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Genetic analysis of breeding traits in a Charolais cattle population segregating an inactive myostatin allele

F. Phocas¹

Institut National de la Recherche Agronomique, UMR1313 Génétique Animale et Biologie Intégrative,
bat 211, F-78352 Jouy-en-Josas

ABSTRACT: The objective of this study was to quantify the effects of the Charolais-specific inactive myostatin allele on phenotypic means and genetic parameters of heifer breeding traits. Records were registered from 1996 to 2006 in 282 herds dedicated to the on-farm French Charolais purebred progeny test. Data consisted of 36,867 female calf records, including 17,518 inseminated heifers that were bred by 186 genotyped sires, of which 43 were heterozygous and 6 were double muscled bulls. Six traits were analyzed under a univariate animal model accounting for maternal effects and myostatin sire genotype: calving difficulty, birth and weaning weights, muscle and skeleton scores at weaning, and fertility of artificially inseminated heifers. The inactive myostatin allele had a large positive effect on weaned heifer muscle score, unfavorable effects on calving difficulty and skeleton score, and small effects on birth and weaning weight. This allele did not induce an

adverse effect on heifer fertility. Univariate estimates of polygenic variance parameters were almost unaffected by the estimation of the myostatin sire genotype, except for heifer morphology traits. Direct and maternal genetic variances and covariances were significantly reduced under a model accounting for the myostatin sire genotype effect on muscle score. The myostatin genotype explained 45% of the direct genetic variance and had a pleiotropic action across both direct and maternal effects on muscle score. Because the myostatin sire genotype had no significant effect on birth weight, the multitrait sire analysis concerned only the 5 other traits. Accounting for the myostatin sire genotype, estimates of polygenic correlation between skeleton score and muscle score, on the one hand, and calving difficulty on the other hand, were largely modified: from a negative estimate of -0.3 to 0.0 and from a positive estimate of 0.4 to 0.7 , respectively.

Key words: beef cattle, calving difficulty, double muscling, fertility, genetic parameter, myostatin

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INTRODUCTION

The so-called double muscling phenotype is a muscular hypertrophy due to an increase in the volume of muscle cells, which is explained by disruptive mutations in the myostatin gene (Grobet et al., 1997, 1998). It is associated with some breeding problems such as reduced fertility, dystocia, reduced calf survival, and milking cow ability (Ménissier, 1982; Hanset et al., 1989). However, cattle showing the syndrome have greater meat yield and meat quality (lean and tender meat) as reviewed by Arthur (1995). Literature information on the effects of double muscling is mainly available for the Belgian Blue breed (Ménissier, 1982; Hanset et al., 1989), crossbred populations (Arthur et al., 1989; Casas et al., 1999, 2004; Short et al., 2002), and South Devon cattle (Wiener et al., 2002). However,

the double-muscled syndrome is found in many breeds of cattle and is often due to different alleles of the myostatin gene. In the Charolais breed, a specific inactivated myostatin mutation, named Q204X, segregates and corresponds to a cytosine to thymine substitution in the second exon of the myostatin gene (Grobet et al., 1998; Dunner et al., 2003). There is no evidence that different alleles of the myostatin gene playing a similar role in muscular hypertrophy should also have similar pleiotropic effects on other traits. Furthermore, the literature is mainly focused on dystocia, growth, conformation, and carcass traits. Few references focus on female breeding traits, and only in the Belgian Blue breed (Hanset et al., 1989) or crossbreds (Arthur et al., 1989; Casas et al., 1999; Short et al., 2002). Consequently, the first aim of the study was the estimation of myostatin pleiotropic effects on Charolais breeding traits, such as calving difficulty (**CD**), birth weight, weaning weight (**WW**), morphology, and fertility of heifers. A second objective was to assess the impact of the myostatin genotype on the estimation of genetic pa-

¹Corresponding author: florence.phocas@jouy.inra.fr
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Table 1. Number of records according to sire myostatin genotype and corresponding phenotypic means for breeding traits recorded on Charolais heifers

Item	Total data set	Normal sires	Heterozygous sires	Double muscled sires
Number of sires	186	137	43	6
Average number of daughters/sire	198	216	166	17
Total birth records	36,867	29,629	7,136	102
Total weaning records	31,442	25,349	6,010	83
Total reproductive records	17,518	14,229	3,273	16
Mean calving difficulty ¹	1.34	1.38	1.30	1.40
Mean birth weight, kg	45.2	44.6	45.9	45.6
Mean weaning weight, kg	267.1	265.7	271.5	250.4
Mean muscle score ²	59.8	59.0	62.7	68.4
Mean skeleton score ³	65.5	65.4	65.9	58.9
Mean fertility, %	56.6	56.9	55.3	68.7

¹Calving difficulty score ranges from 1 for unassisted calving to 4 for cesarean section.

