Effect of breed body size and the muscular hypertrophy gene in the production and carcass traits of concentrate-finished yearling bulls[1]

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ABSTRACT: To examine the extent of the effect of muscular hypertrophy character in beef of northern-Spanish breeds, animal performance and carcass characteristics of 152 finishing steers from 5 genotypes were studied: 32 yearling bulls from a rustic Asturiana de la Montaña (AM) breed, 96 yearling bulls from Asturiana de los Valles (AV) breed, divided in 3 groups depending on the presence of the gene responsible for double-muscling (i.e., 32 AV *mh/mh*, 32 AV *mh*/+, 32 AV +/+), and 24 yearling bulls from AM × AV cross were used. Each genotype was composed of 8 animals per year (4 animals per pen) for 4 yr, except for the AM × AV genotype, which was only evaluated in the last 3 yr of the experiment. All animals were fed indoors with concentrate meal and barley straw ad libitum. Average daily gains in AV animals (1.41 kg/d) were greater ($P < 0.01$) than in AM (1.12 kg/d), whereas AM × AV were intermediate (1.29 kg/d) to these. No significant differences ($P = 0.604$) in ADG were found among the 3 AV genotypes. Longer fattening periods ($P < 0.001$) were taken for AM animals to reach acceptable BW at slaughter. Double-muscled animals (AV *mh/mh*) were found to have the best feed efficiencies when expressed as G:F ($P < 0.001$). However, residual feed intake calculated on a daily basis showed a greater efficiency in AV *mh/mh* and AM than in other genotypes. Carcasses from double-muscled animals had greater BW, yield, conformation and compactness index, and less fat cover than the other genotypes ($P < 0.001$). Carcasses from AM breed were the lightest and had the worst conformation, whereas those from AM × AV generally presented intermediate characteristics between AV and AM. Double-muscled animals had the greatest LM weight and area. The sixth-rib dissection revealed a greater percentage of muscle (84.6%) and decreased percentages of subcutaneous fat (1.1%), intermuscular fat (4.7%), bone (8.5%), and other tissues (1.2%) in AV *mh/mh* compared with other genotypes. Water-holding capacity was greatest in AM and least in AV *mh/mh*. In conclusion, double-muscled AV bulls would provide the greatest economic returns at intensive feeding systems because of their greater efficiency, reduced feeding costs, greater carcass weight and conformation, and greater lean yields, though some LM characteristics (reduced fat content and water-holding capacity) could negatively affect the sensory attributes of the meat compared with other genotypes with greater fatness.

Key words: carcass composition, double-muscled, efficiency, fattening, growth rate, rusticity

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INTRODUCTION

The demand of consumers for leaner meats has increased due to concerns about food quality and health. Leaner beef can be obtained by restricting the feed intake and growth rate of an animal, thus reducing carcass fat, but can negatively affect several physical and chemical characteristics of meat and thus sensorial appreciation by the consumer (Savell and Cross, 1988). Lean meat can also be produced from double-muscled genotypes, whose meat is quite tender after a short period of postmortem aging (Arthur, 1995). In Europe, a premium price is paid for carcasses of double-muscled

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animals because of their greater lean yields and greater proportions of high value cuts, making them an interesting choice for beef producers.

It is recognized that rustic breeds or early maturing animals deposit greater fat amounts, whereas lean genotypes or late-maturing animals (i.e., double-muscled) produce leaner beef (Aldai et al., 2007a). The effects of double-muscling in cattle were initially reviewed by Arthur (1995) based on studies performed before the mutation disrupting the myostatin function was identified (Dunner et al., 1997; Grobet et al., 1998). Later, crossbred cattle have been used for studying double-muscling effects on production and carcass traits by mating F_1 females coming from double-muscled sires with sires carrying different levels of mutation (Casas et al., 2001; Wheeler et al., 2001; Albrecht et al., 2006). The majority of research, however, has been with the Belgian Blue breed (considered to be one of the leanest breeds), although different breeds of double-muscled animals may exhibit different live performance and carcass characteristics.

The present work was designed to study differences in production and carcass traits of 5 genotypes from northern-Spain, coming from 2 different pure breeds, rustic and early maturing Asturiana de la Montaña (**AM**) bulls, and late-maturing Asturiana de los Valles (**AV**) bulls with different presence of the double-muscling gene, managed under intensive feeding conditions and slaughtered at traditional BW.

MATERIALS AND METHODS

All animals were cared for under the guidelines established by the European Union.

Animals, Diets, and Experimental Design

Ninety-six AV yearling bulls, 32 AM yearling bulls and 24 AM × AV crossed yearling bulls were studied. The AV breed is a breed adapted to extensive production systems, whereas the AM breed is characterized by small to medium-sized rustic animals adapted to less favored mountain areas (Cañón et al., 1994). Asturiana de los Valles animals were divided in 3 groups depending on the presence of 11-bp deletion in the coding sequence of the myostatin gene causing double-muscling in cattle (Grobet et al., 1998): double-muscled (AV *mh/mh*, n = 32), heterozygote (AV *mh*/+, n = 32), and normal (AV +/+, n = 32).

