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[1]CENSYRA-SERIDA-Somió, C/ Camino de los Claveles 604, E-33203 Gijón (Asturias), Spain
[2]Dpto. de Produccion Animal, Facultad de Veterinaria E-28040 Madrid, Spain

FELIX GOYACHE[1]; LUIS J. ROYO[1], ISABEL ALVAREZ[1] and JUAN P. GUTIÉRREZ[2]

Testing a continuous variation in preweaning expression of muscular hypertrophy in beef cattle using field data

Summary

The hypothesis of a continuous variation in the expression of muscular hypertrophy has been tested using field data. A modification of NEUVY and VISSAC's cularity index method (Culard Index) was assayed. Expression of muscular hypertrophy showed a broad phenotypical variability. Environmental factors affecting expression of muscular hypertrophy characterised by Culard Index were calving season, age of dam, sex of calf, muscularity of dam, muscularity of sire and age of calf at weaning. In addition, Culard Index influences significantly preweaning growth traits confirming double muscled calves' higher preweaning growth ability. Culard Index score showed moderate heritability. Expression of muscular hypertrophy could be a relatively different trait with respect to latent muscular hypertrophy that would be, in turn, determined by a partially dominant major gene. Calving Index could be an interesting tool to make use of the observable differences in expression of muscular hypertrophy.

Key Words: beef cattle; muscular development; heritability; culard index; preweaning traits; Asturiana de los Valles.

Zusammenfassung

Titel der Arbeit: **Einflussfaktoren, Variation unk Erblichkeit der Ausprägung von Muskelhypertrophien bei Saugkälbern von Fleischrindern**

Die Hypothese einer kontinuierlichen Variation in der Ausprägung der Muskelhypertrophie wurde mittels Felddaten getestet, Hierzu wurde eine Modifikation der Methode nach Neuvy und Vissac für den Geburtsindex angewendet. Die Ausprägung der Muskelhypertrophie zeigte eine starke , phänotypische Variabilität auf. Die Umweltfaktoren, die die Ausprägung der Muskelhypertrophie beinflussten waren AbKalbzeitMuskelbeschaffenheit der Elterntiere. Geschlecht der Kälber Zum Entwöhnungszeitpunkt. Der Grad der Ausprägung der Muskelhypertrophie beeinflusste zudem die Wachstumsmerkmale der Kälben vor Eutwöhnung Kälber mit Muskelhipertrophie zeigten ein stärkeres Wadistumsvermögen auf. Die Ausprägung der Muskelhypertrophie ist jedodi nur schwach vererbbar. Die phenotypische Ausprägeng der Muskelhypertrophie Könte neben der genetischen. Bestimmung ein zusätzliches zuchtmerkmal dar stellen. Der veränderte Geburts index nach Neuvy und Vissac könte ein nützliches Werkzeng sein, um die Unterschiede in der Ausprägung in der Muskelhypertrophie in der Praxis zur Anwendung zu bringen, z.B. in Zuchtprogrammen von Rindervassen mit hoher Frequenz an Tieren mit Muskelhypertrophie.

Schluesselwoerter: Fleischvassen, Entwicklung der Muskulatur, Vererbbarkeit, Muskelhypertrophieindex, Vorentwönnungsmerkmale, Asturiana de los Valles

Introduction

Monogenic determination of Muscular Hypertrophy (MH) has been established since the 80's (HANSET and MICHAUX 1985). On a molecular level, MH would be determined by a partially dominant mutation in bovine MSTN gene, which encodes myostatin (GROBET et al. 1997). However there is a high variability in phenotypic expression of muscular hypertrophy. Observed individual differences in expression of MH do not match with expectation if observable degree of MH were only dependent on a major gene. For instance, Blanc-Bleu Belge cattle and other cattle breeds, such as Asturiana de los Valles, have the same mutation of the myostatin gene (an 11-bp deletion in the coding sequence) (GROBET et al. 1997) responsible of double muscled phenotype, but degree of expression of MH varies widely both inter and intra breeds. Seemingly, individual differences in the MH expression seem to be susceptible to change by selection as it has been successfully done in Blanc-Bleu Belge cattle (Hanset 1999, personal communication). Difficulties in finding out the causes of MH expression variability in cattle are not new, being the conceivable presence of modifier genes with additive effect affecting the expression of partially dominant gene the most accepted hypothesis to explain these differences (Menissier 1982).

