

Relationship between feed efficiency and slaughter traits of French Charolais bulls

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ABSTRACT: Improving feed efficiency is of interest to French beef producers so as to increase their profitability. To enable this improvement through selection, genetic correlations with production traits need to be quantified. The objective of this study was to estimate the genetic parameters for growth, feed efficiency (FE), and slaughter performance of young beef bulls of the French Charolais breed. Three feed efficiency criteria were calculated: residual feed intake (RFI), residual gain (RG), and ratio of FE. Data on feed intake, growth, and FE were available for 4,675 Charolais bulls tested in performance test stations and fed with pelleted diet. Between 1985 and 1989, 60 among 510 of these bulls were selected to procreate one generation of 1,477 progeny bulls which received the same pelleted diet at the experimental farm in Bourges. In addition to feed intake, growth, and FE traits, these terminal bulls also had slaughter traits of carcass yield, carcass composition, and weight of visceral organs collected. Genetic parameters were estimated using linear mixed animal models. Between performance test bulls and terminal bulls, the genetic correlation of RFI was 0.80 ± 0.18 ; it was $0.70 \pm$

0.21 for RG and 0.46 ± 0.20 for FE. For carcass traits, RFI was negatively correlated with carcass yield (-0.18 ± 0.14) and muscle content (-0.47 ± 0.14) and positively with fat content (0.48 ± 0.13). Conversely, RG and FE were positively correlated with carcass yield and muscle content and negatively with fat content. For the three FE criteria, efficient animals had leaner carcass. For visceral organs (as a proportion of empty body weight), RFI was genetically correlated with the proportions of the 5th quarter (0.51 ± 0.17), internal fat (0.36 ± 0.14), abomasum (0.46 ± 0.20), intestines (0.38 ± 0.17), liver (0.36 ± 0.16), and kidneys (0.73 ± 0.11). Conversely, RG and FE were negatively associated with these traits. The high-energy expenditure associated with the high-protein turnover in visceral organs may explain this opposite relationship between FE and the proportion of visceral organs. Selection for final weight and RFI increased growth and FE in progeny, and also improved carcass yield and muscle content in the carcass. To conclude, determinations of growth and feed intake in performance test stations are effective to select bulls to improve their growth, FE, and muscle content in carcass.

Key words: Charolais bulls, feed efficiency, genetic parameters, selection response, slaughter traits

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J. Anim. Sci. 2019.97:2308–2319
doi: 10.1093/jas/skz108

INTRODUCTION

The production of specialized beef breeds in France (Charolais, Limousin, and Blonde d'Aquitaine) has been increasing in recent decades

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Received January 7, 2019.
Accepted April 2, 2019.

as a consequence of improvements to breeding and management practices. The weight of male calves at 210 d has increased by an average of 30 kg in the last 15 yr (Griffon et al., 2017) and the carcass weight of young bulls rose by 56 kg between 1996 and 2016 (IDELE, 1997; IDELE, 2017a). At the same time, the consumption of forage and concentrates per adult animal increased by 10% to 20% and 29%, respectively (Inosys Réseau Elevage, 2016). Between 1998 and 2013, feeding costs increased by 50% (Inosys Réseau Elevage, 2016), whereas the price of the carcass kilogram improved only by 15% (IDELE, 2017b). For these reasons, beef producers are becoming increasingly concerned about the efficient use of feed by their animals.

For several decades now, the selection programs for candidate artificial insemination (AI) sires belonging to specialized beef breeds in France have included an in-station performance test during which growth, muscle score, and feed efficiency (FE) are recorded. Genetic correlations between the performance of these candidates and their subsequent male progeny on end-user farms were estimated by Fouilloux et al. (1999) and Bouquet et al. (2010) with respect to growth and carcass traits, but feed intake (FI) was not recorded on these terminal farms, and the carcass fat score was the only body composition measure. To estimate the genetic relationship between FE and the body composition of terminal young bulls, an experiment was conducted at the Institut National de la Recherche Agronomique (INRA) experimental farm in Bourges where FI and detailed slaughter traits were recorded individually relative to young Charolais bull progeny.

The objective of this study was therefore to estimate the genetic parameters for the growth, FE, and slaughter traits of young Charolais beef bulls relative to their sire performance for growth and FE as recorded by performance test stations.

MATERIALS AND METHODS

Animal Management

Two generations of French Charolais bulls were used during this study. The first comprised bulls tested by performance test stations, whereas the second was the progeny of some of these performance-tested bulls. The latter had been fattened on an experimental farm. During this experiment, all the animals were kept indoors and handled with care, in compliance with INRA's ethics policy in accordance with the guidelines for

animal research issued by the French Ministry of Agriculture (<https://www.legifrance.gouv.fr/eli/decret/2013/2/1/2013-118/jo/texte>).

Performance-tested bulls. Between 1979 and 2014, French AI co-operatives purchased candidate male Charolais calves from farms after weaning at an average age of 298 ± 33 d. These animals were screened by performance test stations to select the best candidates for semen production. On arrival for testing, the calves were allocated to contemporary groups as a function of their age and weight. During their stay at the test station, the calves were adapted to a test diet for at least 4 wk and then tested for at least 12 wk. During the adaptation period, the calves were switched from a roughage diet to a complete pelleted diet composed of 29% dehydrated alfalfa hay, 29% dehydrated beet pulp, and 21% bran, plus other ingredients to ensure a balanced diet. The energy value of the ration was 0.73 "Unité Fourragère Viande" (UFV)/kg, where one UFV corresponds to the net energy of 1-kg barley. This composition of the pelleted diet had remained consistent across the years and different stations, with laboratory controls of its composition along the testing period. An automatic concentrate dispenser ensured the individual distribution of pellets to each animal. The young bulls were fed ad libitum. The dispensers were calibrated at least once a month to ensure accurate distribution. To measure growth, all animals were weighed on 2 consecutive days to establish their initial body weight and then every 28 d throughout the test period. At the end of the test, they were weighed again on 2 consecutive days to establish their final weight (FW). Performance-tested bulls were scored to evaluate their muscle and skeletal development (Fouilloux et al., 1999; FGE, 2016). The animals were also judged on their ability to produce semen of sufficient quantity and quality that would enable their potential commercial use as an AI sire.

