Published January 20, 2015

Impact of selection for residual feed intake on breeding soundness and reproductive performance of bulls on pasture-based multisire mating[1]

Z. Wang,*[2] M. G. Colazo,† J. A. Basarab,‡ L. A. Goonewardene,*† D. J. Ambrose,*† E. Marques,§ G. Plastow,* S. P. Miller,# and S. S. Moore*

*Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton T6G 2C8, Canada; †Alberta Agriculture and Rural Development, Edmonton T6H 5T6, Canadda; ‡Alberta Agriculture and Rural Development, Lacombe Research Centre, Lacombe, Alberta T4L 1W1, Canada; §Beefbooster Inc., Calgary, Alberta T1Y 5E4, Canada; and #Center for Genetic Improvement of Livestock, University of Guelph, Guelph, Ontario N1G 2W1, Canada

ABSTRACT: There is concern in the beef industry that selecting bulls for feed efficiency based on residual feed intake (RFI) may have a negative impact on bull reproductive performance and fertility. Here we investigated the impact of selection of bulls for low RFI on breeding soundness evaluation (BSE), reproductive performance, and fertility of bulls under natural service in multisire mating groups on pasture. Of the 412 RFI-tested bulls available, 98 (23.8%) were culled for performance, type, temperament, or other reasons, and 88 (21.4%) were culled for failing BSE, for an overall cull rate of 45.1%. From among the 314 bulls subjected to BSE, 32 (10.2%), 20 (6.4%), and 36 (11.4%) were culled for poor feet and legs, scrotal circumference, and semen quality, respectively. The BSE traits were not different ($P > 0.10$) between bulls categorized as either inefficient (+RFI) or efficient (–RFI), but the proportion of bulls that failed to meet the 60% minimum sperm motility requirement tended ($P = 0.07$) to be greater in the –RFI group than in the +RFI group (10.2% vs. 4.4%, respectively). In a subpopulation of 115 bulls, individual progressive sperm motility was greater ($P < 0.05$) in +RFI (85%) than –RFI (80%) bulls. A multisire natural mating experiment was conducted during 2 consecutive breeding seasons (2006 to 2007 and 2007 to 2008) using 18 +RFI and 18 –RFI bulls. The overall calving rate (calves born/cows exposed) was 72.9%. Mean number of progeny per sire was significantly greater ($P < 0.01$) in –RFI bulls (18.3) than in +RFI bulls (11.8). Selection for feed efficiency based on RFI appears to have no detrimental impact on reproductive performance and fertility in beef bulls bred in multisire groups on pasture. However, the decreased sperm motility and the greater number of progeny per sire associated with –RFI status need further investigation.

Key words: beef cattle, bull fertility, residual feed intake, selection

J. Anim. Sci. 2012.90:2963–2969
doi:10.2527/jas2011-4521

INTRODUCTION

Feed costs represent approximately one-half of the total cost of production for most classes of livestock, and improvement in feed efficiency is a major consideration in breeding programs (Kennedy et al., 1993). Residual feed intake (**RFI**) is recognized as a robust measure of feed efficiency and is defined as the difference between the actual feed intake (**FI**) of an animal and its expected feed requirements for maintenance and production (Arthur et al., 2001b). Selection for feed efficiency traits has been reported to have a negative impact on reproductive performance and fertility in mice (Nielsen et al., 1997; Rauw et al., 2000; Hughes and Pitchford, 2004), swine (Estany et al., 2002), and poultry (Hagger, 1994). Selecting for feed efficiency has led to a decrease in litter size in mice (Brien et al., 1984; Nielsen et al., 1997) and in pigs (Kerr and Cameron, 1995). This decrease in litter size was explained in mice by differences in ovulation rate (Brien et al., 1984; Nielsen et al., 1997).

[1]The authors acknowledge the financial support of grant 2007F042R from the Alberta Livestock and Meat Agency and Beefbooster Inc., grant rgpin341312-07 from the National Science and Engineering Research Council of Canada, and the participation of Three Cross Cattle Ltd., Airdrie, Alberta, Canada, and Namaka Farms, Strathmore, Alberta, Canada.

[2] Corresponding author: zhiquan@ualberta.ca

Received July 27, 2011.
Accepted March 21, 2012.