²Muscle score is the sum of 5 subjective measurements assessing the calf muscular frame. It ranges from 0 to 100 points.

³Skeleton score is the sum of 5 subjective measurements assessing the calf skeletal frame. It ranges from 0 to 100 points.

rameters, in particular on genetic correlations between breeding traits.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from the existing French national database of cattle herds named SIG.

Data

Records were extracted from the French national database of cattle. Records concerned 282 Charolais herds located in Burgundy and Vendée that are dedicated to on-farm purebred progeny testing. Those herds had a large number of progeny born in 1996 to 2006 bred by 186 sires genotyped for the myostatin gene. Data editing consisted of selecting records from those sires and from contemporary groups with over 4 heifer records per herd-year. The final research data set included data of 36,867 female calves, from 24,213 dams, for CD, birth weight (**WO**) and **WW**, muscle (**MS**) and skeleton (**SS**) scores at weaning, and fertility. Fertility was measured by calving success following the first insemination on only 17,518 heifers selected for reproduction after weaning. Birth traits (**WO** and **CD**) were directly recorded by breeders. Calving difficulty was scored 1 for unassisted calving and 4 for a cesarean section. Weaning weight was adjusted to 210 d. Muscle and skeleton scores were scored over 100 points from visual appraisal. Muscle score was a sum of scores of 5 different subjective measurements to assess the calf muscular frame: width at withers, width behind withers, hindquarter width, curve of rump, and loin thickness. Skeleton score was a sum of scores of 5 other subjective measurements to assess the calf skeletal frame: stature, canon bone circumference, withers hooks length, hooks spins length, and spins width. Technicians belonging to agricultural institutes, which are independent of the breed societies, measured the **WW** and performed the

scoring for **MS** and **SS**. Table 1 presents the numbers of records and raw means of traits according to myostatin sire genotypes and the female populations that are concerned by the measurements: either heifers alive at birth (birth traits) and at weaning (weaning traits) or inseminated heifers (fertility). The small number (6) of double muscled sires is explained by the French Charolais breeding goal: the Q204X allele frequency should not increase in the purebred Charolais cow population, where this frequency is estimated at about 12% (Allais et al., 2008). Consequently, only 2 double muscled sires had over 30 daughters recorded at birth, corresponding to 10 and 6 heifer reproductive records, respectively.

Statistical Analyses

Data were analyzed by animal linear models using ASREML software (Gilmour et al., 2000). To easily derive genetic correlations across traits, discrete traits (like **CD** and fertility) were analyzed under linear models, knowing that estimates of genetic correlations are not affected by the statistical treatment (linear or threshold model) of the categorical trait (Kadarmideen et al., 2003).

The relationship matrix included 3 generations of ancestors that accounted for 69,463 animals in total. Apart from the animal effects, other random effects were maternal genetic and dam permanent environmental effects for all traits except fertility. Those effects had near zero variances for fertility, and, consequently, were ignored. Random mating bull effects were fitted for fertility, although they explained less than 0.3% of the phenotypic variance.

Fixed effects were the contemporary group herd-birth year for **CD** and **WO**; herd-year-weaning group for **WW**, **MS**, and **SS**; and herd-year-reproduction group for fertility. Because no reproduction group was indicated, following the strategy of Robinson and Johnston (2003), the reproduction group was defined within herd-year by 60-d intervals between last AI of a first group and first AI of a second group. The age of the

dam was also fitted for all traits into 6 classes: 3 classes for primiparous dams (<25 mo, 25 to 30 mo, >30 mo), 2 classes for the 2nd calving dams (below and over 42 mo) and the last class for multiparous cows over 42 mo. For birth and weaning traits, the last fixed effect was the birth period (5 levels: January to February, March to June, July to August, September to October, and November to December). For fertility, the heat synchronization treatment (no/yes), AI agent, and week day of the AI were also fitted, as well as the female age class at first AI (12 to 18 mo, 19 to 27 mo, and 28 to 30 mo) and the breeding period (5 levels: September to October, November to January, February to March, April to May, and June to August).