Terminal bulls. For this experiment, 60 Charolais performance-tested bulls were selected from the 510 tested at 2 stations (Creuzier-le-Neuf and Château-Gontier in France) over a 5-yr period (1985 and 1989). Selection was performed by applying the following rules. The 510 animals were ranked on a selection index that combined FW and residual feed intake (RFI) negatively: $\text{Index}_i = 0.44 (\text{FW}_i - \text{FW}_a) - 0.66 (\text{RFI}_i - \text{RFI}_a)$, where the i and a subscript represented the animal and the contemporary group average, respectively. Each year, at each station, 3 high-merit and 3 low-merit

bulls were selected, to reach a total of 30 high-merit and 30 low-merit bulls. These 60 bulls were then used to inseminate purebred Charolais females at the INRA experimental farm in Bourges. Their progeny were born between 1988 and 2009 and weaned on average at 221 ± 3 d. In the terminal barn, groups of 7 calves were placed in pens equipped with Calan Gates (American Calan, Northwood, NH) that enable the individual measurement of FI. The calves were adapted to the terminal diet over a 6- to 8-wk period. They were fed ad libitum with the same pelleted diet as their sire, the performance test bulls. Any feed that had been refused was weighed every Monday, Wednesday, and Friday to calculate their FI. At the start of the test period, the calves were weighed on 2 consecutive days to establish initial body weight. They were then weighed every 14 d to monitor their growth. All the calves were tested until 15 mo of age and this was pursued until 19 mo of age in half of the animals. The age at slaughter was 451 ± 10 and 570 ± 11 d, respectively, in the 2 groups. At the end of the test period, the terminal bulls were weighed on 2 consecutive days to establish their FW and then slaughtered at the experimental slaughterhouse of INRA in Theix. The slaughter protocol was the same at 15 or 19 mo of age. The weights of the hot carcasses were recorded. After 24 h chilling, the 6th rib was excised and dissected to estimate the carcass muscle and fat contents. Among the visceral organs, the 5th quarter fat, rumen, omasum, abomasum, intestines, liver, lungs, heart, kidneys, and spleen were weighed.

Description of Traits

The number of animals for which growth and FI records available were 4,675 and 1,477 at the performance test stations and experimental terminal farm, respectively. For slaughter traits, 1,427 progeny were recorded.

The initial and final weights were used to compute the average daily gain (ADG) and mid-test weight. The metabolic mid-weight (MMW) was calculated as the mid-weight^{0.75}. The automatic concentrate dispenser recorded the daily FI of the performance-tested bulls. The daily FI of terminal bulls was calculated 3 times a week (Monday, Wednesday, and Friday mornings) by subtracting refused feed from the weight of pellets distributed during the 2 (or three) previous days and dividing by 2 (or 3). Eventually FI was calculated as the average of all daily FI records.

Feed intake and ADG were used to calculate 3 FE criteria: residual feed intake (**RFI**), residual gain (**RG**), and FE. RFI was the difference between observed and expected FI, computed by a regression of FI on MMW and ADG, using Proc GLM of SAS/STAT software, version 9.4 of the SAS System for Linux (Copyright 2002 to 2012 by SAS Institute Inc., Cary, NC). A separate model was fitted for each data set, including the fixed effect of the contemporary group and age (at the start or end) as covariate. For performance test bulls, the model was

$$FI = CG + \beta_1 (MMW) + \beta_2 (ADG) + \beta_3 (\text{initial age}) + RFI,$$

where CG was the fixed effect of the contemporary group (year*station*group), β_1 was the partial regression of FI on MMW, β_2 was partial regression of FI on ADG, and β_3 was the partial regression of FI on age at the start. The model for terminal bulls was

$$FI = \text{year} + \beta_1 (MMW) + \beta_2 (ADG) + \beta_3 (\text{final age}) + RFI,$$

where β_3 was the partial regression of FI on the age at the end. RG was the difference between ADG and the expected ADG, computed by a regression of ADG on MMW and FI, using Proc GLM of SAS/STAT software. The same environmental effects as for RFI were used to adjust the regression models of the performance test and terminal bull RG. FE was ADG divided by FI and represented the gain in body weight per 1 kg of feed consumed.

For slaughter traits, the weights of the hot carcass and organs were expressed relatives to the empty body weight (**EBW**). The weights of muscle and fat in the carcass were estimated using the following predictive equations, as developed by Robelin and Geay (1975) with the independent variables expressed in kg:

$$\begin{aligned} \text{Muscle weight} = & -7.89 + 0.77992 (\text{hot carcass}) \\ & - 76.9654 (6^{\text{th}} \text{ rib fat}) \\ & + 9.6196 (6^{\text{th}} \text{ rib muscle}) \\ & - 0.5065 (5^{\text{th}} \text{ quarter fat}), \end{aligned}$$

$$\begin{aligned} \text{Fat weight} = & -3.56 + 0.1072 (\text{hot carcass}) \\ & + 79.788 (6^{\text{th}} \text{ rib fat}) \\ & - 9.851 (6^{\text{th}} \text{ rib muscle}) \\ & + 0.6887 (5^{\text{th}} \text{ quarter fat}). \end{aligned}$$

The carcass muscle and fat contents were then calculated by dividing the estimated muscle and fat weights by the weight of the hot carcass.

Statistical Analysis

Genetic parameters were estimated using the restricted estimation of maximum likelihood (REML) method with WOMBAT software (Meyer, 2007). For performance test bulls, the model included a contemporary group (205 groups) as fixed effect and age at the start as covariates. For terminal bulls, the model included the fixed effects of years (22 yr), age of the dam (3, 4, 5, 6 yr and over) and twinning (single or twin) and the slaughter age as a covariate. Because of the selection of sires, the performances of terminal bulls were analyzed using a multitrait model simultaneously with the RFI and FW of performance test bulls to take into account of the selection process. The relationship

matrix thus included 34,163 animals, up to the 5th generation.

To obtain the phenotypic correlations, traits were first corrected using the Proc GLM of SAS with the same fixed effects and covariates as the genetic model. Then, correlations were computed using Proc CORR of SAS.

Selection Response

The selection responses to the index combining high FW and low RFI of the 30 low-merit and 30 high-merit performance test bulls were computed for FI, FW, ADG, RFI, carcass composition, and visceral organs of the terminal bulls. To estimate the difference between low-merit and high-merit groups, traits were adjusted for the same fixed effects and covariates as in the genetic model. The estimated differences were standardized by the phenotypic standard deviation of each trait.

Table 1. Means and standard deviations (SD) of the traits studied in the performance tested and terminal bulls

Trait ¹	Performance-tested bulls			Fattening bulls		
	Number	Mean	SD	Number	Mean	SD
Start age, d	4,675	357	35	1,477	275	10
Start weight, kg	4,675	548	58	1,477	349	41
FI, kg/d	4,675	11.40	1.15	1,477	10.62	1.31
MMW, kg	4,675	126.8	9.0	1,477	108.1	8.8
ADG, kg/d	4,675	1.46	0.23	1,477	1.45	0.20
Final age, d	4,675	481	36	1,477	509	60
FW, kg	4,675	730	66	1,477	682	87
RFI, kg/d	4,675	0.00	0.47	1,477	0.00	0.82
RG, kg/d	4,675	0.00	0.18	1,477	0.00	0.14
FE, kg/kg	4,675	0.13	0.02	1,477	0.14	0.02
EBW, kg	–	–	–	1,427	590	78
HCW, kg	–	–	–	1,427	402.4	57.4
MW, kg	–	–	–	1,427	285.4	42.0
FW, kg	–	–	–	1,427	59.6	14.6
5 th QW, kg	–	–	–	1,427	183.7	25.0
Leather, kg	–	–	–	1,427	53.2	8.2
5 th QFW, kg	–	–	–	1,427	16.0	5.8
Rumen, kg	–	–	–	1,427	12.6	2.3
Omasum, kg	–	–	–	1,427	4.5	1.0
Abomasum, kg	–	–	–	1,427	2.1	0.5
Intestines, kg	–	–	–	1,427	12.0	2.3
Liver, kg	–	–	–	1,427	6.8	1.0
Lung, kg	–	–	–	1,427	4.1	0.6
Heart, kg	–	–	–	1,427	2.3	0.4
Kidneys, kg	–	–	–	1,427	1.2	0.2
Spleen, kg	–	–	–	1,427	1.2	0.3

¹Trait abbreviations: FI = daily feed intake; MBW = metabolic mean-weight; ADG = average daily gain; FW = final weight; RFI = residual feed intake; RG = residual gain; FE = feed efficiency; EBW = empty body weight; HCW = hot carcass weight; MW = muscle weight; FW = fat weight; 5th QW = 5th quarter weight; 5th QFW = 5th quarter fat weight.