Calves were suckled by their mothers from birth (i.e., winter) to weaning (i.e., early autumn). After weaning, male calves were fattened indoors by feeding a typical Spanish finishing diet that included a concentrate meal (84% barley, 10% soy, 3% fat, and 3% minerals and vitamins, on DM basis) and barley straw, both ad libitum. Chemical and fatty acid composition of the concentrate meal was previously published by Aldai et al. (2007b). Fattening was carried out in housing facilities of the SERIDA Research Institute and lasted an average of 229 ± 4.8 d.

Overall, a total of 152 animals were distributed in 5 experimental groups according to breed and presence or absence of the myostatin gene mutation (i.e., AV *mh/mh*, AV *mh*/+, AV +/+, AM, AM × AV). The aforementioned experimental genotypes were composed of 8 animals per year in 2 replicates (4 animals per pen). The 10 pens were regarded as the experimental units and randomly assigned to each genotype in each year. This experimental design was maintained during 4 yr (2001 to 2004), except for the AM × AV genotype, which was only studied in the last 3 yr of the study (i.e., 2002 to 2004).

All animals were slaughtered in a commercial abattoir according to standard procedures (Real Decreto 147/1993; OJEC, 1999) when they reached typical endpoints of approximately 475 to 500 kg for AM and 525 to 550 kg for other genotypes.

Production Traits

Initial BW was recorded at the beginning of the finishing period over 2 consecutive days. After that, animals were weighed every 3 wk until slaughter. Before slaughter, animals were weighed twice (on the day before slaughter and on the day of slaughter) to get the final average BW. Average daily gain was calculated as the difference between final and initial BW divided by the number of days. During the fattening period, the daily food offered was recorded for each experimental unit (i.e., on a per pen basis), and the rejected amounts were weighed and subtracted from the offered amounts when appropriate to calculate the daily food consumed per pen. Average daily feed intake per animal was calculated dividing it by 4 (i.e., the number of animals per pen). Feed conversion was calculated as kilograms of BW per kilogram of concentrate and also as kilograms of carcass weight per kilogram of concentrate. Residual feed intake (**RFI**) was calculated as the difference between actual ADFI and that predicted on the basis of requirements for production and maintenance (Koch et al., 1963). Daily feed intake was regressed on ADG and metabolic BW (**$BW^{0.75}$**) at mid-test of each year, including the effect of year, and the residual error terms were taken as the RFI values, with smaller (negative) values representing more efficient animals than greater (positive) ones (Archer et al., 1997; Basarab et al., 2003).

Carcass Measurements

After slaughtering and dressing, HCW was recorded and carcasses were chilled at 3°C. Cold carcass weight was calculated by subtracting 2% of the HCW, and carcass yield percentage was obtained from the relation between BW at slaughter and cold carcass weight. Twenty-four hours postmortem, carcasses were classified by visual assessment of conformation and degree of fat cover by an experienced evaluator. For conformation, development of carcass profiles, in particular the essential components, were taken into consideration according to EUROP classification (E: excellent, U: very good, R: good, O: fair, P: poor), and for degree of fat cover the amount of fat on the carcass outside and inside the thoracic cavity was taken into account using a classification range from 1 to 5 (1: low, 2: slight, 3: average, 4: high, 5: very high; OJEC, 1981a,b, 1991a,b). Each level of both scales was divided in 3 subclasses (i.e., conformation; R+, R, R−; fat cover: 3+, 3, 3−) to a transformed scale ranging from 1 to 15, with 15 as the best conformation and the thickest fat cover. Carcass length was measured according to the methodology described by De Boer et al. (1974) and compactness index as the ratio between carcass weight and carcass length.

The rib joint of the left half carcass (i.e., sixth through ninth rib) was removed and transported to the laboratory for further analysis. Total weight of the sixth rib was recorded and the LM separated from the rib, weighed, and the area measured by a digital planimeter (Planix 7, Tamaya Technics Inc., Tokyo, Japan). The rest of the rib was frozen at −20°C for further detailed dissection into lean, subcutaneous fat, intermuscular fat, bone, and other tissues (i.e., blood vessels, ligaments, tendons). Dissection data from the sixth rib were used to predict the carcass composition according to Oliván et al. (2001).

Water-holding capacity was determined in the LM of the ninth rib 48 h postmortem according to 2 measurements: expressible juice, as the release of juice from meat during application of external pressing (i.e., filter-paper press method, Grau and Hamm, 1953), and drip loss, as the formation of exudates from meat without application of external forces (Honikel, 1998).

Statistical Analysis

Data on animal performance and carcass characteristics were subjected to a general linear model procedure (PROC GLM, SAS Inst. Inc., Cary, NC) including the effects of genotype (i.e., AV *mh/mh*, AV *mh*/+, AV +/+, AM, and AM × AV), year, and the interaction between genotype and year in the model, and considering pens as experimental units (i.e., 2 replicates per genotype within each year). Initial age and BW were included as covariables in the model for the analysis of live performance traits. For the analysis of carcass traits, age at slaughter was included as a covariable. The LSMEANS and PDIFF options were used for generating least squares means, and comparison of treatments was done by Tukey test. Polynomial regressions incorporating linear and quadratic coefficients were conducted using the REG procedure of SAS to evaluate the relationship between selected variables. When the quadratic effects were not significant ($P > 0.05$), models were then reprocessed with only the linear effect. Partial correlations between performance and carcass variables were obtained using PROC GLM, including genotype and year as fixed effects.