Presence of mutation causing MH can be desirable in cattle to obtain certain meat characteristics such as leanness or tenderness. However, modulation of MH expression could be interesting to avoid undesirable effects of double muscling affecting animal welfare, such as calving problems. Since large-scale genotyping of myostatin gene in a given cattle population is not realistic in economic terms it would be useful to develop new tools to take advantage of MH expression variability. In order to achieve the use in breeding programs of the observed individual differences in MH expression it is necessary to implement a methodology able to measure objectively the phenotypical degree of MH. The use of some indices assuming a continuous variation of MH expression has been proposed (NEUVY and VISSAC 1962; ROLLINS et al. 1972). However, none of them has been employed on a large scale. In addition, papers concerning its use in real conditions are scarce and based on narrow samples (LOGEAY and VISSAC 1970; VALLS et al. 1972).

"Asturiana de los Valles" (AV) is a Spanish beef cattle breed, exploited mostly in traditional conditions in the mountains of the north of Spain (GOYACHE et al. 2000). MH presence at the AV breed has been related since the 30's, and its diffusion into the breed has been continuous due to economical reasons. MH affects dramatically the sale price of animals. Culard carcasses have a carcass price per Kg up to 40% higher to normal ones. In this market conditions, knowledge and use of muscular hypertrophy is a major goal in AV improvement program. Despite the presence of MH in almost all sires, there is still a high percentage of phenotypically normal cows, regardless their actual myostatin genotype, to maintain good maternal characteristics. It is possible to find a high variability of MH expression in calves.

The objective of this paper is to test the ability of a new index to characterise the observable variation in expression of MH assuming a continuous variation of the trait and to estimate environmental and genetic factors affecting preweaning muscular hypertrophy expression using AV breed field data.

Material and methods

The Regional Government of Principado de Asturias, through the Asturiana de los Valles Breeders Association (ASEAVA), have implemented performance recording (CORECA database) based on nuclei grouping farms according to their proximity and their production system arising from small farm size (GOYACHE et al. 2000; GOYACHE and GUTIERREZ 2001).

Degree of observable muscularity, as a measure of the degree of expression of a possible subjacent MH, is usually recorded categorically in AV breed improvement program. Sires and dams are phenotypically assessed according to their general muscularity as 0 (poor muscular development), 1 (good muscular development) and 2 (excellent muscular development) by trained ASEAVA's classifiers. Muscularity of calves at birth is assessed by breeders following the same methodology. Class 0 is expected to include genotypically normal animals and heterozygous animals with a poorer expression of MH characteristics. Class 2 is expected to contain all the phenotypically double muscled animals.

Table 1.
Characters considered building Cularity Index, age of maximum expression of each character, and AV performance recording modification

Character*	Score	AV modification	Age of maximum expresivity**
A. Macroglosy	0,1,2	No	Birth. Dessapear in three weeks old calves
B. Muscularity of shoulders	0,1,2	x2	From 3 months to 1 year
C. Compacity degree	0,1,2	†	All life
Rear legs	0,1,2	†	All life
D. Abdomen retraction	0,1,2	†	From 3 months to 1 year
E. Pelvic inclination	0,1,2	†	All life
F. Attachment point of the tail	0,1,2	†	All life
G. Muscularity of legs	0,1,2	x2	From 3 months to 1 year
H. Shoulders and hindquarters depressions	0,1,2	No	From 3 months to 1 year
I. Fineness of bones	0,1,2	†	All life
Total score	20	20	

*NEUVY Y VISSAC 1968; **VISSAC et al. 1971; † The same score than in the original method