Univariate analyses were performed to determine the impact of myostatin sire genotype on each of the 6 traits, separately. A likelihood ratio test was performed to test the significance level of the sire genotype on each heifer trait. The *P*-value was derived from a chi-square distribution with 2 degrees of freedom (3 possible sire genotypes). Genetic parameters were estimated with both models accounting or not for the sire genotype as a fixed effect. Because 88% of the heifer dams are expected to be normal homozygous (and the last 12% only heterozygous) at the myostatin gene, the allelic substitution effect can be approximated by the effect estimated for the double muscled sire genotype because 94% of their daughters are expected to be heterozygous and only 6% double muscled. Whatever the mutant allele frequency, the contrast of progeny from double muscled sires vs. progeny of normal sires would cleanly estimate the allelic substitution effect under 3 conditions: additive gene action, no assortative mating, and a large sample of sires from each genotype. When considering that double muscled sires and heterozygous sires are drawn from the same genetic population, the heterozygous sire genotype effect should be one-half the effect observed for double muscled sires. Hence, another way to approximate the allelic substitution effect is to double the heterozygous sire genotype effect. Due to the small number of double muscled sires accounted for in our analysis, this last alternative should be preferred. The dominance, additive, or recessive effects of the Q204X allele on heifer traits could not be assessed because heifer genotypes were not available.

A multivariate analysis was performed for CD, WW, MS, SS, and fertility because they were the 5 traits exhibiting significant differences (*P*-value up to 10%) according to sire genotypes. For multivariate analysis, the maternal genetic effect was not accounted for, but a global maternal effect (including both genetics and permanent environment) was fitted for CD, WW, MS, and SS. Indeed, data information was not sufficient to estimate maternal genetic correlations (Heydarpour et al., 2008). Ignoring maternal genetic effects under an animal model may induce large overestimation of direct genetic variances (Meyer, 1992), and in consequence, may provoke bias in the estimation of direct genetic correlations. Because the focus was on getting

unbiased estimates of direct genetic correlations across heifer breeding traits, a sire model was considered for the multitrait analysis. The sire relationship matrix included 3 generations of ancestors that accounted for 784 sires in total. For each trait, the same fixed effects as in the univariate analysis were fitted in the multitrait model.

RESULTS AND DISCUSSION

Myostatin Sire Genotype Effects on Heifer Birth Traits

The goodness-of-fit of the model accounting for the effect of myostatin sire genotype on CD was not clearly better than the fit of the simple polygenic model: the *P*-value of the likelihood ratio (LR) test was only 10% (Table 2). However, this low significance level is probably due to the joint facts of a small effect of heterozygous sire on CD and a low number of records from double muscled sires. The effect of double muscled sire genotype on the birth condition of daughters was as large as the effect of the parity of the dams (i.e., primiparous versus second-calving dams). Short et al. (2002) found an allelic substitution effect equal to about 0.6 phenotypic SD on dystocia score of Piedmontese crossbred calves. This effect seemed to be additive. Here, the allelic substitution is only estimated to be 0.2 phenotypic SD on CD. Casas et al. (1999) did not find any significant contrast between CD of heterozygous and normal Piedmontese crossbred calves, but a significant increase of 19% in the proportion of CD for double muscled calves compared with heterozygous ones.

The LR test did not reveal any significant effect of the myostatin genotype on WO. Because of the nonsignificant LR test, it was decided to drop the WO records for running the multitrait analysis.