RESULTS

Production Traits

Daily BW gains and performance indexes are presented in Table 1. At the beginning of the fattening period, calves from different genotypes had similar ages, ranging between 253 and 270 d. At this time, AM calves were lighter (206 kg) than AV breed (average of 235 kg, $P = 0.059$), whereas AM × AV had intermediate BW (217 kg). The longest fattening period ($P < 0.001$) was observed in AM calves (251 d). There were no differences in the fattening period of the other 4 genotypes, averaging 222 d for AV and 230 d for AM × AV.

Postweaning ADG was affected by breed ($P < 0.001$) but not significantly by the presence of the myostatin gene mutation, despite double-muscled (*mh/mh*) animals showing numerically greater values than other AV genotypes. At the time of slaughter, AM calves were the oldest (532 d, $P < 0.001$) and the lightest (496 kg, $P = 0.003$). Conversely, AV animals were the youngest (473 d) and the heaviest (539 kg). The age of AM × AV animals did not differ from AV genotypes (495 d), and their BW at slaughter was between that of AV +/+ and AM.

The AV +/+ and AV *mh*/+ animals showed the greatest ADFI, whereas AM animals showed the least. Intermediate intakes were recorded for AM × AV and AV *mh/mh* animals. In general, animals with larger body size ate greater amounts of concentrate per day, except for AV *mh/mh* animals, which also showed the greatest ($P < 0.001$) feed conversion. Differences in G:F between genotypes were even greater when concentrate intakes were related to the final carcass weights ($P < 0.001$), which were also related to differences between genotypes in carcass dressing percentages. In contrast to the least G:F found in the AM breed, RFI values showed a greater ($P < 0.001$) feed efficiency of AV *mh/mh* and AM genotypes compared with the others, though the interaction with year was also significant ($P < 0.001$).

Carcass Characteristics

Results of carcass and meat quality measurements are given in Table 2. The AV animals showed the greatest ($P < 0.001$) cold carcass weight. Differences within AV genotype were also observed, with AV *mh/mh* animals showing a greater carcass weight (339 kg) compared with other AV genotypes (307 kg). The AM and AM × AV animals showed the lightest carcass weights (278 kg). Carcass yield in AV animals was also greater ($P < 0.001$) than in AM, with AM × AV bulls being intermediate. Within the AV breed, AV *mh/mh* animals showed greater carcass yields (62.7%) than AV *mh*/+ and AV +/+ (57.1%).

Regarding carcass visual assessment, AV animals showed the best conformation index (most muscular, average of 11.5), whereas AM animals showed the least (7.7). As expected, conformation within AV calves was related to the level of presence of myostatin gene mutation, with AV *mh/mh* animals having a better ($P < 0.001$) conformation (13.9) than AV *mh*/+ and AV +/+ (10.6 and 9.9, respectively). Opposite results were obtained for the degree of fat cover, with AV *mh/mh* animals showing minimal fat cover (2.43) and other genotypes showing greater amounts (average value of 4.69). As a result, a negative and linear relationship between carcass conformation and degree of fat cover across genotypes ($y = 9.30 - 0.49x$; $R^2 = 0.61$; $P < 0.001$) was found.

The AV *mh*/+ and AV +/+ animals had the longest carcasses (128 cm, $P = 0.001$), whereas the shortest carcasses were obtained from AV *mh/mh* and AM animals (125 cm). In general, AV carcasses were the most compact (average of 2.50), whereas AM carcasses were the least compact (2.17, $P < 0.001$). Within the AV breed, double-muscled carcasses showed the greatest compactness (2.73), whereas AV +/+ animals had the least (2.34). Compactness was positively correlated with carcass conformation across genotypes ($r = 0.93$, $P < 0.001$) and, therefore, with the presence of myostatin gene and carcass weight.

The weight of the sixth rib did not differ between genotypes. However, significant differences in LM weight ($P = 0.001$) and area ($P < 0.001$) were observed. Muscles obtained from AV *mh/mh* animals were heavier and bigger in area (383 g and 72.9 cm^2), whereas AV +/+, AM × AV, and AM showed the least values. A positive and linear regression between LM weight and carcass conformation ($y = 150.9 + 16.1x$; $R^2 = 0.46$; $P < 0.001$) was observed. Dissection of the sixth rib was also a good reflection of LM weight. In general, AV *mh/mh* animals had a greater percentage ($P < 0.001$) of lean (84.6%) and smaller percentages of fat (1.15% subcutaneous fat, 4.74% of intermuscular fat), bone (8.47%), and other components (1.21%). Other genotypes (i.e., AV +/+, AM, and AM × AV) had less lean (76.1%) and greater total fat contents (12.6%). The AV *mh*/+, AV +/+, and AM animals had the greatest bone percentage (10.1%). A negative and linear regression between muscle and fat content across genotypes ($y = 22.1 - 1.1x$; $R^2 = 0.68$; $P < 0.001$) was observed.