RESULTS

Descriptive Statistics

Descriptive statistics of the traits measured in performance test and terminal bulls are shown in Table 1. The terminal bulls were younger at the start of the test period than the performance test bulls (differences of -82 d and -199 kg). They also ate 0.78 kg less feed per day, but the ADG was quite similar. Because of the longer test period, the age of terminal bulls at the end was older than that of performance test bulls ($+28$ d) but their FW was lower (-48 kg). After adjusting for environmental effects, the R^2 of the multiple regression of FI on MMW and ADG was 0.64 for performance test bulls and 0.53 for terminal bulls. The lower R^2 of the terminal bull model resulted in a greater phenotypic variability of RFI in these bulls. For the RG trait, the R^2 of the performance test bull model was 0.27 and the R^2 of the terminal bull model was 0.48 . Performance test bulls displayed greater phenotypic variability for RG than terminal bulls. FE values were the same in both data sets: on average, the bulls converted 13% – 14% of feed into ADG.

Phenotypic and Genetic Parameters

Overall, the genetic parameters were better estimated in performance test bulls with lower standard errors (SE) (Table 2). The heritability coefficients of FI were the same in both data sets (0.36 ± 0.05 and 0.36 ± 0.07), and almost the same for ADG (0.27 ± 0.04 vs. 0.31 ± 0.06) and FW (0.37 ± 0.04 vs. 0.33 ± 0.06). For the 3 FE traits, the heritability

coefficients were greater for terminal bulls than in performance test bulls. Feed intake, ADG and FW were positively correlated with each other. As expected, RFI was not phenotypically and genetically correlated with ADG in either the performance test bulls or terminal bulls. Similarly, RG was not phenotypically and genetically correlated with FI in the 2 data sets. RFI was also independent of FW, whereas RG was slightly correlated with FW. Residual feed intake was markedly correlated with FI (0.84 ± 0.03 and 0.77 ± 0.06), whereas RG was markedly correlated with ADG (0.81 ± 0.04 and 0.80 ± 0.05). Residual feed intake and RG were moderately negatively correlated (-0.29 ± 0.11 and -0.45 ± 0.13) in both data sets. The FE ratio was markedly correlated with ADG (0.81 ± 0.04) in performance test bulls and slightly less so (0.57 ± 0.11) in terminal bulls. The FE ratio was closely correlated with RG (0.99 ± 0.04 and 0.91 ± 0.03) in both data sets. Genetic correlations between FE and FI or RFI were tenuous for performance test bulls and FE was negatively correlated with FI (-0.49 ± 0.12) and RFI (-0.77 ± 0.07) in terminal bulls.

The genetic correlations between performance test traits and terminal traits are shown in Table 3. For FI, ADG, and FW, the correlations were close to 1 (>0.95). They were strong for RFI (0.80 ± 0.18) and RG (0.70 ± 0.21) but only moderate for FE (0.46 ± 0.20). The performance test RFI was markedly positively correlated with terminal bull FI (0.69 ± 0.16) but not with ADG and FW. The performance test RG was markedly correlated with the terminal bull ADG (0.67 ± 0.21), moderately with FW (0.41 ± 0.20), but not with FI. The performance test bull FE was correlated with the FW (0.53 ± 0.21), ADG

Table 2. Heritability (diagonal, \pm SE), genetic (above diagonal, \pm SE), and phenotypic¹ correlations between traits in each data set¹

	Trait ²	FI	ADG	FW	RFI	RG	FE
Performance test bulls	FI	0.36 ± 0.05	0.66 ± 0.06	0.84 ± 0.03	0.84 ± 0.03	0.10 ± 0.11	0.09 ± 0.11
	ADG	0.51	0.27 ± 0.04	0.64 ± 0.06	0.15 ± 0.11	0.81 ± 0.04	0.81 ± 0.04
	FW	0.78	0.58	0.37 ± 0.04	0.06 ± 0.10	0.22 ± 0.10	0.17 ± 0.10
	RFI	0.62	0.00	0.00	0.26 ± 0.04	-0.29 ± 0.11	-0.22 ± 0.11
	RG	0.00	0.85	0.23	-0.39	0.21 ± 0.04	0.99 ± 0.04
	FE	0.03	0.86	0.23	-0.34	0.99	0.23 ± 0.04
Terminal bulls	FI	0.36 ± 0.07	0.44 ± 0.12	0.75 ± 0.06	0.77 ± 0.06	-0.16 ± 0.15	-0.49 ± 0.12
	ADG	0.53	0.31 ± 0.06	0.80 ± 0.06	-0.04 ± 0.16	0.80 ± 0.05	0.57 ± 0.11
	FW	0.70	0.72	0.33 ± 0.06	0.10 ± 0.15	0.28 ± 0.14	0.17 ± 0.16
	RFI	0.72	0.02	0.02	0.36 ± 0.07	-0.45 ± 0.13	-0.77 ± 0.07
	RG	0.00	0.83	0.27	-0.29	0.35 ± 0.07	0.91 ± 0.03
	FE	-0.45	0.49	0.06	-0.71	0.83	0.35 ± 0.07

¹ $|r_p| < 0.03$: P not significant; $|r_p| > 0.05$: $P < 0.01$; $|r_p| > 0.10$: $P < 0.0001$.

²Trait abbreviations: FI = daily feed intake; ADG = average daily gain; FW = final weight; RFI = residual feed intake; RG = residual gain; FE = feed efficiency.

(0.66 ± 0.22), and RG (0.70 ± 0.21) of the terminal bulls, but was independent of FI and RFI.

Slaughter Traits

All the phenotypic and genetic correlations with respect to terminal bulls are presented in Supplementary Table. This part will focus on relationship between FE traits and slaughter traits. Most of slaughter traits had a greater genetic correlation with RFI, RG, and FE than a phenotypic correlation (Table 4). Empty body weight displayed moderate heritability (0.27 ± 0.06) and was phenotypically correlated with RFI (0.10) and RG (0.24).

Carcass traits. The carcass accounted for a very high proportion of EBW (68%). It contained

mainly for muscle (71%) and a small amount of fat (15%). The heritability coefficients of carcass composition traits were moderate to high (0.31 ± 0.07 for fat and muscle contents; 0.51 ± 0.08 for carcass yield). Carcass yield and muscle contents were negatively correlated with RFI and positively with RG and FE. The carcass fat content was positively correlated with RFI and negatively with RG and FE.