However, published reports on the direct impact of RFI on male reproductive performance or fertility are lacking. In bulls, scrotal circumference (**SC**) is an important fertility variable as it has been shown to be highly associated with testes weight, sperm output, semen quality traits, and age of puberty in heifer progeny (Almquist et al., 1976; Brinks et al., 1978; Coulter and Foote, 1979; Gregory et al., 1991). Two previous studies showed no correlation between selection for RFI and SC (Arthur et al., 2001a; Schenkel et al., 2004). In addition, penile extension, SC, semen concentration, sperm motility and abnormalities, and overall breeding soundness were not significantly different among 62 Bonsmara bulls with positive, intermediate, and negative RFI values (Fox et al., 2004). Although these studies have shown no negative relationship between RFI and SC or other breeding soundness traits, there still remains a concern in the beef industry that selecting bulls for –RFI (efficient bulls) will affect bull reproductive performance and fertility (J. Stewart-Smith, Beefbooster, Inc.,Calgary, Alberta, Canada, personal communication). Beef breeders fear that the more efficient bulls might be less active in the multisire mating group and thus have reduced reproductive performance and fertility on pasture. This concern needs to be addressed to ensure that industry benefit accrues through the adoption of RFI-based bull selection. The objective of this study was to assess the impact of selection for low RFI on breeding soundness, reproductive performance, and fertility of bulls under natural service in multisire mating groups on pasture.

MATERIALS AND METHODS

All animals were cared for according to the Canadian Council on Animal Care (1993) guidelines.

All the bulls (n = 412) available for this study were terminal cross (**TX**, a terminal cross paternal line) young bulls of Beefbooster, Inc., which were RFI-tested at the GrowSafe Test Facility (Olds College, Olds, Alberta, Canada) from 2004 to 2008. The RFI test duration was approximately 84 to 87 d each year. The GrowSafe RFI tests were started from November to January in each testing year, and the test protocol and RFI calculations followed those described by Basarab et al. (2003, 2007). The diet consisted of 30.2% barley grain, 52.4% oats grain, 12.3% alfalfa silage, and 5.1% protein and trace mineral supplements (as-fed basis; 71.1% diet DM; 11.08% MJ ME/kg DM diet). All 412 bulls were pooled together to calculate the RFI for each individual animal. As 150 bulls were eventually culled before semen quality exams, the RFI was recalculated for the remaining 262 animals.

A multisire mating study was conducted during 2 consecutive breeding seasons in 2007 (Three Cross Cattle Ltd., Airdrie, Alberta, Canada) and 2008 (Three Cross Cattle Ltd. and Namaka Farms, Strathmore, Alberta, Canada).

Calculation of Growth and Efficiency Traits

The bulls arrived at the GrowSafe RFI test facility approximately 30 to 40 d before the start of the FI and growth test. Bulls were placed into a feedlot pen fitted with 10 GrowSafe System feeding stations (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) for the automatic monitoring of individual animal FI and adjusted to their final test diet over a 28-d adjustment period. The adjustment period was followed by an 84 to 87 d test period. Animals were weighed on 2 consecutive days at the start and end of the test and in between at 14-d intervals. Bull on-test BW, midtest BW, and ADG were calculated by a linear regression of the BW of the animal on day following methods outlined by Basarab et al. (2007). The estimation of maintenance requirements was captured by using midtest BW to the three-quarters power (**BWT$^{0.75}$**; NRC, 1996). It has previously been shown that BWT$^{0.75}$ is proportional to fasting energy expenditure, such that metabolic requirements are scaled with body size. Residual feed intake was obtained as a linear function of standardized DMI (**SDMI**; 10 MJ ME/kg DM) on BW and growth rate as suggested by Basarab et al. (2003) as

$$\text{RFI} = \text{SDMI} - (\beta_0 + \beta_1\text{ADG} + \beta_2\text{MMWT}),$$

where β_1 and β_2 are partial regression coefficients, β_0 is the intercept, and MMWT is the metabolic midtest BW, which is BWT$^{0.75}$.

Breeding Soundness Evaluation

A certified veterinarian performed all breeding soundness evaluation (**BSE**) in the middle of April each year, and weaning BW, preweaning ADG, 365-d BW, 365-d SC, front and hind feet score, temperament score, and semen quality (density, motility, and morphology) were determined. Ninety-eight of the 412 bulls were culled because of light weaning BW, preweaning ADG, 365-d BW, and temperament. Therefore, only 314 of the 412 bulls were subjected to BSE. An additional 52 bulls were culled because of poor SC (<32 cm) or undesirable front and hind feet scores, resulting in only 262 bulls subjected to semen collection and evaluation.