Water-holding capacity of LM based on expressible juice or drip loss confirmed differences between genotypes ($P < 0.01$). Meat from double-muscled animals lost greater amounts of water (23.1 and 2.42% for expressible juice and drip loss, respectively), whereas meat from AM animals lost the smallest amounts (20.3 and 0.95%, respectively). Although meat from other genotypes gave intermediate values, AV +/+ and AM × AV were closer to AM than AV *mh*/+ animals. A

Table 1. Production performance (mean ± SE) of concentrate-finished yearling bulls from different genotypes

Item	Genotype[1]						Effect[2]			
	AV *mh/mh*	AV *mh*/+	AV +/+	(AV)	AM	AM × AV	G	Yr	G × Yr	Cov
Initial age, d	257 ± 6	253 ± 9	253 ± 10	(254 ± 5)	270 ± 11	265 ± 10	0.207	<0.001	0.222	—
Initial BW, kg	231 ± 14	248 ± 19	225 ± 11	(235 ± 8)	206 ± 9	217 ± 9	0.076	0.009	0.850	—
Fattening period, d	218^b ± 7	224^b ± 8	226^b ± 11	(222 ± 5)	251^a ± 10	230^b ± 8	<0.001	<0.001	0.609	<0.001
ADG, kg/d	1.45^a ± 0.04	1.38^a ± 0.06	1.39^a ± 0.05	(1.41 ± 0.03)	1.12^b ± 0.02	1.29^{ab} ± 0.03	<0.001	0.127	0.889	0.374
BW at slaughter, kg	541^a ± 9	541^a ± 9	535^{ab} ± 8	(539 ± 5)	496^c ± 10	511^{bc} ± 8	0.003	0.090	0.347	0.124
Age at slaughter, d	472^b ± 9	466^b ± 11	479^b ± 16	(473 ± 7)	532^a ± 13	495^b ± 14	<0.001	<0.001	0.158	0.319
ADFI, kg/d	6.72^c ± 0.16	7.13^{ab} ± 0.16	7.25^a ± 0.17	(7.03 ± 0.10)	6.39^d ± 0.21	6.93^{bc} ± 0.23	<0.001	<0.001	0.011	0.978
G:F,[3] kg/kg	0.217^a ± 0.006	0.195^b ± 0.010	0.192^b ± 0.007	(0.202 ± 0.005)	0.177^b ± 0.007	0.186^b ± 0.007	<0.001	0.044	0.487	0.287
G:F,[4] kg/kg	0.136^a ± 0.004	0.113^b ± 0.006	0.109^{bc} ± 0.004	(0.119 ± 0.004)	0.097^c ± 0.004	0.104^{bc} ± 0.003	<0.001	0.054	0.458	0.213
RFI,[5] kg/d	-0.322^a ± 0.059	0.135^b ± 0.073	0.275^b ± 0.042	(0.029 ± 0.069)	-0.253^a ± 0.057	0.248^b ± 0.062	<0.001	0.069	<0.001	<0.001

[a–d]Within a row, means without a common superscript differ ($P < 0.05$).
[1]Genotypes: AV = Asturiana de los Valles breed; *mh/mh* = double muscled; *mh*/+ = heterozygote; +/+ = normal; (AV) = average of 3 AV genotypes; AM = Asturiana de la Montaña breed.
[2]G = genotype; Cov = covariable effect of initial BW.
[3]kg of BW per kg of concentrate.
[4]kg of carcass weight per kg of concentrate.
[5]RFI = residual feed intake.

Table 2. Carcass characteristics (mean ± SE) of concentrate-finished yearling bulls from different genotypes