Fifth quarter traits. On average, the 5th quarter accounted for 31% of EBW. Its heritability coefficient was moderate (0.18 ± 0.05); it was positively correlated with RFI (0.51 ± 0.17) and negatively with RG (−0.44 ± 0.18) and FE (−0.56 ± 0.17). Leather had a high heritability (0.41 ± 0.08); it was not correlated with RFI but was negatively correlated with

Table 3. Genetic (±SE) correlations between performance test bull traits (rows) and terminal bull traits (columns)

Trait ¹	FI	ADG	FW	RFI	RG	FE
FI	0.96 ± 0.13	0.73 ± 0.20	0.86 ± 0.17	0.56 ± 0.18	0.06 ± 0.23	−0.38 ± 0.20
ADG	0.69 ± 0.15	0.95 ± 0.19	0.84 ± 0.18	0.23 ± 0.18	0.60 ± 0.20	0.16 ± 0.20
FW	0.78 ± 0.14	0.99 ± 0.14	0.99 ± 0.14	0.18 ± 0.19	0.48 ± 0.19	0.09 ± 0.19
RFI	0.69 ± 0.16	−0.06 ± 0.22	0.18 ± 0.21	0.80 ± 0.18	−0.54 ± 0.22	−0.78 ± 0.19
RG	0.14 ± 0.18	0.67 ± 0.21	0.41 ± 0.20	−0.17 ± 0.19	0.70 ± 0.21	0.50 ± 0.20
FE	0.17 ± 0.18	0.66 ± 0.22	0.53 ± 0.21	−0.11 ± 0.20	0.70 ± 0.21	0.46 ± 0.20

¹Trait abbreviations: FI = daily feed intake; ADG = average daily gain; FW = final weight; RFI = residual feed intake; RG = residual gain; FE = feed efficiency.

Table 4. Means, standard deviations (SD) and heritability (±SE) of slaughter traits, and genetic (±SE) and phenotypic correlations between slaughter and feed efficiency traits in terminal bulls¹

	Mean	SD	h ²	RFI ²		RG ²		FE ²	
				r _p	r _g	r _p	r _g	r _p	r _g
Empty body weight, kg	590.17	77.84	0.27 ± 0.06	0.10	0.15 ± 0.16	0.24	0.19 ± 0.16	−0.01	0.05 ± 0.17
Carcass, % ³	68.12	1.75	0.51 ± 0.08	−0.16	−0.18 ± 0.14	0.18	0.37 ± 0.13	0.18	0.32 ± 0.14
Muscle, % ⁴	70.91	2.42	0.31 ± 0.07	−0.27	−0.47 ± 0.14	0.09	0.43 ± 0.15	0.20	0.51 ± 0.14
Fat, % ⁴	14.74	2.51	0.31 ± 0.07	0.31	0.48 ± 0.13	−0.06	−0.47 ± 0.15	−0.22	−0.55 ± 0.13
5 th quarter, % ³	31.23	2.60	0.18 ± 0.05	0.07	0.51 ± 0.17	−0.08	−0.44 ± 0.18	−0.07	−0.56 ± 0.17
Leather, % ³	9.05	0.99	0.41 ± 0.08	−0.05	0.01 ± 0.15	−0.09	−0.36 ± 0.13	−0.03	−0.19 ± 0.14
5 th quarter fat, % ³	2.69	0.78	0.33 ± 0.07	0.29	0.36 ± 0.14	0.00	−0.41 ± 0.15	−0.16	−0.46 ± 0.14
Rumen, % ³	2.16	0.40	0.32 ± 0.07	−0.11	0.06 ± 0.16	−0.05	0.02 ± 0.16	0.04	−0.04 ± 0.16
Omasum, % ³	0.77	0.18	0.14 ± 0.05	−0.03	0.10 ± 0.20	−0.01	−0.11 ± 0.20	0.02	−0.17 ± 0.20
Abomasum, % ³	0.36	0.08	0.14 ± 0.05	0.07	0.46 ± 0.20	−0.05	−0.11 ± 0.20	−0.06	−0.55 ± 0.19
Intestines, % ³	2.05	0.35	0.21 ± 0.06	0.05	0.38 ± 0.17	−0.02	−0.25 ± 0.18	−0.02	−0.34 ± 0.17
Liver, % ³	1.17	0.16	0.24 ± 0.06	0.12	0.36 ± 0.16	0.02	−0.23 ± 0.18	−0.03	−0.38 ± 0.17
Lung, % ³	0.70	0.09	0.13 ± 0.05	−0.04	−0.26 ± 0.19	−0.05	0.07 ± 0.20	0.01	0.17 ± 0.20
Heart, % ³	0.39	0.05	0.35 ± 0.07	0.06	0.18 ± 0.15	−0.07	−0.10 ± 0.16	−0.07	−0.19 ± 0.15
Kidneys, % ³	0.20	0.03	0.28 ± 0.06	0.15	0.73 ± 0.11	−0.07	−0.35 ± 0.16	−0.10	−0.58 ± 0.13
Spleen, % ³	0.20	0.04	0.40 ± 0.07	−0.01	−0.08 ± 0.15	0.00	0.17 ± 0.14	0.02	0.16 ± 0.14

¹|r_p| < 0.05: P not significant; |r_p| > 0.05: P < 0.05; |r_p| > 0.10: P < 0.0001.

²Trait abbreviations: RFI = residual feed intake; RG = residual gain; FE = feed efficiency.

³Percentage of empty body weight.

⁴Percentage of carcass weight.

RG (-0.36 ± 0.13). Fifth quarter fat followed the same trend as carcass fat content: heritability was moderate (0.33 ± 0.07), and it was positively correlated with RFI (0.36 ± 0.14) and negatively with RG (-0.41 ± 0.15) and FE (-0.46 ± 0.14).

Digestive tract. For the rumen, heritability was moderate (0.32 ± 0.07) and was not correlated with 3 FE criteria. Omasum had a low heritability (0.14 ± 0.05) and was not correlated with RFI, RG, and FE. The heritability coefficient of abomasum was also low (0.14 ± 0.05) and this trait was strongly correlated with RFI positively (0.46 ± 0.20) and FE negatively (-0.55 ± 0.19). The heritability of intestines was moderate (0.21 ± 0.06) and was positively correlated with RFI (0.38 ± 0.17) and negatively with RG (-0.25 ± 0.18) and FE (-0.34 ± 0.17).

Organ traits. Organs displayed a broad range of heritability (from 0.13 ± 0.05 for the lungs to 0.40 ± 0.07 for the spleen). Residual feed intake had a strong correlation with the kidneys (0.73 ± 0.11), a moderate correlation with the liver (0.36 ± 0.16), and a low correlation with the heart (0.18 ± 0.15). The liver and kidneys were negatively correlated with RG and FE, whereas the spleen was slightly positively correlated with them. The lungs were not correlated with RG and FE and was slightly negatively correlated with RFI (-0.26 ± 0.19).