A modification of the cularity index proposed by NEUVY and VISSAC (1962) was assayed to measure accurately the degree of expression of muscular hypertrophy of calves at weaning. The traits involved and differences with NEUVY and VISSAC's method are shown at Table 1. Doubtful or age dependent traits have been excluded from the new index. Macroglosy disappears quickly after birth. Intermuscular depressions of shoulders and hindquarters are not exclusive of double muscled animals and they can be observed even in poorer muscled animals when they are under a very low feeding regime. Traits scoring muscularity have been more weighted in the determination of the new cularity index than in the original one. The maximum score is still 20 and the minimum (total absence of observable muscular hypertrophy) is 1. CI is supposed to be effective at every economically important age of calf (weaning and fattening) regardless of availability of previous information about calf. Assuming the notation of the involved traits showed in Table 1, CI can be expressed as

$$CI = 2\,B + C + D + E + F + 2\cdot G + I \qquad (1)$$

Each one of the traits building CI is scored as 0, 1 or 2 for no expression, intermediate expression and full expression of MH characteristics, respectively.
CI scores have been recorded at weaning by trained ASEAVA's classifiers. The classifier who carried out CI scores in a given management group was always the same. Performance of classifiers was routinely checked to avoid individual differences in scores. Scores from 1 to 6 are expected to include phenotypically normal muscled calves

at weaning; scores from 7 to 10 are expected to include phenotypically intermediate muscled calves and from 11 to 19 clearly double muscled calves. Notice that classes grouping CI scores, like classifications of degree of observable muscularity in sires, dams or calves at birth, do not match with actual myostatin genotypes of the assessed animals.
Up to 2,604 cularity index observations were available. Because of the non-experimental origin of data, only records including degree of muscularity of sire and dam, weight and degree of muscularity of calf at birth, and weaning weight of calf were accepted for statistical analysis. Records were deleted in all cases of twin calving, uncertain calving number or doubtful calf sex. Records out of range 90 to 270 days of age at weaning were also removed from the analysis. Finally 2,493 records were analysed.

Statistical analysis

The statistical analysis was done with GLM Procedure of SAS (SAS 1999). Sum of squares were estimated using Type III test. DUNCAN's multiple-range test was performed on all main-effect means affecting CI.

Table 2.
Degrees of freedom, mean squares, f-values and significance of phenotypic sources of variation affecting culard index

Sources of variation	d.f.	Mean square	F-value
Management group	37	139.3	11.49***
Month of calving	11	31.5	2.60**
Calving number	5	45.8	3.78**
Sex of calf	1	205.9	16.98***
Muscularity of sire	2	58.1	4.79*
Muscularity of dam	2	767.1	63.27***
Covariate age at weaning	1	221.3	18.25***

*P<0.05; **P<0.01; ***P<0.001

CI analysis model (Table 2) included as fixed effects: management group by year of calving, calving month, calving number, calf sex, muscularity of dam, and muscularity of sire; age at weaning was included as a linear covariate.
CI effect productive characters was analysed as independent variable for birth weight, actual weaning weight, 180-days adjusted weaning weight; dystocia was treated as a continuous trait from 1 (no-assistance) to 4 (caesarea). All fitted models included the same fixed effects: management group by year of calving, calving month, calving number, calf sex, muscularity of dam, and CI as a linear and quadratic covariate. Previous analysis showed that muscularity of sire did not influence significantly on productive traits; in consequence this effect was not included in the fitted model. Preweaning growth trait models included age at weaning as a linear covariate. Dystocia model, included birth weight as a linear covariate to take into account the major influence of calf size on calving ease.

Genetic parameters

Genetic parameters affecting CI, considered as a continuous trait, were analysed with Meyer's DFREML program (1991) under an animal model. The program has been re-started with different *a priori* values of the genetic parameters to avoid confusion arising from the possible existence of local maxima.

Table 3.
Structure of data used for the estimation of genetic parameters of culard index in AV breed

Structure of data	
Number of animals	4,849
Animals with record	2,508
Sires	349
Dams	2,031
Animals in model	4,849
Sires with record and offspring	12
Dams with record and offspring	27
Environmental effects	
Nucleus-year	39
Calving season	3
Calving number	4
Calf sex	2
Age at weaning	1