The SC measurements were taken to the nearest 0.5 cm using a scrotal tape and taken at the point of greatest circumference when both testicles were pulled firmly into the bottom of the scrotum (Barth, 2000). Front and hind feet scores were on a scale of 1 to 5, where 1 = ex-

cellent and 5 = poor. Temperament scores were also on a scale of 1 to 5, where 1 = calm and 5 = very aggressive. Semen was collected by electroejaculation from the 262 bulls using standard procedures and then examined for density and individual progressive motility (motility, %) using a light microscope at 400× magnification. Semen density scores were on a scale of 1 to 5, where 1 = excellent and 5 = poor, and motility scores were on a percentage scale. Bulls yielding semen samples with less than 60% motility were culled (Barth, 2000). Semen smears were prepared and stained with Eosin-Nigrosin for sperm morphology evaluation under 1000× magnification, and bulls yielding semen with less than 70% normal sperm were culled (Barth, 2000). No effort was made to further categorize sperm abnormalities into primary vs. secondary abnormalities.

Multisire Mating Trials

The bulls (n = 36) used in the multisire mating trials were selected from the 142 bulls tested for RFI during the years 2006 to 2007 and 2007 to 2008. The experiment was designed with equal numbers (18 each) of +RFI and –RFI bulls in 2 yr, and the criterion for bull selection was to select the 2 extremes of +RFI and –RFI bulls available in the same group of bulls in each test year. There were no differences in age, 365-d BW, ADG, and 365-d SC between the 2 RFI bull groups. The assignment of test bulls and cows by location during the 2 breeding seasons is shown in Table 1. During the first year, the experiment was carried out at Three Cross Cattle Ltd. Sixteen Beefbooster TX yearling bulls with divergent RFI phenotypes (8 +RFI and 8 –RFI) were selected from a larger population of 34 +RFI and 39 –RFI tested bulls. These 16 bulls were assigned to breed 320 cows in 3 pastures, resulting in a cow-to-bull ratio of 20:1. The first and second pasture groups contained 120 cows assigned to 3 +RFI and 3 –RFI bulls each, and the third group contained 80 cows assigned to 2 +RFI and 2 –RFI bulls. These cows calved from April to May of 2008. In the second year, experiments were conducted in the Three Cross Cattle and Namaka Farms herds. Twenty Beefbooster TX yearling bulls with divergent RFI phenotypes (10 +RFI and 10 –RFI) were selected from 35 +RFI and 34 –RFI bulls. Ten (5 +RFI and 5 –RFI) bulls were assigned to 210 cows (cow-to-bull ratio of 21:1) at Three Cross Cattle Ltd., and the remaining 10 (5 +RFI and 5 –RFI) bulls were assigned to 215 cows (cow-to-bull ratio of 21.5:1) at Namaka Farms. Calving occurred from April to May of 2009. The breeding seasons for both years started on the third week of July, and the bulls stayed in their multisire mating groups on pasture for 50 d.

Table 1. Assignment of bulls and cows to the multisire mating experiment in 2 locations

RFI[1] test and breeding year	Location	No. of bulls		No. cows	Bull:cow ratio
		+RFI[1]	–RFI[1]		
2007	Three Cross[2]	8	8	320	1:20.0
2008	Three Cross[2]	5	5	210	1:21.0
2008	Namaka Farms[3]	5	5	215	1:21.5
Total		18	18	745	1:20.7

[1]RFI = residual feed intake.

[2]Three Cross cattle Ltd., Airdrie, AB, Canada.

3Namaka Farms, Strathmore, AB, Canada.

Parentage Test

All test bulls and their calves born from the multisire mating group in the 2 experimental yr (Table 1) were genotyped using the Igenity marker panel (Merial Ltd./Igenity, Duluth, GA) with a total of 233 SNP markers (Tang et al., 2011) at the Bovine Genomics Laboratory at the University of Alberta. The genotypes of calves from each multisire mating group were analyzed and compared against the genotypes of all potential bulls used in that mating group. The paternity of each calf was then assigned on the basis of the comparative genotyping results. The assigned parentage information was used to determine the fertility and mating ability of the +RFI and –RFI test bulls.