	Genotype[1]						Effect[2]			
Item	AV *mh/mh*	AV *mh/+*	AV +/+	(AV)	AM	AM × AV	G	Yr	G × Yr	Cov
Cold carcass weight, kg	$339^{a} \pm 7$	$312^{b} \pm 5$	$302^{b} \pm 4$	(318 ± 4)	$272^{c} \pm 6$	$285^{c} \pm 5$	<0.001	0.014	0.246	0.419
Carcass yield, %	$62.7^{a} \pm 0.3$	$57.7^{b} \pm 0.3$	$56.5^{bc} \pm 0.3$	(59.0 ± 0.6)	$54.8^{d} \pm 0.4$	$55.8^{cd} \pm 0.3$	<0.001	0.270	0.596	0.678
Conformation	$13.94^{a} \pm 0.17$	$10.57^{b} \pm 0.17$	$9.93^{bc} \pm 0.38$	(11.48 ± 0.39)	$7.72^{d} \pm 0.19$	$9.03^{c} \pm 0.33$	<0.001	0.342	0.045	0.345
Degree of fat cover	$2.43^{b} \pm 0.27$	$4.83^{a} \pm 0.30$	$4.88^{a} \pm 0.25$	(3.76 ± 0.28)	$4.30^{a} \pm 0.41$	$4.77^{a} \pm 0.28$	<0.001	0.001	0.232	0.034
Carcass length, cm	$125^{b} \pm 1$	$128^{a} \pm 1$	$129^{a} \pm 1$	(127 ± 1)	$125^{b} \pm 1$	$127^{ab} \pm 1$	0.001	0.034	0.535	0.356
Compactness index, kg/cm	$2.73^{a} \pm 0.04$	$2.43^{b} \pm 0.03$	$2.34^{bc} \pm 0.03$	(2.50 ± 0.04)	$2.17^{d} \pm 0.03$	$2.23^{cd} \pm 0.02$	<0.001	0.052	0.143	0.408
6th-rib weight, g	1,748 ± 62	1,654 ± 70	1,545 ± 49	(1,649 ± 38)	1,680 ± 91	1,646 ± 38	0.177	0.370	0.751	0.903
LM weight, g	$383^{a} \pm 13$	$335^{ab} \pm 14$	$293^{bc} \pm 11$	(337 ± 10)	$274^{c} \pm 11$	$296^{bc} \pm 21$	0.001	0.038	0.614	0.256
LM area, cm^2	$72.9^{a} \pm 1.6$	$62.7^{b} \pm 1.4$	$57.2^{c} \pm 2.2$	(64.3 ± 1.7)	$52.2^{d} \pm 1.1$	$57.1^{c} \pm 2.0$	<0.001	0.073	0.002	0.891
6th-rib dissection										
Lean, %	$84.6^{a} \pm 0.3$	$78.2^{b} \pm 0.6$	$76.0^{c} \pm 0.6$	(79.6 ± 0.8)	$75.6^{c} \pm 0.6$	$76.7^{bc} \pm 0.7$	<0.001	<0.001	0.530	0.744
Subcutaneous fat, %	$1.15^{b} \pm 0.18$	$2.34^{a} \pm 0.20$	$2.42^{a} \pm 0.17$	(1.81 ± 0.14)	$2.79^{a} \pm 0.28$	$2.44^{a} \pm 0.19$	<0.001	0.039	0.793	0.066
Intermuscular fat, %	$4.74^{c} \pm 0.20$	$8.26^{b} \pm 0.32$	$9.93^{ab} \pm 0.50$	(7.65 ± 0.49)	$9.70^{ab} \pm 0.59$	$9.96^{a} \pm 0.34$	<0.001	0.027	0.754	0.942
Total fat, %	$5.75^{c} \pm 0.26$	$10.36^{b} \pm 0.44$	$12.26^{ab} \pm 0.54$	(9.46 ± 0.62)	$12.94^{a} \pm 0.71$	$12.49^{a} \pm 0.41$	<0.001	0.009	0.729	0.531
Bone, %	$8.47^{b} \pm 0.16$	$10.05^{a} \pm 0.23$	$10.28^{a} \pm 0.21$	(9.60 ± 0.20)	$9.85^{a} \pm 0.20$	$9.39^{ab} \pm 0.46$	<0.001	0.312	0.682	0.692
Others, %	$1.21^{c} \pm 0.04$	$1.39^{bc} \pm 0.05$	$1.45^{ab} \pm 0.06$	(1.35 ± 0.03)	$1.60^{a} \pm 0.06$	$1.42^{ab} \pm 0.06$	<0.001	0.125	0.124	0.187
Expressible juice, %	$23.1^{a} \pm 1.0$	$22.4^{ab} \pm 0.7$	$21.4^{b} \pm 0.6$	(22.3 ± 0.4)	$20.3^{c} \pm 0.4$	$21.6^{b} \pm 0.5$	<0.001	<0.001	0.002	0.819
Drip loss, %	$2.42^{a} \pm 0.28$	$1.63^{ab} \pm 0.20$	$1.32^{c} \pm 0.11$	(1.79 ± 0.16)	$0.95^{c} \pm 0.05$	$1.56^{ab} \pm 0.06$	0.004	0.565	0.619	0.284

[a–d]Within a row, means without a common superscript differ ($P < 0.05$).

[1]Genotypes: AV = Asturiana de los Valles breed; *mh/mh* = double muscled; *mh/+* = heterozygote; +/+ = normal; (AV) = average of 3 AV genotypes; AM = Asturiana de la Montaña breed.

[2]G = genotype; Cov = covariable effect of age at slaughter.

positive and linear relationship between drip loss and carcass conformation ($y = -0.64 + 0.22x$; $R^2 = 0.56$; $P < 0.001$) was found, whereas a negative linear relationship between drip loss and total fat content (dissection data from the sixth rib; $y = 2.94 - 0.13x$; $R^2 = 0.38$; $P < 0.001$) and a quadratic relationship between drip loss and carcass fat cover ($y = 3.61 - 0.84x + 0.07x^2$; $R^2 = 0.65$; $P < 0.01$) were found.

Differences ($P < 0.001$) between years were observed for the majority of the variables studied. However, ADG, carcass yield and conformation, sixth-rib weight, percentages of bone and other components, and drip loss were not affected by year. In general, no interactions between genotype and year were observed among the variables studied.

Correlations

Partial correlation coefficients between live performance and carcass variables are presented in Table 3. Average daily gains were positively correlated with cold carcass weight ($r = 0.67$; $P < 0.001$), conformation index ($r = 0.32$; $P = 0.077$), carcass length ($r = 0.51$; $P = 0.004$), and compactness index ($r = 0.59$; $P = 0.001$). Feed conversion values (G:F ratio calculated per BW or carcass weight) also correlated positively with previously mentioned carcass traits, whereas ADFI and BW at slaughter correlated positively with carcass weight, length, and compactness. In addition, ADG and G:F showed negative correlations with fat cover degree. However, all these performance traits in general showed weak and nonsignificant correlations with the rib and LM variables, with the exceptions of those between BW at slaughter and LM area ($r = 0.43$; $P = 0.016$), and between ADFI and expressible juice ($r = 0.56$; $P = 0.001$). The length of fattening period positively correlated with sixth-rib weight ($r = 0.53$; $P = 0.002$), whereas age at slaughter correlated positively with carcass fat cover degree ($r = 0.34$; $P = 0.065$) and negatively with the percentage of waste tissues ($r = -0.40$; $P = 0.024$). Residual feed intake values showed weak correlations with carcass traits, except for positive correlations with expressible juice and drip loss.

