficient female cattle and all of them were conducted on *B. taurus*. One of the first results were reported by Arthur et al. (2005), who evaluated Angus females from 2 selection lines divergent for RFI (difference in the estimated breeding value of 0.8 kg DM/d) in the first 3 breeding seasons. The authors found no difference in pregnancy, calving or weaning rates, but negative RFI (most efficient) females calved 5 d later during the breeding season than positive RFI females ($P = 0.07$). Basarab et al. (2007) classified cows according to the RFI of their offspring and observed results similar to those reported by Arthur et al. (2005) regarding pregnancy, calving, and weaning rates and the delay of 5 to 6 d in days to calving of cows whose offspring were more efficient.

In contrast to the present study in which negative RFI *Bos indicus* females had a shorter interval between the first and second calving, other studies demonstrated the same or a slightly delayed performance (especially in the first calving) of negative RFI *B. taurus* females compared with positive RFI animals, apparently without a negative effect on lifetime performance. There are certain inconsistencies in the results published up to now, probably due to the difficulty of evaluating fertility traits in a large number of beef cows tested for RFI in similar environments and management conditions.

Genetic Evaluation

The RFI values observed within the breed and contemporary animals shows the wide variation in the feed intake of animals (males and females), a fact justifying feed efficiency studies to generate technologies that could significantly reduce the amount of raw materials necessary for beef cattle production systems and consequently the environmental impacts of the activity.

The heritability estimates are consistent with the values reported in the literature for subcutaneous

fat thickness of both *B. taurus* (Schenkel et al., 2004; Pires et al., 2017) and *B. indicus* (Santana et al., 2014), as well as for scrotal circumference (Schenkel et al., 2004; Silva et al., 2013; Pires et al., 2017). However, the heritability for days to calving obtained in the present study was higher than that reported for *B. taurus* (Mu et al., 2016) and *B. indicus* (Forni and Albuquerque, 2005), whereas the heritability for RFI was lower than either *B. taurus* (Mu et al., 2016) or *B. indicus* (Santana et al., 2014). Although the heritabilities estimated using part of the present feed efficient database are high for the traits involved in the calculation of RFI, 0.41 to 0.53 for DMI, ADG, and metabolic mid-test weight (Grion et al., 2014; Ceacero et al., 2016), the estimates obtained for RFI are lower than those reported in the literature (Del Claro et al., 2012).

In cattle, scrotal circumference is an important fertility trait that shows a considerable positive genetic correlation with the reproductive integrity of young bulls and a negative correlation with the percentage of major and minor semen defects (Silva et al., 2013). The genetic correlations between subcutaneous fat thickness and male and female fertility were of low magnitude but consistent in terms of signaling genetic synergism, that is, selection for greater fat thickness could have a tendency to increase the animal's breeding value for greater fertility. Low synergistic genetic correlations between fat thickness and scrotal circumference have also been reported in other studies (Schenkel et al., 2004; Yokoo et al., 2010; Pires et al., 2017). Similarly, low synergistic genetic correlations were found between fat thickness (or body condition score) and age at first calving (Caetano et al., 2013) or days to calving (Mercadante et al., 2006; Laurence et al., 2016). These results confirm the evidence of phenotypic relationships between higher subcutaneous fat deposition and greater female fertility discussed earlier.

The genetic correlation between the male and female fertility traits evaluated in this study was close to zero (-0.06) and similar to the correlation (-0.10) estimated by Forni and Albuquerque (2005). However, stronger correlations have been reported between scrotal circumference and age at first calving (-0.71 to -0.42) and between scrotal circumference and heifer pregnancy at 14 mo of age (0.43) (Terakado et al., 2015; Pires et al., 2017), confirming that scrotal circumference is a proxy of sexual precocity in cattle. Forni and Albuquerque (2005) found a high genetic correlation (0.76) between days to calving and age at first calving, suggesting that days to calving may also be an indicator of sexual precocity.