Statistical Analysis

The impact of RFI (+RFI and –RFI) on culling in the bulls tested (n = 412) during the years 2004 to 2008 was determined by χ^2 tests using the FREQ procedure (SAS Inst. Inc., Cary, NC). When cell sizes were less than 5 for culling reasons, a Fisher's test was used to compare RFI status. The continuous variables for growth, efficiency, and SC were subjected to ANOVA with the fixed effects of bull RFI status (+RFI and –RFI) and year of test. The GLM procedure of SAS was used to determine the significant fixed effects and obtain least-squares means and SE for all continuous traits. Medians of +RFI and –RFI bulls for the score traits, sperm motility, and morphology were compared by a Kruskal-Wallis test (Kruskal and Wallis, 1952) for nonparametric data using the NPAR-A1WAY procedure of SAS. The number of progeny per sire for the trial bulls was analyzed using the GENMOD procedure of SAS with a model that included fixed effects of bull RFI status and contemporary group [breeding year (2007 and 2008) and herd (Three Cross and Namaka Farms)] and assuming a Poisson distribution. The correlations between RFI of bulls and their growth, feed efficiency, and BSE traits were computed using the correlation procedure of SAS.

Table 2. Descriptive statistics for growth, feed efficiency, and breeding soundness evaluation traits and their phenotypic correlations with residual feed intake (RFI) for all 262 bulls available for semen quality evaluation

Traits	No.	Mean[1] (Median[2])	SD	r_p[3]	*P*-value level
On-test BW, kg	262	338.6	36.19	−0.02	0.69
ADG, kg/d	262	1.7	0.27	0.00	1.00
Feed intake, kg DM/d	262	8.9	1.40	0.53	0.00
FCR[4], kg DM feed/kg gain	262	5.2	1.27	0.35	0.00
Midpoint BW, kg	262	418.6	43.52	0.00	0.98
Metabolic midpoint BW, kg	262	112.6	8.79	0.00	1.00
RFI, kg DM/d	262	0.0	0.82		
Breeding soundness evaluation					
Age, d	262	355.3	17.08	0.01	0.88
365-d BW, kg	262	560.4	40.17	−0.02	0.69
365-d SC,[5] cm	262	36.0	2.44	−0.01	0.82
Front feet score	262	(2.0)	—	0.00	0.96
Hind feet score	262	(2.0)	—	0.03	0.61
Temperament score	262	(2.0)	—	-0.01	0.86
Semen density score	262	(3.0)	—	-0.05	0.38
Normal sperm morphology, %	262	(85.0)	—	0.07	0.21
Sperm motility, %	262	(85.0)	—	0.11	0.05

[1]For continuous traits, both mean and SE for each trait were calculated.

[2]For discontinuous traits, only the medians were calculated.

[3]Phenotypic correlation

[4]Feed conversion ratio and is defined as per kg of body weight gain required for kg of feed intake of dry mater

5The 365-d scrotal circumference (SC, cm) = actual SC + [(365 − age at measurement, in days) × (actual SC/age at measurement, in days)].

RESULTS

Descriptive statistics (means or median scores) for growth, efficiency, and BSE traits, together with the phenotypic correlations of all traits with RFI for all 262 bulls available for semen quality evaluation, are shown in Table 2. Feed intake and feed conversion ratio (**FCR**) were positively correlated with RFI ($P < 0.01$; Table 2). None of the BSE traits, with the exception of sperm motility, were positively correlated with RFI.

The impact of RFI on culling reasons for bulls tested for RFI (n = 412) during the years 2004 to 2008 are shown in Table 3; the reasons for culling did not differ ($P = 1.0$) between the +RFI and –RFI bull groups. Culling reasons for only those RFI bulls (n = 314) subjected to BSE are presented in Table 4. Bulls that failed the BSE for reasons relating to feet and leg problems, SC, and semen quality did not differ ($P \geq 0.13$) between the 2 RFI groups (Table 4). A slightly greater ($P = 0.07$) proportion of –RFI bulls failed to meet the 60% minimum motility requirement compared with +RFI bulls (10.24% vs. 4.44%, respectively).

Table 3. Cull reasons for inefficient (+) and efficient (–) residual feed intake (RFI) beef bull tested during the years 2004 to 2008

	+RFI		–RFI		
Item	No.	Percentage	No.	Percentage	*P*-value
Total bulls tested for RFI	213	51.69	199	48.31	
Culling reasons					
Performance,[1] type, temperament	50	23.47	48	24.12	0.77
Bulls culled for BSE[2]	44	26.99	44	29.14	1.0
Total bulls culled	94	44.13	92	49.50	0.84

[1]Performance includes weaning BW, preweaning ADG, and yearling BW

[2]BSE = breeding soundness evaluation.