DISCUSSION

Regarding animal performance variables, it is important to note that, although initial ages of genotypes were not statistically different, AM were lighter at the beginning of the trial. Moreover, after a longer period of time in the feedlot (251 d vs. an average of 224 d for other genotypes), final slaughter weight was not as great (496 kg) as in the other groups (511 kg for AM × AV and an average of 539 kg for AV). This was probably due to different growth rates inherent to the breed itself, which is further supported by the absence of significant covariable effects of initial age and BW on ADG. Animals from AM breed are rustic and early maturing with the ability to accumulate greater fat amounts, whereas AV animals, which are more specialized in beef production, are characterized by being late-maturing, having larger adult size and less fat content (Alberti et al., 2008). In general, ADG in AV and AM breeds (1.41 and 1.12 kg/d, respectively) were similar to those reported by Piedrafita et al. (2003) when 7 Spanish regional beef breeds were studied (AV 1.41 and AM 1.03 kg/d), or by Alberti et al. (2008) when 15 European breeds were compared (AV 1.30 and AM 1.12 kg/d). However, the effects of the double-muscling gene on postweaning ADG remain unclear. In the present study, numerically greater ADG were observed in AV *mh/mh* calves (1.45 kg/d), although not significantly different from the BW gains obtained by AV *mh/+* and AV +/+ animals (average of 1.39 kg/d). These findings are in accordance with those of Short et al. (2002) in the Piedmontese breed, and Wiener et al. (2002) in the South Devon breed, who found no differences in ADG between animals with 0, 1, or 2 copies of the gene causing double-muscling. Other studies conducted by Nott and Rollins (1979) and Arthur et al. (1989), where the genetic influence on double-muscling was recognized but no formal test for genotyping was available, also found similar performances of double-muscled and normal animals at yearling weights. In contrast, other researchers have reported greater preweaning but reduced postweaning growth rates for double-muscled compared with normal calves (Vissac and Perreau, 1968; Vissac et al., 1973; Geay et al., 1982). Aforementioned results are in opposition to those observed in double-muscled AV (K. Osoro, unpublished data) and Rubia Gallega calves (Monserrat and Sánchez, 1991). Superior growth rates of double-muscled animals in pre- or postweaning stages were also observed in studies involving breeds with medium growth potential (Falliez, 1966; Trillat, 1967). These contradictory results might be indicative of other genes apart from the myostatin gene, which could also be related to BW gains at later stages in life (Kambadur et al., 1997; McPherron and Lee, 1997; Grobet et al., 1998). Overall, the observed ADG values in this study for double-muscled AV bulls (1.45 kg/d) were greater than those found by Hornick et al. (1998) in double-muscled Belgian Blue animals fed ad libitum from 300 to 630 kg of final BW, promoting rapid growth (1.32 kg/d), or by Coopman et al. (2007) in double-muscled Belgian Blue animals between 7 (189 kg) and 20 (628 kg) mo of age.

Regarding ADFI, Arthur (1995) and some earlier studies by Trillat (1967) and Geay et al. (1982) indicated that double-muscled animals have a reduced appetite, resulting in less feed intake during the postweaning period. Arthur (1995) also pointed out that this decrease in feed intake was related to a reduced size of the digestive tract. Additionally, Cima (1996) observed less rumen weight (30% less) and whole gut weight (13% less) in the AV breed than what would be expected in animals of the same size with normal conformation. This could limit their feed intake capacity and hence reduce their growth rates compared with

Table 3. Partial correlation coefficients (r) and significance (*P*-values) between performance and carcass variables in concentrate-finished yearling bulls after adjusting for the effects of genotype and year[1]