The allelic substitution effect was also estimated to about 20% of phenotypic SD on heifer birth weight (i.e., +1 kg is expected for a heterozygous compared with a normal female calf). Casas et al. (1999) estimated this contrast to +3 kg in Piedmontese crossbreds accounting for male and female calves. They did not find any significant contrast of birth weights between double muscled and heterozygous calves. However, most of the results in the literature found rather an additive gene action on WO with the magnitude of the allelic substitution effect ranging from 0.2 to 0.4 phenotypic SD. Short et al. (2002) found a larger and additive allelic substitution effect equal to about 0.4 phenotypic SD on birth weight. In a crossbred experimental population, Casas et al. (2004) looked at the effect of the inactive myostatin allele on WO within the Charolais sire line (Q204X allele) or Belgian Blue × British Breed sire line (nt821 allele). They found an allelic substitution effect of +2 kg at birth for both alleles. Vinet et al. (2006) compared the effects of the myostatin gene polymorphism on calf WO and conformation at 4 mo in a double muscled synthetic sire line, INRA95. In this

Table 2. Estimates of sire myostatin genotype effects on heifer traits (in contrast to normal sire genotype effects)

Trait	Heterozygous genotype (SE)	Double muscled genotype (SE)	Likelihood ratio test	P-value
Calving difficulty ¹	+0.06 (0.017)	+0.19 (0.065)	5.6	0.10
Birth weight, kg	+0.5 (0.26)	+0.6 (0.82)	1.0	0.84
Weaning weight, kg	+0.1 (1.43)	−8.2 (4.40)	8.0	0.02
Muscle score ²	+2.8 (0.51)	+9.0 (1.71)	45.4	<0.001
Skeleton score ³	−0.6 (0.46)	−5.1 (1.42)	12.4	<0.001
Fertility, %	+0.3 (1.53)	+4.75 (13.6)	6.2	0.07

¹Calving difficulty score ranges from 1 for unassisted calving to 4 for cesarean section.

²Muscle score is the sum of 5 subjective measurements assessing the calf muscular frame. It ranges from 0 to 100 points.

³Skeleton score is the sum of 5 subjective measurements assessing the calf skeletal frame. It ranges from 0 to 100 points.

population, 6 different inactive alleles of the myostatin gene were segregating. The authors found a significant contrast between 134 normal and 228 Q204X/Q204X calves of 0.5 phenotypic SD for WO, and 0.2 phenotypic SD between WO of 337 heterozygous and the 134 normal calves, corresponding to +1.5 kg at birth. This last result was consistent with our finding on Charolais purebred female calves.

Myostatin Sire Genotype Effects on Heifer Weaning Traits

The maximum significant LR test was for MS (Table 2). The allelic substitution effect was estimated to be 0.6 phenotypic SD of MS from the contrast between heterozygous and normal sire genotypes and 0.9 phenotypic SD when considering the contrast between double muscled and normal sire genotypes. Vinet et al. (2006) estimated the contrast between Q204X/Q204X and normal calves to be equal to 0.85 phenotypic SD on calf MS at 4 mo, whereas the contrast between heterozygous and normal calves was only 0.2 phenotypic SD. The Q204X allele effect seemed to be partially recessive on MS.

The LR test for skeletal score (Table 2) was also highly significant. The allelic substitution effect was estimated to be −0.15 phenotypic SD of SS from the contrast between heterozygous and normal sire genotypes and −0.60 phenotypic SD when considering the contrast between double muscled and normal sire genotypes. No information was found in the literature to discuss that result, apart from the well-known reduction in the weight of the skeleton of double muscled animals (Arthur, 1995). Given that SS was highly correlated with WW, the results were consistent with those presented below for WW.

The LR test indicated a significance level of 2% for the myostatin sire genotype on WW, although the contrast between heterozygous and normal sire genotypes was null. The contrast was −8 kg (i.e., about −0.3 phenotypic SD of WW) between double muscle and normal sire calves. The discrepancy between the 2 estimates of the allelic substitution effect may be due to the sampling genetic background of the 6 double muscled sires. The data seemed rather to indicate a null effect of the

Q204X allele on WW. Wiener et al. (2002) in South Devon cattle and Vinet et al. (2006) in the INRA95 sire line also found a nonsignificant contrast for WW between genotypes. On the contrary, Casas et al. (1999) found that heterozygous Piedmontese crossbred calves were significantly heavier than the 2 homozygous types, which had similar WO at weaning. However, their results were not confirmed by Short et al. (2002) in Piedmontese crossbreds, where no significant effect of the mutant allele was detected for WW. Once again, Casas et al. (2004) for the 11-pair deletion mutation of the Belgian Blue Breed and the Q204X mutation of the Charolais breed found a significant increase in the WW of the heterogeneous calves (+10 kg), 2 homozygous types having similar WW in the Belgian Blue crossbreds.