The data on progeny per sire for the 36 bulls used in the multisire mating experiment are presented in Table 5. The mean age, adjusted 365-d BW and SC, and median scores for feet, temperament, and semen characteristics at BSE for all bulls tested during the years 2006 to 2007 and 2007 to 2008 are also presented in Table 5. With the exception of decreased number of progeny per sire in the +RFI and decreased sperm motility in –RFI bulls, no differences ($P \geq 0.13$) were observed between +RFI and –RFI bulls in any of the other traits evaluated. Despite the decreased sperm motility, the average progeny per sire was significantly ($P < 0.01$) greater for –RFI bulls (Table 5).

DISCUSSION

With the exception of sperm motility, none of the BSE traits was associated with RFI in the present study.

Table 4. Cull reasons after breeding soundness evaluation (BSE) in inefficient (+) and efficient (–) residual feedintake (RFI) beef bulls tested during the years 2004 to 2008

	+RFI		–RFI		
Item	No.	Percentage	No.	Percentage	*P*-value
Total bulls tested for BSE	163	51.90	151	48.10	
Culling reasons					
BSE: feet and legs	19	11.66	13	8.61	0.13
BSE: scrotal circumference	9	5.52	11	7.28	0.52
BSE: semen quality[1]	16	9.82	20	13.24	0.48
Density[2]	2	1.48	0	0.00	n/a
Morphology[2]	8	5.93	7	5.51	0.71
Motility[2]	6	4.44	13	10.24	0.07
Bulls culled for BSE	44	26.99	44	29.14	1.0

[1]Semen density, morphology, and individual motility were based on Western Canadian Association of Bovine Practitioners guidelines.

[2]Percentages for sperm density, morphology, and motility for +RFI (n = 135) and –RFI (n = 127) bulls were based on 262 bulls that were available for semen evaluation.

Table 5. Comparison of breeding soundness evaluation (BSE) traits for inefficient (+) and efficient (–) residual feed intake (RFI) bulls tested during the years 2006 to 2007 and 2007 to 2008 and number of progeny for those bulls used in the multisire mating experiment

		+RFI			–RFI			
Category	Traits	No.	Mean[1] (Median[2])	SE	No.	Mean[1] (Median[2])	SE	*P*-value
Bulls RFI tested	Age, d	69[3]	343.57	1.22	73[3]	345.27	1.19	0.23
	365-d BW, kg	69	553.87	6.10	73	551.79	5.91	0.98
	ADG, kg/d	69	1.84	0.03	73	1.84	0.03	0.90
	365-d SC[4], cm	69	36.73	0.38	73	36.37	0.37	0.40
	Front feet score	65[3]	(2.00)	—	69[3]	(3.00)	—	0.61
	Hind feet score	65	(2.00)	—	69	(2.00)	—	0.11
	Temperament score	65	(2.00)	—	69	(2.00)	—	0.74
	Semen density score	55[3]	(2.00)	—	60[x]	(3.00)	—	0.29
	Normal sperm morphology, %	55	(87.00)	—	60	(82.00)	—	0.66
	Sperm motility, %	55	(85.00)	—	60	(80.00)	—	0.04
Bulls in mating experiment	No. sire	18	1.24	0.16	18	-1.05	0.13	<0.01
	No. progeny	213	—	—	330	—	—	—
	Avg progeny/sire	11.8	—	2.48	18.3	—	2.47	<0.01
	Age, d	18	347.4	3.12	18	347.0	3.31	0.92
	365-d BW, kg	18	562.9	12.49	18	546.6	13.25	0.38
	ADG, kg/d	18	1.8	0.05	18	1.8	0.06	0.76
	365-d SC, cm	18	37.5	0.61	18	36.6	0.65	0.35

[1]For continuous traits, both mean and SE for each trait were calculated.

[2]For discontinuous traits, only the medians were calculated.

[3]Bulls that did not pass their SC test were not examined for conformation, and those that did not pass conformation were not semen sampled.

[4]Scrotal circumference.