Carcass variable[2]		Performance variable								
		IBW	FP	ADG	BWS	Age	ADFI	G:F[3]	G:F[4]	RFI
CCW	r	0.21	−0.14	0.67	0.92	−0.09	0.48	0.47	0.52	−0.07
	P	0.267	0.437	0.000	0.000	0.648	0.007	0.007	0.002	0.726
CY	r	−0.17	0.16	0.09	−0.02	−0.05	−0.02	0.07	0.24	0.02
	P	0.347	0.400	0.645	0.905	0.807	0.906	0.716	0.187	0.931
Conf	r	0.00	−0.22	0.32	0.14	−0.05	−0.02	0.34	0.42	−0.18
	P	0.984	0.238	0.077	0.458	0.778	0.930	0.061	0.017	0.322
FC	r	0.12	0.12	−0.36	−0.14	0.34	−0.28	−0.26	−0.35	−0.18
	P	0.509	0.517	0.047	0.467	0.065	0.133	0.161	0.057	0.334
CL	r	0.15	−0.16	0.51	0.71	−0.13	0.35	0.38	0.34	−0.06
	P	0.405	0.403	0.004	0.000	0.492	0.050	0.036	0.065	0.745
CI	r	0.17	−0.13	0.59	0.79	−0.06	0.47	0.40	0.48	0.01
	P	0.364	0.484	0.001	0.000	0.759	0.008	0.027	0.007	0.974
RW	r	−0.50	0.53	0.24	0.14	0.13	0.23	0.13	0.19	0.32
	P	0.005	0.002	0.201	0.441	0.498	0.211	0.482	0.298	0.077
LMW	r	−0.28	0.19	0.27	0.10	−0.22	0.05	0.26	0.33	0.03
	P	0.122	0.319	0.136	0.601	0.230	0.807	0.158	0.066	0.876
LMA	r	0.30	−0.17	0.23	0.43	−0.20	0.08	0.16	0.21	−0.24
	P	0.106	0.355	0.221	0.016	0.276	0.664	0.395	0.260	0.201
MU	r	−0.10	0.08	−0.12	−0.23	−0.20	−0.22	−0.05	0.02	−0.10
	P	0.585	0.675	0.515	0.216	0.270	0.231	0.777	0.905	0.604
SC	r	−0.10	0.23	−0.05	−0.014	0.25	−0.07	−0.03	−0.07	−0.02
	P	0.607	0.219	0.797	0.941	0.167	0.719	0.862	0.711	0.936
IT	r	0.00	−0.18	0.26	0.17	0.15	0.30	0.16	0.09	0.19
	P	0.998	0.344	0.166	0.368	0.428	0.106	0.405	0.642	0.316
TF	r	−0.3	−0.07	0.20	0.14	0.22	0.23	0.12	0.05	0.15
	P	0.857	0.709	0.277	0.458	0.241	0.215	0.516	0.791	0.409
BO	r	0.30	−0.02	−0.14	0.24	0.06	0.03	−0.14	−0.14	−0.10
	P	0.102	0.932	0.463	0.184	0.729	0.877	0.454	0.466	0.585
OT	r	−0.12	0.01	−0.12	−0.29	−0.40	−0.22	−0.00	−0.04	−0.07
	P	0.527	0.972	0.521	0.115	0.024	0.237	0.992	0.838	0.710
EJ	r	0.01	−0.03	0.10	0.16	0.19	0.56	−0.16	−0.14	0.54
	P	0.947	0.889	0.578	0.387	0.302	0.001	0.375	0.466	0.002
DL	r	−0.10	−0.08	−0.07	−0.23	−0.09	0.28	−0.23	−0.20	0.45
	P	0.669	0.737	0.767	0.313	0.685	0.206	0.310	0.384	0.035

[1]IBW = initial BW; FP = fattening period; BWS = BW at slaughter; age = age at slaughter; RFI = residual feed intake.

[2]CCW = cold carcass weight; CY = carcass yield; Conf = conformation score; FC = fat cover degree; CL = carcass length; CI = compactness index; RW = rib weight; LMW = LM weight; LMA = LM area; MU = muscle; SC = subcutaneous fat; IT = intermuscular fat; TF = total fat; BO = bone; OT = other tissues; EJ = expressible juice; DL = drip loss.

[3]BW-to-feed ratio.

[4]Carcass weight-to-feed ratio.

other breeds. Moreover, Boucqué et al. (1984) and Fiems et al. (1995) also found some special requirements in finishing double-muscled Belgian Blue bulls. These authors confirmed the need for extra protein in the diet compared with animals with normal conformation (Boucqué et al., 1980; Levy et al., 1980; Anderson et al., 1988), and these results have been more recently confirmed by Fiems et al. (1998) and De Campeneere et al. (1999). A 25% greater energy requirement of double-muscled compared with non-double-muscled calves was also confirmed by Vermorel et al. (1994) and De Campeneere et al. (2001). In the present study, all genotypes were fed the same concentrate meal but less ADFI was observed in double-muscled AV animals (6.72 kg/d) compared with the other AV genotypes (average of 7.19 kg/d). For AV double-muscled animals, ADFI was less but G:F was greater (0.22) than those reported by Hornick et al. (1998) in double-muscled Belgian Blue animals when finishing ad libitum (9.7 kg/d and 0.14, respectively).

As a consequence of the reduced ADFI while achieving increased ADG, AV double-muscled animals showed better feed efficiencies (greater G:F and smaller RFI values) than other genotypes. A better efficiency (G:F) of double-muscled animals has been previously reported by Geay et al. (1982). By contrast, RFI calculated on the basis of daily feed intake showed a similar efficiency between AV *mh/mh* and AM animals, being less in the other genotypes. Because RFI is phenotypically independent of ADG and $BW^{0.75}$ by definition (Koch et al., 1963), it implies that AM bulls ate less feed than those expected in a daily basis. However, considering the longer fattening periods taken in AM to attain acceptable final BW, even though target BW is less, the absolute amounts consumed were greater compared with other genotypes, thus increasing total feeding costs.