Myostatin Sire Genotype Effects on Heifer Fertility

The LR test (Table 2) did not clearly select the model accounting for the effect of myostatin sire genotype on fertility: the significance threshold was only 7%. The Q204X allele seemed to have a null effect, or even a slightly favorable effect (1 to 10% of phenotypic SD), on heifer fertility. Because information came from breeders and not from the experiment station, it was checked that these results were not biased by MS phenotypic selection of the normal heifers. Average MS of the inseminated heifers (Table 3) were very close to the average MS of all animals at weaning (Table 1) recorded before selection occurred for breeding. Heifer selection was clearly performed on greater SS and WW, and no counter-selection of double muscled or heterozygous heifers seemed to occur. On raw data (Table 1), fertility of heifers bred by heterozygous sires is less (−1.5%) than fertility of heifers bred by normal sires. However, the corresponding BLUP estimate is +0.3% with SE of 1.53%, clearly indicating no effect of sire genotype on fertility. The large, but nonsignificant, estimate of +4.7% for fertility of heifers sired by double muscled bulls was consistent with raw data, but is probably due to sampling error of the 2 sires or their 16 daughters. Indeed, this result seemed to be inconsistent with the literature (e. g., Ménéssier, 1982; Arthur et al., 1989;

Table 3. Phenotypic means for breeding traits recorded on artificially inseminated Charolais heifers according to their sire myostatin genotype

Mean trait	Total data set	Normal sires	Heterozygous sires	Double muscled sires
Calving difficulty ¹	1.33	1.36	1.24	1.12
Birth weight	45.7	45.3	47.1	44.1
Weaning weight, kg	271.1	269.4	278.5	258.9
Muscle score ²	60.8	59.9	64.2	68.3
Skeleton score ³	67.0	66.9	67.7	64.3
Fertility, %	56.6	56.9	55.3	68.7

¹Calving difficulty score ranges from 1 for unassisted calving to 4 for cesarean section.

²Muscle score is the sum of 5 subjective measurements assessing the calf muscular frame. It ranges from 0 to 100 points.

³Skeleton score is the sum of 5 subjective measurements assessing the calf skeletal frame. It ranges from 0 to 100 points.

Arthur, 1995), where double muscled Belgian Blue heifers had a 4% less nonreturn rate (Hanset et al., 1989) than normal heifers. It also can be thought from the experiment of Arthur et al. (1989) that the inactivated myostatin gene has rather a recessive effect on female fertility. However, no information based on genotypes rather than visual classification of animals was found in the literature of the last 10 yr. Fertility is a difficult trait to analyze due to its huge phenotypic variability (Table 4). In most analyses of on-farm data, the environmental effects considered for modeling heifer fertility are only the age of the heifer, her mating group, and her bull mate. In the present study, other large effects were also fitted such as the weekday of the AI (an AI on Monday had -2.7% less success than an AI on Wednesday) or the synchronization treatment (-4.2% on heifer fertility).

Impact of Myostatin Sire Genotype on Direct and Maternal Genetic (Co)variances Within Trait

Tables 4 and 5 present genetic and phenotypic parameters estimated by a univariate animal model for birth traits, WW, and fertility, and for morphology traits, respectively. Table 4 presents the results for a model not accounting for the myostatin genotype because almost the same variance components were estimated for CD, WO, WW, and fertility whether or not the myostatin sire genotype was accounted for. Parameters for weaning traits and fertility are quite similar to those previously estimated on the French Charolais population (Phocas and Laloë, 2004; Phocas, 2007). On the con-

trary, the direct-maternal genetic correlations for birth traits are clearly not statistically different from zero in this study, whereas previous estimates were negative (about -0.4). This was probably due to the fact that only female traits were recorded here, whereas male and female calves were both accounted for in the previous analysis.