When all 262 bulls subjected to semen evaluation were taken into account, there was a tendency for a greater proportion of –RFI bulls failing to meet the 60% minimum requirement for sperm motility than +RFI bulls. Moreover, when the subset of 115 bulls subjected to semen evaluation during the years 2006 to 2007 and 2007 to 2008 was considered, median sperm motility was greater in +RFI than in –RFI bulls. Therefore, from our results, it may be inferred that a greater proportion of bulls selected for –RFI may fail to meet minimum requirements for sperm motility. Recent work from the University of Guelph also found decreased sperm motility in bulls selected for –RFI (S. P. Miller, personal communication. However, Fox et al. (2004) reported no differences in semen concentration, sperm motility, and abnormalities and overall breeding soundness among 62 Bonsmara bulls with positive, intermediate, and negative RFI values, which are in partial agreement with the present study. It is noteworthy that the percentage of sperm with morphological abnormalities was not different between the 2 RFI groups. In this regard, Barth and Waldner (2002) showed that a vast majority of bulls that have 70% morphologically normal sperm will have >60% sperm motility if the semen is properly handled. It must be recognized that the scoring procedure for motility is somewhat subjective and can be affected by many factors, such as temperature, time, concentration, contamination, and method of collection (Barth, 2000; Agdex, 2002). Hence, sperm motility should not be used as a sole measure of bull fertility (Agdex, 2002). Barth and Waldner (2002) reported that an individual motility of 70.2% was observed in bulls with above-average SC. They considered the quality of the semen to be questionable when the individual motility was between 40% and 59% and the proportion of morphologically normal sperm was between 59% and 69%. In the present study, we followed the Western Canadian Association of Bovine Practitioners BSE guidelines (Barth, 2000); therefore, 60% and 70% minimum requirements were set for motility and morphology, respectively. Furthermore, there is little emphasis placed on primary vs. secondary sperm abnormalities in this system of evaluation. Although it appears in this study the decreased motility score in –RFI compared with +RFI bulls had no impact on fertility, the relatively greater proportion of –RFI bulls failing to meet the 60% motility requirement chosen in the present study needs further investigation. It should be noted that in this study animals were culled for different reasons because of management protocols, after which they were not available for subsequent analysis of several BSE traits.

Despite decreased sperm motility in –RFI bulls and a greater proportion of –RFI bulls failing to meet the minimum motility requirement, the mean number of

progeny per bull was significantly greater in the –RFI group, suggesting that selection for –RFI may have a positive effect on reproductive performance and bull fertility. The reason for the result is uncertain but may be related to –RFI bulls having more stored energy reserves because of reduced maintenance requirements and feeding activity, thus having more energy reserves for breeding activity. In a recent study, Durunna et al (2011) reported that feeding event behaviors (feeding duration, head down time, and feeding frequency) were decreased in efficient bulls during GrowSafe testing periods, and this may suggest that the efficient bulls might also have more time available for breeding. However, whether these feeding event behaviors observed in the GrowSafe system will translate to less time grazing on pasture and more time for breeding remains unknown.

It must be noted, however, that 2 +RFI bulls, 1 at each farm, produced no progeny during the trial. Both bulls had passed the BSE and semen quality exams. When these 2 bulls were removed from the analysis the number of progeny per sire for the +RFI was 13.3 ± 2.6 and for the –RFI was 18.3 ± 2.4, and this difference was not significant.

Estimates of heritability for SC, motility, and total sperm abnormalities as reported by Garmyn et al. (2011) are 0.46, 0.05, and 0.25, respectively. Therefore, SC and sperm abnormalities are responsive to selection and could be optimized by selective breeding. However, similar responses to selection would not be expected for sperm motility. Furthermore, none of the BSE traits investigated in this study were correlated with RFI, and therefore, they appear to be independent.

The rate of culling yearling bulls was independent of RFI and averaged approximately 45%in both –RFI and +RFI groups. Of those bulls subjected to BSE, the culling rate did not differ between the 2 groups (26.99% and 29.14% for + RFI and –RFI bulls, respectively). However, these culling rates are considerably greater than the 10% reported by McDermott et al. (1994) for beef herds in Ontario, Canada.