Selection Response

The differences in traits between high-merit and low-merit animals are presented in Table 5. In the performance test bulls, the marked differences regarding RFI and FW were consistent with the selection of these 2 traits (-1.56 and 2.29 phenotypic SD unit). These differences were smaller but still significant for terminal bulls (-0.17 and 0.53 phenotypic SD unit). Feed intake and ADG were greater in high-merit animals than in low-merit animals (0.27 and 0.49). The same trend was observed for carcass yield (0.33) and muscle content (0.22). High-merit animals had less fat in the carcass (-0.27). The liver weight related to EBW was greater in high-merit animals (0.14). The other 5th quarter components did not differ between high-merit and low-merit animals.

DISCUSSION

Residual feed intake had a heritability coefficient of 0.26 for performance test bulls and 0.36 for terminal bulls. This result was in line with estimates in the literature. In their review, Berry and

Table 5. Differences between high-merit and low-merit performance test and terminal bulls

	Trait ¹	Delta ²	Delta/SD ³
Performance test bulls	RFI, kg/d	-0.74^{***}	-1.56
	Final weight, kg	106^{***}	2.29
Terminal bulls	RFI, kg/d	-0.14^*	-0.17
	Final weight, kg	28^{***}	0.53
	FI, kg/d	0.27^{**}	0.27
	ADG, kg/d	0.08^{***}	0.49
	Carcass, %EBW	0.53^{***}	0.33
	Fat, %carcass	-0.62^{***}	-0.27
	Muscle, % carcass	0.51^{**}	0.22
	Abomasum, %EBW	-0.01 NS	-0.08
	Intestines, %EBW	0.00 NS	0.01
Kidneys, %EBW	0.00 NS	0.03	
Liver, %EBW	0.02^*	0.14	

¹Trait abbreviations: RFI = residual feed intake; FW = final weight; FI = daily feed intake; ADG = average daily gain.

²Delta is the estimated difference between high-merit and low-merit selected bulls or between the progeny of high-merit and low-merit selected bulls. *P*-value: NS = no significant; * <0.05 ; ** <0.001 ; *** <0.0001 .

³Phenotypic standard deviations of traits.

Crowley (2013) reported a range of heritability coefficients for RFI from 0.14 to 0.62 , thus embracing our own estimates. In addition, Zhang et al. (2017) found an RFI heritability of 0.22 (0.07). And more recently, Polizel et al. (2018) and Coyne et al. (2018) noted that the heritability of RFI was 0.28 (0.07) and 0.50 (0.05), respectively. Our results, bolstered by findings in the literature, suggest that the trait might be sufficient heritable to enable potentially effective genetic selection in the French Charolais population.

Because of the regression properties, phenotypic correlations between RFI and FI were positive and high (0.62 for performance test bulls and 0.72 for terminal bulls). Our findings were consistent with those of Berry and Crowley (2013) who reported an average phenotypic correlation of 0.66 between FI and RFI. Genetic correlations between FI and RFI were even stronger: 0.84 for performance test bulls and 0.77 for terminal bulls, consistent with the average genetic correlation of 0.72 reported by Berry and Crowley (2013). Polizel et al. (2018) reported same level of correlation between phenotype (0.65) and genotype (0.61 ± 0.11), as did Coyne et al. (2018), who found 0.72 for phenotypic and 0.70 ± 0.04 for genetic correlations. Selection for a low RFI would therefore be effective in significantly reducing FI. In our study, the genetic correlations between RFI and ADG or FW did not differ significantly from zero (no greater than

0.15 ± 0.11). Therefore, in the French Charolais population, selection for RFI would not have an impact on growth capacity (FW or ADG). In their review, Berry and Crowley (2013) reported that on average there was no genetic correlation between RFI and ADG or body weight, although in some studies a correlation different from zero could be found. For example, Nkrumah et al. (2007) found a genetic correlation between RFI and ADG of 0.46 (±0.45) in a composite Canadian population. In Wagyu population, Hoque et al. (2006) reported a genetic correlation of 0.25 (±0.16) between RFI and ADG and 0.19 (±0.15) between RFI and body weight. More recently, Polizel et al. (2018) found negative genetic correlation between RFI and ADG (-0.19 ± 0.05). Although RFI is by construction phenotypically uncorrelated with metabolic body weight and ADG, Kennedy et al. (1993) explained that genetic correlation different from zero could be found in some populations.

Residual gain was not correlated with FI: both genetic correlations between RG and FI were indeed not significantly different from zero. The genetic correlations estimated between RG and FW were significant and slightly positive (0.22 and 0.28) because FW was the sum of the mid-test weight and half of the weight gain during the test. As expected, we found a moderate negative relationship between RG and RFI in our 2 bull populations (-0.29 and -0.49). Crowley et al. (2010) and Coyne et al. (2018) investigated the relationship between RG and other performance traits; during their studies, RG was highly correlated to ADG, similar to the high genetic correlations (more than 0.80) estimated in our study. Crowley et al. (2010) also found a negative genetic correlation between RFI and RG (-0.46 ± 0.11).

Most of the studies that investigated FE used the feed conversion ratio ($FCR = FI/ADG$, the inverse of FE). In our study, no correlation was found between FE and FI in performance test bulls. However, in terminal bulls, the genetic correlation was -0.49 ± 0.12 . In their review, Berry and Crowley (2013) found an average genetic correlation of 0.39 between FCR and FI. However, the range of correlations between FCR and FI was very broad (-0.57 to 0.90). Coyne et al. (2018) found a positive genetic correlation between FCR and FI (0.33 ± 0.09). We saw positive genetic correlations between FE and ADG in performance test (0.81) and terminal bulls (0.57). Similarly, Berry and Crowley (2013) found an average genetic correlation of -0.62 and Coyne et al. (2018) determined a value of -0.53 (0.07). Between FE and

FW, we found different relationships between the 2 bull populations, where FE was correlated with FW in performance test bulls but no relationship was found in terminal bulls. Berry and Crowley (2013) reported an average phenotypic correlation of -0.01 (-0.67 to 0.35) and a genetic correlation of -0.03 (-0.62 to 0.88) between FCR and FW.

Residual feed intake and the FE ratio were negatively correlated, particularly in terminal bulls. In their review, Berry and Crowley (2013) found an average genetic correlation of 0.75 between FCR and RFI, whereas Coyne et al. (2018) estimated a genetic correlation of 0.47 (0.08). In our study, the genetic correlation between FE and RG was very high and close to 1 in both performance test and terminal bulls. In their study, Crowley et al. (2010) and Coyne et al. (2018) found a strong negative relationship between FCR and RG. The 3 FE criteria were obviously correlated inter se, although these correlations were not equal to one. These results suggest that different biological determinants may be involved in the expression of FE and each of these criteria could be used to characterize differences in FE between animals.