For morphology traits (Table 5), and in particular for MS, genetic parameters were significantly different when accounting for the myostatin sire genotype in the model. As expected, the phenotypic and direct genetic variances were reduced under such a model. The variance reductions would have probably been larger if heifer genotypes, rather than sire genotypes, could have been fitted (Hoeschele, 1988). Maternal heritabilities of MS and SS, and direct heritability of SS were kept almost constant at about 0.04, 0.06, and 0.25, respectively. The direct heritability of MS dropped from 0.38 to 0.25. The direct-maternal genetic correlation for SS was kept almost constant at about -0.45 , whereas the corresponding correlation for MS increased from -0.45 to -0.11 as the maternal genetic variance was reduced from 4.2 to 3.4. This last phenomenon revealed some pleiotropic and negative action of the myostatin gene across maternal and direct effects of MS. However, only a small amount (4%) of the phenotypic variability is explained by the maternal genetics.

Impact of Myostatin Sire Genotype on Direct Genetic Correlations Across Traits

For the multivariate sire analysis, maternal genetic effects were ignored, but they were still accounted for

Table 4. Genetic parameters for calving difficulty (CD), birth weight (WO), weaning weight (WW), and fertility under polygenic animal univariate models (SE in parentheses)

Parameter	CD	WO	WW	Fertility
Phenotypic variance	0.310	28.72	790.0	2,410
Direct genetic variance	0.012	5.70	133.6	26.0
Maternal genetic variance	0.023	1.57	61.83	0
Permanent environment/ σ_p^2	0.11 (0.012)	0.12 (0.010)	0.13 (0.012)	0
Direct heritability	0.04 (0.010)	0.20 (0.031)	0.17 (0.030)	0.01 (0.005)
Maternal heritability	0.07 (0.014)	0.05 (0.013)	0.08 (0.017)	0
Direct-maternal genetic correlation	-0.07 (0.165)	-0.27 (0.118)	-0.39 (0.104)	—

Table 5. Genetic parameters of morphology traits at weaning (SE in parentheses) for univariate animal models

Parameter ¹	Muscle score		Skeleton score	
	Polygenic model	Model with myostatin gene	Polygenic model	Model with myostatin gene
σ_p^2	101.1	97.70	67.93	67.54
σ_d^2	38.72	24.89	17.25	15.70
σ_m^2	4.24	3.43	3.84	4.03
C^2	0.04 (0.011)	0.04 (0.011)	0.07 (0.011)	0.07 (0.011)
h^2_d	0.38 (0.051)	0.25 (0.038)	0.25 (0.040)	0.23 (0.038)
h^2_m	0.04 (0.013)	0.03 (0.011)	0.06 (0.014)	0.06 (0.015)
Rdm	-0.45 (0.119)	-0.11 (0.153)	-0.46 (0.104)	-0.44 (0.104)

¹ σ_p^2 = phenotypic variance; σ_d^2 = direct genetic variance; σ_m^2 = maternal genetic variance; C^2 = permanent environment/ σ_p^2 ; h^2_d = direct heritability; h^2_m = maternal heritability; Rdm = direct-maternal genetic correlation.

as a part of the permanent maternal random effect for CD, WW, MS, and SS of heifers. Table 6 presents the results both for the polygenic sire model and for the sire model accounting for the myostatin genotype as a fixed effect. Heritabilities were kept constant across models for CD, WW, SS, and fertility and were very similar to previous univariate estimates under the animal model. On the contrary, the drop in MS heritability when accounting for myostatin sire genotype was larger than in the univariate animal model analysis. Under the animal model, the myostatin sire genotype explained about one-third of the additive genetic variance, whereas it explained 45% of the genetic variance under a sire model. This last figure is a better estimate of the contribution of the myostatin gene to the genetic variance of MS due to the lack of knowledge of heifer genotypes under the animal model.

Under a polygenic model, the genetic correlations statistically different from zero (absolute value over twice the SE) were mainly the correlations between SS and the 4 other traits. The maximum correlation was estimated between SS and WW (over 0.8). Intermediate positive correlations were estimated between SS and fertility (0.5) or CD (0.4), and between CD and WW (0.4). Moderate negative correlations were estimated between MS and SS (-0.3) or fertility (-0.4).