Scrotal circumference measurement is associated with testes weight, sperm output, high semen quality traits, and age of puberty in heifer progeny (Almquist et al., 1976; Brinks et al., 1978; Coulter and Foote, 1979; Gregory et al., 1991). A very high proportion (93.63%) of bulls at 1 yr of age exceeded the suggested minimum SC of 28 to 32 cm recommended for several common beef cattle breeds in Canada (Barth, 2000). In the present study, a minimum SC of 32 cm was chosen; although it may be considered high for yearling bulls, the culling rate due to SC did not differ between the RFI groups, nor was there any correlation between SC and RFI. Our results support the findings of 3 previous studies. In this regard, Arthur et al. (2001a) did not observe significant phenotypic ($r_p = 0.10$, $r_p = 0.0$) or genetic ($r_g = -0.03$, $r_g = -0.10$) correlations between SC and RFI or FCR in Angus bulls. In addition, Schenkel et al. (2004) also reported that no significant phenotypic and genetic correlations between SC and RFI were observed in young purebred beef bulls of 6 breeds in Ontario bull test stations from 1991 to 2000. Last, Fox et al. (2004) reported no differences in SC among 62 Bonsmara bulls with positive, intermediate, and negative RFI values. This suggests that selecting for improved feed efficiency on the basis of –RFI will not have any detrimental effect on SC of bulls. Two other independent studies have reported that –RFI and +RFI cows did not differ for pregnancy, calving, and weaning rates for cows selected for postweaning RFI (Arthur et al., 2005) and for cows that produced –RFI and +RFI progeny (Basarab et al., 2007). However, –RFI heifers have been reported to have increased age at puberty (Donoghue et al., 2011; Shaffer et al., 2011).

This small effect of –RFI on sperm motility and heifer age at puberty may be due to the FI testing procedure favoring later-maturing animals as first proposed by Basarab et al. (2007). These authors have hypothesized that because postweaning FI tests occur with a mixture of pre- and postpubertal animals, bulls or heifers not reaching puberty (later maturing) until the end of the test would have decreased RFI values compared to bulls or heifers reaching puberty at the start of the test because of the energy expenditures associated with sexual development and activity. It could also be that because + RFI animals are fatter, they reach puberty sooner because of the positive effects that fat reserves have on the onset of puberty.

Implications

Results from this study demonstrate that RFI is an alternative measure of efficiency independent of growth and body size that provides an opportunity to identify more efficient cattle with no detrimental impact on reproductive performance and fertility in beef bulls bred in multisire groups on pasture. Scrotal circumference, the number of progeny per sire, breeding soundness traits, and most reproduction traits were not associated with RFI in yearling bulls. Sperm motility, however, appears to be slightly less in bulls selected for –RFI, although no effect on siring ability was found in this study. It is expected that benefits to the beef industry will accrue by the adoption of RFI-based bull selection. However, additional studies are warranted to further examine the relationship between RFI and sperm motility and to confirm that selection for improved feed efficiency (–RFI) will not compromise bull fertility.

LITERATURE CITED

Agdex. 2002. Breeding soundness evaluation of bulls. Albertra Agriculture and Rural Development, Agdex 423/15-1. Accessed August 16, 2012. http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex3545.

Almquist, J. O., R. F. Branas, and K. A. Barber. 1976. Postpuberal changes in semen production of Charolais bulls ejaculated at high frequency and the relation between testicular measurements and sperm output. J. Anim. Sci. 42:670–676.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805–2811.

Arthur, P. F., R. M. Herd, J. F. Wilkins, and J. A. Archer. 2005. Maternal productivity of Angus cows divergently selected for post-weaning residual feed intake. Aust. J. Exp. Agric. 45:985–993.

Arthur, P. F., G. Renand, and D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and efficiency in young Charolais bulls. Livest. Prod. Sci. 68:131–139.

Barth, A. D. 2000. Bull Breeding Soundness Evaluation. 2nd ed. West. Can. Assoc. Bovine Pract., Saskatoon, Saskatchewan, Canada.

Barth, A. D., and C. L. Waldner. 2002. Factors affecting breeding soundness classification of beef bulls examined at the Western College of Veterinary Medicine. Can. Vet. J. 43:274–284.

Basarab, J. A., D. McCartney, E. K. Okine, and V. S. Baron. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87:489–502.

Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Can. J. Anim. Sci. 83:189–204.

Brien, F. D., L. G. Sharp, W. G. Hill, A. Robertson. 1984. Effects of selection on growth, body composition, and food intake in mice. Genet. Res. 44:73–85.

Brinks, J. S., M. J. McInerney, and P. J. Chenoweth. 1978. Relationship of age of puberty in heifers to reproductive traits in young bulls. Proc. West. Sect. Am. Soc. Anim. Sci. 29:28–30.