Several studies and reviews (Lobley, 2003; Herd and Arthur, 2009; Fitzsimons et al., 2017; Cantalapiedra-Hijar et al., 2018) have attempted to explore the biological determinants involved in differences in FE. Globally, Herd and Arthur (2009) suggested that the biological determinants concerned 5% body composition, 2% feeding patterns, 37% protein turnover, metabolism and stress, 9% heat increment of fermentation, 10% digestibility, 10% activity, and 27% other determinants. During our study, we specifically investigated the relationship between FE and the carcass and 5th quarter composition. Indeed, Webster (1989) stated that the partitioning of nutrients towards lean or fat deposition has a marked effect on FE and that differences in visceral mass between animals may have significant effects on thermogenesis, because protein turnover in visceral organs, a costly energy mechanism, is much greater compared with the protein turnover in skeletal muscle.

First, we investigated the phenotypic relationship between FE and carcass traits. We showed that RFI was negatively correlated with the dressing percentage and muscle content but positively with fat content. In Angus breed cattle, Herd et al. (2009) also found a negative phenotypic association with the dressing percentage and positive association with rib fat depth. Richardson et al. (2001) found a positive association with rib and rump fat depth and a negative

association with protein gain in an Angus population. Nevertheless, some studies did not find any phenotypic association between RFI and carcass traits. In Nellore cattle, Gomes et al. (2012), Bonilha et al. (2013), Zorzi et al. (2013), and Fidelis et al. (2017) could not demonstrate any association between RFI and carcass fatness. In Angus x Hereford cattle, Sainz et al. (2006), Bulle et al. (2007), and Cruz et al. (2010) did not determine any relationship between RFI and carcass traits. However, the latter results were obtained during physiology experiments involving a limited number of recorded animals.

Our estimates of genetic relationships revealed a strong negative genetic correlation between RFI and muscle content in the carcass and a positive correlation with fat content. Few studies have investigated the genetic correlations between FE and carcass traits. When studying 381 animals of different breeds, Nkrumah et al. (2007) showed a negative genetic association between RFI and carcass lean meat area and lean meat yield, and a positive genetic association with carcass grade fat. Robinson and Oddy (2004) found a positive genetic association between RFI and carcass intramuscular fat percentage. Crowley et al. (2011) showed a negative genetic correlation between the sire RFI recorded at the performance test station and in their progeny with carcass weight and conformation, and a positive correlation with carcass fatness. In a multibreed analysis, Coyne et al. (2018) also found a positive genetic correlation between RFI and carcass fat and a negative correlation with carcass conformation.

The present study demonstrated positive genetic correlations between RG and dressing percentage and muscle content, and negative genetic correlations with the carcass fat content. Crowley et al. (2011) also found a positive genetic association with carcass weight and conformation, but there was no relationship with carcass fat. With FE, the same trend was observed with respect to carcass traits. Those authors also found a positive genetic association with carcass weight and conformation but not with fat content. Coyne et al. (2018) estimated a positive genetic relationship between FCR and fat depth and intramuscular fat. They also found a negative genetic correlation with carcass conformation. For rump and rib fat, Robinson and Oddy (2004) showed a positive genetic association with FCR. However, Nkrumah et al. (2007) did not find genetic relationship between FCR and lean meat and fat in the carcass. To conclude, in the French Charolais population, selection for any of

the 3 FE criteria (i.e., efficient animals) will increase the dressing percentage and muscle content and decrease fat content.

As a second step, we studied the relationship between FE and several organs traits. According to Herd and Arthur (2009), 37% of energy metabolism is due to turnover and metabolism requirements. Cantalapiedra-Hijar et al. (2018) defined turnover as a continuous process of protein degradation and synthesis for the renewal of tissues. This phenomenon is essential for metabolic regulation, cellular repair, and rapid adaptation to environmental changes, among other functions. In his review, Lobley (2003) noted that the rate of protein synthesis is greater in splanchnic organs than in peripheral tissues such as muscle. Because turnover is linked to tissue renewal, it is possible to imagine that more energy will be used for protein turnover the greater the proportion of visceral organs.

Our results showed that FE was genetically associated with a lower proportion of the 5th quarter, and more specifically with limited 5th quarter fat. A similar trend was shown with respect to the carcass fat content. In our young bull population, high FE was strongly associated with reduced fat accretion. Webster (1985) noted that the greater the proportion of fat in the gains, the poorer the food conversion efficiency. For other components of the 5th quarter, the intestines, liver and kidneys were positively correlated with RFI and negatively with RG and FE. Efficient animals with lower proportion of these visceral organs might therefore require less metabolic energy to achieve the protein turnover process for tissue renewal. Overall, genetic correlations between visceral traits and RFI or FE were greater than the correlation with RG.

In his review, Lobley (2003) noted that the liver accounts for 25% of the energy expenditure of steers, with 4% to 15% of protein synthesis. He also showed that the gut represents 23% of energy expenditure, with 32% to 45% of protein synthesis. Indeed, between 5% and 7% of the EBW of animals accounts for 48% of energy expenditure. Basarab et al. (2003) found that animals with a high RFI had, in raw mass terms, a larger stomach and intestine, liver, and more kidney fat and trim. Bonilha et al. (2013) found larger kidneys in high-RFI animals. Fitzsimons et al. (2014) found a positive correlation between the reticulo-rumen and RFI. Some studies did not find any differences in organ weights, but determined differences in cell size. Lam et al. (2018) studied the rumen epithelium and did not find any difference in rumen weight between inefficient and efficient animals. However, the size of

epithelium cells in the ventral blind sac and across sacs was larger in efficient animals. Montanholi et al. (2017) found a larger hepatocyte size in the livers of efficient animals with respect to the portal triad and central vein, but no difference in liver weight. Nevertheless, Richardson et al. (2001), Sainz et al. (2006), Gomes et al. (2012), Meale et al. (2017), and Fidelis et al. (2017) could not find difference between RFI and visceral organ traits. In their study of crossbred steers, Mader et al. (2009) noted a negative correlation between RFI and the heart, which was not consistent with our findings. Moreover, they found a positive relationship between FE and spleen, which was also not consistent with our results.

Apart from the work by Basarab et al. (2003) on 148 steers, the studies cited used fewer than a hundred animals. During our study, we noted that phenotypic correlations are weaker than genetic correlations in the 1,427 terminal bulls. The lack of power of some studies may explain why no significant phenotypic relationship between FE and organs traits are found in the literature. Combining the results of carcass and visceral organ traits allowed us to show that efficient animals had more muscle than fat and a lower proportion of some visceral organs. A putative strategy in those animals may be that they use more energy to deposit protein and maintain it in muscles than expending it to maintain organs. However, Fitzsimons et al. (2017) noted from a review of some studies the possible presence of differences in protein turnover and degradation between the muscles of individual animals, which might contribute to FE potential. Cantalapiedra-Hijar et al. (2018) suggested that efficient animals might have a lower protein turnover in muscle and organs.