When considering the myostatin sire genotype, the correlation estimate between WW and SS stayed re-

markably constant (over 0.8) due to the absence of a sufficient effect of the myostatin sire genotype on heifer WW. On the contrary, some large differences were observed in other correlation estimates. In particular, the correlation between MS and SS tended toward zero, indicating that the previous negative estimate was only due to the pleiotropic effect of the myostatin gene on MS and SS. The correlation between SS and CD was also greatly increased with a new estimate of about 0.7; the previous estimate was less due to the opposite sign of the myostatin genotype effect on both traits. Such a result questioned the general tendency to consider that estimates of genetic correlation close to zero correspond to traits that are genetically unlinked. In fact, the mathematical rule applying to independent variables should always be kept in mind: the correlation between 2 independent variables is zero, but a null correlation does not mean that 2 variables are independent.

The only literature information available on differences in genetic correlations when accounting for the myostatin genotype concerned the South Devon cattle where the same allele (nt821) as in the Belgian Blue Breed is segregating (Wiener et al., 2002). Three traits of their paper were almost comparable with CD, MS, and WW. Contrary to the present study, the authors found no significant correlation between CD and WW, whatever the genetic model. As in the present study, they found almost no correlation between MS and WW

Table 6. Heritabilities (h^2), maternal contribution to phenotypic variance (C^2), and direct additive genetic correlations across heifer traits: figures with asterisks (*) for a sire model accounting for myostatin genotype, polygenic sire model otherwise (SE in parentheses)

Trait	h^2	C^2	CD	WW	MS	SS	Fertility
CD ¹	0.03 (0.008)	0.18	0.03 (0.008)*	0.51 (0.128)*	-0.10 (0.158)*	0.68 (0.105)*	0.15 (0.255)*
WW ²	0.19 (0.033)	0.07	0.38 (0.147)	0.17 (0.032)*	0.23 (0.126)*	0.82 (0.046)*	0.44 (0.226)*
MS ³	0.31 (0.049)	0.09	0.23 (0.154)	0.03 (0.125)	0.17 (0.032)*	-0.02 (0.131)*	-0.53 (0.208)*
SS ⁴	0.28 (0.046)	0.02	0.40 (0.149)	0.83 (0.044)	-0.28 (0.112)	0.23 (0.039)*	0.44 (0.226)*
Fertility	0.01 (0.006)	—	0.07 (0.267)	0.24 (0.248)	-0.44 (0.240)	0.47 (0.242)	0.01 (0.006)*

¹CD = calving difficulty score.

²WW = weaning weight.

³MS = muscle score.

⁴SS = skeleton score.

whatever the genetic model and also between MS and CD under a polygenic model. This last correlation became moderately positive (0.2) when the myostatin genotype was accounted for in their study, whereas the correlation remained null in the present analysis.

Implications for Beef Cattle Selection Schemes

Estimates of genetic correlations across breeding traits validated the traditional behavior of Charolais breeders, which consists of selecting replacement heifers among calves with high SS and moderate MS, to maximize the weaned calf crop per cow. For decades, breeders put emphasis on female SS and selected against double muscling genotypes in the Charolais cow population. Hence, breeders indirectly reduced CD risk, but also improved WW and heifer fertility. Identification of the myostatin gene and its variation in cattle has been an important finding of the end of the 1990s because it enables management of its allele frequency in the beef cattle population, depending on the economic breeding goals. A deliberate effort was made in the last century either to increase the frequency of double muscling (Belgian Blue, Piedmontese cattle) when considering that the favorable effects on beef traits are overwhelming the unfavorable ones on breeding traits, or to eradicate it when the breeding goal favored breeding traits as in hardy breeds such as Gascon cattle. Another system proposed was a terminal sire breeding system whereby normal females are mated to double muscled sires and all progeny slaughtered, the breeding female herd being kept free from double muscling. Further investigation is still needed to propose alternative and efficient methods of selection within beef cattle breeds for high female breeding performance and high quality and quantity of beef production. For instance, accounting for the myostatin genotype separately, Charolais breeders should be aware that selection on a high polygenic component of the SS would provoke a strong increase in CD due to the high genetic correlation between the polygenic components of the 2 traits.

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