Canadian Council on Animal Care. 1993. Guide to the Care and Use of Experimental Animals. Vol. 1. E. D. Olfert, B. M. Cross, and A. A. McWilliams, ed. Can. Counc. Anim. Care, Ottawa, Ontario, Canada.

Coulter, G. H., and R. H. Foote. 1979. Bovine testicular measurements as indicators of reproductive performance and their relationship to productive traits in cattle: A review. Theriogenology 11:297–311.

Donoghue, K. A., P. F. Arthur, J. F. Wilkins, and R. M. Herd. 2011. Onset of puberty and early-life reproduction in Angus females divergently selected for post-weaning residual feed intake. Anim. Prod. Sci. 51:183–190.

Durunna, O. N., Z. Wang, J. A. Basarab E. S. Okine, and S. S. Moore. 2011. Phenotypic and genetic relationships among feeding behavior traits, feed intake, and residual feed intake in steers fed grower and finisher diets. J. Anim. Sci. 89:3401–3409.

Estany, J., D. Villalba, J. Tibau, J. Soler, D. Bahot, and J. L. Noguera. 2002. Correlation response to selection for litter size in pigs: I. Growth, fat deposition, and feeding behavior traits. J. Anim. Sci. 80:2556–2565.

Fox, J. T., G. E. Carstens, E. G. Brown, M. B. White, S. A. Woods, T. H. Welsh Jr., J. W. Holloway, B. G. Warrington, R. D. Randel, D. W. Forrest, and D. K. Lunt. 2004. Net feed intake of growing bulls and relationships with performance, fertility and ultrasound composition traits. Pages 117–120 in Beef Cattle Research in Texas. Web Site Publication by the Department of Animal Science, Texas A&M University, College Station, TX. Accessed from January to December 2005.

Garmyn, A. J., D. W. Moser, R. A. Christmas, and J. Minick Bormann. 2011. Estimation of genetic parameters and effects of cytoplasmic line on scrotal circumference and semen quality traits in Angus bulls. J. Anim. Sci. 89:693–698.

Gregory, K. E., D. D. Lunstra, L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for puberty and scrotal traits of beef cattle. J. Anim. Sci. 69:2795–2807.

Hagger, C. 1994. Relationships between income minus feed cost and residual feed consumption in laying hens. Poult. Sci. 73:1341–1344.

Hughes, T. E., and W. S. Pitchford. 2004. How does pregnancy and lactation affect efficiency of female mice divergently selected for post-weaning net feed intake? Aust. J. Exp. Agric. 44:501–509.

Kennedy, B. W., J. H. J. van der Werf, and T. H. E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. J. Anim. Sci. 71:3239–3250.

Kerr, J. C., and N. D. Cameron. 1995. Reproductive performance of pigs selected for components of efficient lean growth. J. Anim. Sci. 60:281–290.

Kruskal, W. H., and W. A. Wallis. 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47:583–621.

McDermott, J. J., S. W. Martin, and O. B. Allen 1994. Reproductive performance of Ontario beef breeding herds. Prev. Vet. Med. 18:99–113.

Nielsen, M. K., B. A. Freking, L. D. Jones, S. M. Nelson, T. L. Vorderstrasse, and B. A. Hussy. 1997. Divergent selection for heat loss in mice: II. Correlated responses in feed intake, body mass, body composition, and number born through fifteen generations. J. Anim. Sci. 75:1469–1476.

National Research Council. 1996. Nutrient Requirements of Beef Cattle. Natl. Acad. Press, Washington, DC.

Rauw, W. M., P. Luiting, M. Bakken, T. Schuurman, C. J. M. de Veer, and O. Vangen. 2000. Behavioural differences in non- reproductive adult females in a long term selection experiment for litter size in mice. Appl. Anim. Behav. Sci. 66:294–296.

Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. Can. J. Anim. Sci. 84:177–185.

Shaffer, K. S., P. Turk, W. R. Wagner, and E. E. D. Felton. 2011. Residual feed intake, body composition, and fertility in yearling beef heifers. 2011. J. Anim. Sci. 89:1028–1034.

Tang, G., X. Li, G. Plastow, S. S. Moore, and Z. Wang. 2011. Developing marker assisted models for evaluating growth traits in Canadian beef cattle genetic improvement. Livest. Sci. 138:62–68.