To test the selection of young Charolais bulls with respect to FE, our study investigated genetic correlations across 2 generations of Charolais bulls and differences in selection responses between traits in performance test and terminal bulls. Performance test bulls were selected using a synthetic index that combined their FW and RFI, as recommended by the Institut de l'Élevage in France (IDELE, 2005). With the animals being fed the same pelleted diet, we showed that this selection increased the growth and FI of progeny. This was not a surprise because, genetically, FW was highly correlated with ADG (0.64 ± 0.06) and FI (0.84 ± 0.03). However, simultaneous selection against RFI allowed the increase in FI (0.27 SD unit) to be lower than the responses of FW (0.53 SD unit) and ADG (0.49 SD unit), leading to a reduction in RFI (-0.17 SD unit). The progeny were

more efficient. Herd et al. (1997) investigated the response to selection based on RFI only and showed that progeny from low-RFI parents ate less and were more efficient. No difference was observed with respect to live weight and growth. Richardson et al. (2001) demonstrated the same trend. They also investigated body composition and found no difference in dressing percentage, although low-RFI animals displayed more protein gain and less carcass fat. The selection on FW and RFI in our study not only improved the growth and efficiency of progeny, but also improved muscle growth capacity as revealed by the positive responses of dressing percentage and muscle content in carcass and a reduction in the carcass fat content.

This study was based on animals fed with a high-digestibility diet and both sires and progeny received the same pelleted diet. Interactions between genetic traits and other diets (roughage or silage diets) were not explored during this study. Further investigations will now be necessary to link FE studies and management practices on French farms.

CONCLUSION

Feed efficiency is a heritable trait in the French Charolais breed and RFI is not associated with FW and ADG. This relationship enables the selection of this trait without this having any effects on growth traits. RG is also useful to select animals with a high daily gain without an antagonist effect on FI. RFI, RG, and FE have a consistent relationship with carcass composition traits: efficient animals have a greater proportion of muscle, procuring an advantage in terms of beef value. The 3 FE criteria were also associated with a reduction in 5th quarter fat. Residual feed intake and FE were markedly associated with several organ traits, which indicates that selection for RFI and FE may reduce the proportion of these visceral organs and hence the impact of energy expenditure on protein turnover.

Selection for a high FW associated with a low RFI showed that it is possible to improve growth, FE, and carcass composition simultaneously: the progeny display better growth, are more efficient, and have leaner carcasses, in line of the selection goals of AI co-operatives. This study investigated the selection of RFI and FW under the same high-digestibility pelleted diet. Genetic parameters for FE under different feed systems need to be investigated to identify a potential genotype \times environment interaction. Indeed, several feed conditions apply on French farms and selection for FE needs to be profitable for all livestock systems.

SUPPLEMENTARY DATA

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

Conflict of interest statement. None declared.

ACKNOWLEDGMENTS

We would like to thank the technical staff at the INRA experimental slaughterhouse, 63122 Saint-Genès-Champanelle, France, for their assistance. S.T. was the beneficiary of a grant from APIS-GENE.

LITERATURE CITED

- 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. doi:10.4141/A02-065
- Berry, D. P., and J. J. Crowley. 2013. Genetics of feed efficiency in dairy and beef cattle. *J. Anim. Sci.* 91:1594–1613. doi:10.2527/jas.2012-5862.
- Bonilha, E. F., R. H. Branco, S. F. Bonilha, F. L. Araujo, E. Magnani, and M. E. Mercadante. 2013. Body chemical composition of Nellore bulls with different residual feed intakes. *J. Anim. Sci.* 91:3457–3464. doi:10.2527/jas.2012-5437.
- Bouquet, A., M.-N. Fouilloux, G. Renand, and F. Phocas. 2010. Genetic parameters for growth, muscularity, feed efficiency and carcass traits of young beef bulls. *Livest. Sci.* 129:38–48. doi:10.1016/j.livsci.2009.12.010
- Bulle, C., F. C., P. V. Paulino, A. C. Sanches, and R. D. Sainz. 2007. Growth, carcass quality, and protein and energy metabolism in beef cattle with different growth potentials and residual feed intakes. *J. Anim. Sci.* 85:928–936. doi:10.2527/jas.2006–373
- Cantalapiedra-Hijar, G., M. Abo-Ismaïl, G. E. Carstens, L. L. Guan, R. Hegarty, D. A. Kenny, M. McGee, G. Plastow, A. Relling, and I. Ortigues-Marty. 2018. Review: biological determinants of between-animal variation in feed efficiency of growing beef cattle. *Animal* 12(s2):s321–s335. doi:10.1017/S1751731118001489.
- Coyne, J. M., M. M. Judge, S. Conroy, and D. P. Berry. 2018. Variance component estimation of efficiency, carcass and meat quality traits in beef cattle. *Proc. World Congr. Genet. Appl. Livest. Prod. Electronic Poster Session-Biology-Feed Intake and Efficiency.* 1:912.
- Crowley, J. J., R. D. Evans, N. Mc Hugh, T. Pabiou, D. A. Kenny, M. McGee, D. H. Crews, and D. P. Berry. 2011. Genetic associations between feed efficiency measured in a performance test station and performance of growing cattle in commercial beef herds. *J. Anim. Sci.* 89:3382–3393. doi:10.2527/jas.2011–3836
- Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr, R. D. Evans, and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. *J. Anim. Sci.* 88:885–894. doi:10.2527/jas.2009-1852.
- Cruz, G. D., J. A. Rodríguez-Sánchez, J. W. Oltjen, and R. D. Sainz. 2010. Performance, residual feed intake, digestibility, carcass traits, and profitability of angus-hereford steers housed in individual or group pens. *J. Anim. Sci.* 88:324–329. doi:10.2527/jas.2009-1932.
- FGE. 2016. Référentiel technique du contrôle des taureaux en station d'évaluation SE et CI.
- Fidelis, H. A., S. F. M. Bonilha, L. O. Tedeschi, R. H. Branco, J. N. S. G. Cyrillo, and M. E. Z. Mercadante. 2017. Residual feed intake, carcass traits and meat quality in nellore cattle. *Meat Sci.* 128:34–39. doi:10.1016/j.meatsci.2017.02.004.
- Fitzsimons, C., D. A. Kenny, and M. McGee. 2014. Visceral organ weights, digestion and carcass characteristics of beef bulls differing in residual feed intake offered a high concentrate diet. *Animal* 8:949–959. doi:10.1017/S1751731114000652.
- Fitzsimons, C., M. McGee, K. Keogh, S. M. Waters, and D. A. Kenny. 2017. Molecular Physiology of Feed Efficiency in Beef Cattle. In: *Biology of Domestic Animals*, editor, CG Scanes and RA Hill. CRC Press, FL, Boca Raton, USA. p. 122–165
- Fouilloux, M.-N., G. Renand, J. Gaillard, and F. Ménéssier. 1999. Genetic parameters of beef traits of Limousin and Charolais progeny-tested AI sires. *Genet. Sel. Evol. GSE.* 31:465–489. doi:10.1186/1297-9686-31-5-465
- Gomes, R. C., R. D. Sainz, S. L. Silva, M. C. César, M. N. Bonin, and P. R. Leme. 2012. Feedlot performance, feed efficiency reranking, carcass traits, body composition, energy requirements, meat quality and calpain system activity in Nellore steers with low and high residual feed intake. *Livest. Sci.* 150:265–273. doi:10.1016/j.livsci.2012.09.012
- Griffon, L., P. Boulesteix, A. Delpuch, A. Govignon-Gion, J. Guerrier, O. Leudet, S. Miller, R. Saintilan, E. Venot, and T. Tribout. 2017. La sélection génétique des races bovines allaitantes en France: un dispositif et des outils innovants au service des filières viande. *INRA Prod. Anim.* 30:107–124. doi:https://doi.org/10.20870/productions-animales.2017.30.2.2237
- Herd, R. M., J. A. Archer, P. F. Arthur, E. C. Richardson, J. H. Wright, K. C. P. Dibley, and D. A. Burton. 1997. Performance of progeny of high vs low net feed conversion efficiency cattle. *Proc. Assoc. Advmt. Anim. Breed Genet.* 12:742–745.
- Herd, R. M., and P. F. Arthur. 2009. Physiological basis for residual feed intake. *J. Anim. Sci.* 87(14 Suppl):E64–E71. doi:10.2527/jas.2008-1345.
- Herd, R. M., S. Piper, J. M. Thompson, P. Arthur, B. McCorkell, and K. C. P. Dibley. 2009. Benefits of genetic superiority in residual feed intake in a large commercial feedlot. *Proc. Assoc. Advmt. Anim. Breed Genet.* 18:476–479.
- Hoque, M. A., P. F. Arthur, K. Hiramoto, and T. Oikawa. 2006. Genetic relationship between different measures of feed efficiency and its component traits in Japanese Black (Wagyu) bulls. *Livest. Sci.* 99:111–118. doi:10.1016/j.livprodsci.2005.06.004
- IDELE. 1997. 1996 : l'année économique lait & viande bovine perspective 1997.
- IDELE. 2005. Répertoire des méthodes et procédures de contrôle des bovins de races à viande.
- IDELE. 2017a. Résultats 2016 des élevages BV suivis par Bovins Croissance. <http://idele.fr/contact/publication/idelesolr/recommends/resultats-2016-des-elevages-bovins-viande-suivis-par-bovins-croissance.html> (Accessed 8 August 2018).
- IDELE. 2017b. Les chiffres clés du GEB bovins 2017.