Regarding carcass characteristics, some of the observed differences between genotypes for traits such as length, compactness, and LM area, and obviously for cold carcass weight, may be partly attributable to differences observed in BW at slaughter as indicated by the significant correlations observed. However, the differences found in the other carcass traits (yield, conformation, sixth-rib characteristics and water holding capacity) would be mostly dependent on genotype regardless of the final BW achieved. Double-muscled animals from the AV breed showed greater carcass yield (62.7%), and similar results were observed by Piedrafita et al. (2003; 63.6%) and Alberti et al. (2008; 62.6%). Increased carcass yields were also obtained by Fiems et al. (2003; 66.6%) and Hornick et al. (1998; 64.3%) in double-muscled Belgian Blue animals. Likewise, greater yields in double-muscled compared with heterozygote (*mh*/+) and normal (+/+) animals were observed elsewhere (Arthur et al., 1989; Casas et al., 2004). In general, differences between heterozygote and normal animals were small. The medium-sized or rustic genotypes studied showed less carcass yields (55.8 and 54.8% for AM × AV and AM, respectively) together with reduced scores for carcass conformation (9.0 and 7.7, respectively) but similar degrees of fat cover to AV *mh*/+ and AV +/+ genotypes, agreeing with the results obtained by Alberti et al. (2008).

Differences in carcass characteristics related to double-muscled animals have been widely reported in Belgian Blue (Bouton et al., 1982; Uytterhaegen et al., 1994; Arthur, 1995; Nürnberg et al., 1999) and Piedmontese cattle (Wheeler et al., 2001; Biagini and Lazzaroni, 2005). Double-muscled animals from this study also produced carcasses with great conformation scores but less degrees of fat cover. As reported in previous studies (Martínez et al., 2003), reduced fat cover scores for *mh/mh* animals was clearly reflected in the sixth-rib dissection, with increased lean but reduced intermuscular and subcutaneous fat percentages. Less fat content of double-muscled compared with normal homozygote animals (+/+) was also reported by Fiems et al. (2000) in Belgian Blue breed. These authors found 12.2% of total dissectible fat (eighth rib), whereas only 5.8% was found in the present study for AV *mh/mh* (sixth rib). Apparently, meat obtained from AV animals seemed to be leaner than meat from Belgian Blue animals. However, it is recognized that a certain amount of fat in meat is desirable to improve sensorial variables (i.e., juiciness and flavor; Farmer, 1994; Osoro et al., 2003). Savell and Cross (1988) recommended a minimum intramuscular fat content of 3% in meat products. Furthermore, some cover of subcutaneous fat can also insulate carcass and slow down the postmortem chilling process, avoiding tenderness problems (i.e., cold shortening). However, it is known that double-muscled animals provide a very tender meat after few days postmortem. Consequently, the influence of carcass fat content could be less important in these animal types compared with non-double-muscled animals that normally need longer aging times (Uytterhaegen et al., 1994; Fiems et al., 2000; Oliván et al., 2004).

There is some evidence suggesting a negative relationship between feed efficiency and fat deposition in growing cattle (e.g., Richardson et al., 2001; Basarab et al., 2003; Nkrumah et al., 2007). In this study, negative correlations between G:F and carcass fat cover were observed. However, no relationship was found between RFI and carcass or rib fat contents. Notwithstanding, AV *mh/mh* animals showing the best feed efficiencies also had the least fat content, and thus positive correlations between RFI values and fatness across genotypes were observed.

The LM weight and area were greater, and bone percentage was less in double-muscled animals. These animals also showed considerably greater muscle to bone ratios (10.0) than heterozygote (7.7) and normal (7.4) animals, in agreement with the results of Thiessen (1974). In general, heterozygote animals showed intermediate characteristics but were closer to normal. This pattern of differences between genotypes (*mh/mh*, *mh*/+, and +/+) has been previously reported in other breeds (Ménissier, 1982; Shahin and Berg, 1985; Arthur et al., 1989; Fiems et al., 2000; Short et al., 2002; Wiener et al., 2002; Casas et al., 1998, 2004). On the whole, scores for carcass traits of the more rustic breed (AM) were typically less, whereas AM × AV animals were quite close to normal (+/+) for most of the studied variables.

Water-holding capacity, measured as a percentage of expressible juice and drip loss, was least in double-muscled, intermediate in *mh*/+, and greater in +/+ animals, as previously found by Oliván et al. (2004) and Aldai et al. (2006) in the AV breed, and by Uytterhaegen et al. (1994) and De Smet et al. (2000) in the Belgian Blue breed. However, AM meat showed the greatest water-holding capacity, whereas AM × AV were intermediate and similar to AV +/+. Water-holding capacity is of particular economic importance due to its relationship with weight losses during storage, freezing and thawing, or meat cooking. It provides information on changes in meat protein structure and can be affected by animal factors (e.g., sex, age, breed, muscle type, preslaughter stress). It can influence meat quality parameters like juiciness, tenderness, and color (Hamm, 1986). Oliván et al. (2003) proposed that water-holding capacity could be positively related to intramuscular fat content. In this study, negative correlations between drip loss and fat contents were found across genotypes, but not within genotypes.

Overall, from the production point of view, double-muscled AV animals, with increased muscle and very small fat and bone percentages, would be more appropriate to meet current demands of consumers. Producers would be benefited because of the increased growth potential and reduced costs of these animals at intensive feeding. In addition, the better conformation of double-muscled AV bulls has a direct impact on financial income because in the European market carcasses are valued primarily by conformation (Drennan et al., 2002). Other genotypes are less appropriate for intensive production despite their greater water-holding capacity, fat content, and in consequence, greater flavor.

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