The genetic correlations between fat thickness and RFI were of medium to strong intensity and antagonistic, that is, a higher breeding value for fat deposition is correlated with a higher breeding value for feed efficiency (higher RFI or feed conversion rate), as reported in other studies on *B. taurus* (Robinson and Oddy, 2004; Schenkel et al., 2004; Santana et al., 2014). The correlations between fat thickness and RFI of the present study have been reported previously and discussed by Ceacero et al. (2016).

The genetic correlation between scrotal circumference and RFI was close to zero. Arthur et al. (2001) and Schenkel et al. (2004) also reported a low genetic correlation between these 2 traits (-0.03 and 0.15 , respectively). Thus, selection for higher feed efficiency will not cause a genetic change in scrotal circumference. Furthermore, because scrotal circumference is genetically correlated with reproductive integrity and semen quality (Silva et al., 2013), it is possible to infer that selection for more efficient animals would have no deleterious effects on male fertility. However, there are published results that support or refute this hypothesis. In phenotypic evaluations generally performed on young bulls, Hafla et al. (2012) found no association of scrotal circumference or sperm motility with RFI but observed a weak and unfavorable association between sperm morphology and RFI. In the study of Wang et al. (2012), there was a larger number of negative RFI bulls that did not meet the minimum desirable criterion for sperm motility when compared with positive RFI bulls, with no differences in the other traits related to reproductive integrity of bulls. However, Awda et al. (2013) and Fontoura et al. (2016) reported a lower scrotal circumference, in addition to reduced sperm motility and viability, in young bulls with low RFI. In young *B. taurus* of a breed adapted to the tropics, testicular measurements and serum testosterone concentration were similar in most and least efficient animals (Kowalski et al., 2017).

Female fertility, which was genetically evaluated in this study only based on days to calving, showed a medium antagonistic correlation with RFI, that is, a lower breeding value for RFI (high feed efficiency) is correlated with a higher breeding value for days to calving (poor fertility). Although days to calving is apparently not very comprehensive trait in terms of fertility since it is related to the date of conception of the female during the breeding season, the trait also includes all females, that is, those that calved and those that did not, and is therefore similar to pregnancy rate or calving rate.

Data about genetic correlations between female fertility traits and feed efficiency are limited. Crowley et al. (2011) reported antagonistic genetic correlations of medium magnitude between age at first calving and RFI and between age at first calving and feed conversion. Mu et al. (2016) found genetic correlations close to zero of first pregnancy rate, repeated pregnancy rate, number of services per conception, and pregnancy duration with RFI. However, the authors reported an antagonistic genetic correlation of medium magnitude (-0.34) between days to calving and RFI. The authors emphasized that because days to calving showed the highest heritability among the traits studied, the trait could be considered the best predictor of female fertility. Wolcott et al. (2014) also reported a negative genetic correlation (-0.50) between days to calving and RFI in Brahman cattle, but not in tropical composite cattle. These results provide evidence of a low to medium genetic association between female fertility and feed efficiency, despite the limitation that the number of animals evaluated for feed efficiency was small in the cited studies, including the present one.

Taken together, the results of the phenotypic and genetic relationships between fat thickness, female fertility and RFI were somehow consistent with each other and with those reported in the literature. There is evidence that more efficient (negative RFI) animals have lower fat thickness phenotypically and genotypically. Furthermore, literature data and the results of the present genetic evaluation indicate that females with phenotypically and genetically greater fat thickness tend to be more fertile. Evidence of a medium genetic antagonism between female fertility and feed efficiency and of a weak genetic antagonism between male fertility and feed efficiency is still limited. Although the relationship between the 3 traits is not direct, body composition probably plays an important role in the phenotypic and genetic relationship between fertility and feed efficiency in cattle.

In conclusion, the phenotypic and genetic association between fertility and RFI seems to be of low to medium magnitude and unfavorable. It is therefore recommended that feed efficiency and fertility traits be considered simultaneously in the selection index to increase the sustainability of beef cattle production systems.

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