- Inosys Réseau Elevage. 2016. Vaches, surfaces, charges... tout augmente sauf le revenu. http://idele.fr/no_cache/recherche/publication/idelesolr/recommends/vaches-surfaces-charges-tout-augmente-sauf-le-revenu.html (Accessed 8 August 2018).
- Kennedy, B. W., J. H. van der Werf, and T. H. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. *J. Anim. Sci.* 71:3239–3250. doi:10.2527/1993.71123239x.
- Lam, S., J. C. Munro, M. Zhou, L. L. Guan, F. S. Schenkel, M. A. Steele, S. P. Miller, and Y. R. Montanholi. 2018. Associations of rumen parameters with feed efficiency and sampling routine in beef cattle. *Animal* 12:1442–1450. doi:10.1017/S1751731117002750.
- Lobley, G. E. 2003. Protein turnover—what does it mean for animal production? *Can. J. Anim. Sci.* 83:327–340. doi:10.4141/A03-019
- Mader, C. J., Y. R. Montanholi, Y. J. Wang, S. P. Miller, I. B. Mandell, B. W. McBride, and K. C. Swanson. 2009. Relationships among measures of growth performance and efficiency with carcass traits, visceral organ mass, and pancreatic digestive enzymes in feedlot cattle. *J. Anim. Sci.* 87:1548–1557. doi:10.2527/jas.2008-0914.
- Meale, S. J., D. P. Morgavi, I. Cassar-Malek, D. Andueza, I. Ortigues-Marty, R. J. Robins, A. M. Schiphorst, C. Migné, M. Pétéra, S. Laverroux, et al. 2017. Exploration of biological markers of feed efficiency in young bulls. *J. Agric. Food Chem.* 65:9817–9827. doi:10.1021/acs.jafc.7b03503.
- Meyer, K. 2007. WOMBAT: a tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). *J. Zhejiang Univ. Sci. B* 8:815–821. doi:10.1631/jzus.2007.B0815.
- Montanholi, Y. R., L. S. Haas, K. C. Swanson, B. L. Coomber, S. Yamashiro, and S. P. Miller. 2017. Liver morphometrics and metabolic blood profile across divergent phenotypes for feed efficiency in the bovine. *Acta Vet. Scand.* 59:24. doi:10.1186/s13028-017-0292-1
- Nkrumah, J. D., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, D. H. Crews, and S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and measures of efficiency with growth and carcass merit of beef cattle. *J. Anim. Sci.* 85:2711–2720. doi:10.2527/jas.2006-767
- Polizel, G. H. G., L. Grigoletto, M. E. Carvalho, P. Rossi Junior, J. B. S. Ferraz, and M. H. de A. Santana. 2018. Genetic correlations and heritability estimates for dry matter intake, weight gain and feed efficiency of Nellore cattle in feedlot. *Livest. Sci.* 214:209–210. doi:10.1016/j.livsci.2018.06.013
- Richardson, E. C., R. M. Herd, V. H. Oddy, J. M. Thompson, J. A. Archer, and P. F. Arthur. 2001. Body composition and implications for heat production of Angus steer progeny of parents selected for and against residual feed intake. *Aust. J. Exp. Agric.* 41:1065–1072. doi:10.1071/ea00095
- Robelin, J., and Y. Geay. 1975. Estimation de la composition de la carcasse des taurillons à partir de la composition de la 6ème côte. *Bull. Tech. CRZV Theix.* 22:41–44.
- Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Livest. Prod. Sci.* 90:255–270. doi:10.1016/j.livprodsci.2004.06.011
- Sainz, R., G. D. Cruz, R. B. Monteiro, J. Rodriguez-Sanchez, D. B. Monteiro, V. Guidi, and R. J. Anaruma. 2006. Carcass composition and visceral organs are similar at harvest in low and high residual feed intake groups of Angus-Hereford steers. *Proc. West. Sect. Am. Soc. Anim. Sci.* 57:401–403.
- Webster, A. J. F. 1985. Differences in the energetic efficiency of animal growth. *J. Anim. Sci.* 61:92–103. doi:10.1093/ansci/61.Supplement_2.92
- Webster, A. J. F. 1989. Bioenergetics, bioengineering and growth. *J. Anim. Sci.* 48:249–269. doi:10.1017/S0003356100040265
- Zhang, F., C. Ekine-Dzivenu, M. Vinsky, J. A. Basarab, J. L. Aalhus, M. E. R. Dugan, and C. Li. 2017. Phenotypic and genetic relationships of residual feed intake measures and their component traits with fatty acid composition in subcutaneous adipose of beef cattle. *J. Anim. Sci.* 95:2813–1824. doi:10.2527/jas2017.1451
- Zorzi, K., S. F. Bonilha, A. C. Queiroz, R. H. Branco, T. L. Sobrinho, and M. S. Duarte. 2013. Meat quality of young Nellore bulls with low and high residual feed intake. *Meat Sci.* 93:593–599. doi:10.1016/j.meatsci.2012.11.030