Since birth and weaning weight were not necessary for genetic analysis, 2,508 records were available. Structure of analysed data is shown in Table 3. Fitted model included five fixed effects: management group by year of calving as a comparison group, period of calving, calving number, sex of calf and age at weaning as a linear covariate. The random effects included the additive genetic effect, the maternal genetic effect, the covariance between both direct and maternal genetic effects being its variance-covariance matrix proportional to the additive numerator relationship matrix, and the residual. Described model was used before to analyse genetic parameters of preweaning growth traits in AV breed (GUTIERREZ et al. 1997).
Total heritability (h^2_T) has been calculated with the formula $h^2_T = (\sigma^2_a + 1.5\sigma_{am} + 0.5\sigma^2_m)/\sigma^2$ (DICKERSON 1947), being σ^2 the phenotypic variance

Results

Phenotypic CI mean, considered as a continuous variable, was 8,6 and had a high coefficient of variation (46.5%). Descriptive statistics of CI by major sources of variation

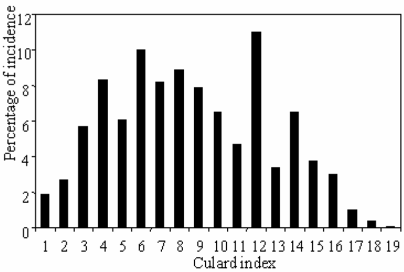

Fig1: frecuency of culard indes score (in porcetage) in te analysed database

are shown in Tables 4 and 5. Phenotypic CI mean seems rather constant despite the influence of calf sex or calving number. As it was expected, CI shows no normal distribution (Kolmogorov Test: 0.091, P<0.01) (Figure 1) and a mode of 12 (11% of the incidence) very close to the 6 incidence (10%). A CI below 7 (phenotypically normal animals) was found in 34.6% of calves, whereas a CI above 10 (double muscled animals) appeared in 33.9% of them. CI shows a close correlation with calf muscularity assessment at birth (r=0.69). 70% of calves assessed as double muscled at birth are weaned with a CI above to 10 (Table 5). Only 6% of double muscled calves at birth presented a CI lower than 7. A 51% of calves classified as 1 at birth had at weaning with CI between 7 and 10, but 36% are weaned with CI above to 10. A 66% of class 0 calves

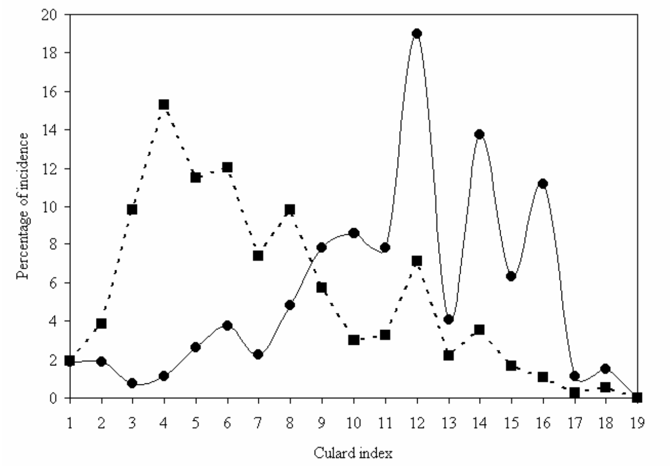

Fig.2: Frecuency of Culard index score (in percentage) by parents' muscularity score (■) Class 0 sires' offspring. (●) Class 2 dam's offspring.

Table 4.
Least squares means, standard errors (s.e.) and mode of culard index as a continuous variable by the major sources of variation

	Number	Mean	s.e.	Mode
Muscularity of sire				
Class 2[a]	1,738	9.6	0.23	12
Class 1[b]	389	9.2	0.14	4
Class 0[c]	366	8.9	0.24	4
Muscularity of dam				
Class 2[a]	269	10.4	0.24	12
Class 1[b]	288	9.4	0.24	12
Class 0[c]	1,936	8.0	0.14	6
Sex of calf				
Male[a]	1,28	9.6	0.17	12
Female[b]	1,213	9.0	0.17	12
Calving number				
First[b]	386	8.7	0.22	12
Second[ab]	366	9.4	0.22	8
Third[a]	345	9.5	0.23	12
Fourth[a]	335	9.6	0.23	12
Form 5 to 9[ab]	939	9.5	0.17	12
More than 9[ab]	122	8.8	0.35	7

Unequal letters express means signifacntly differences for P<0.05

at birth are weaned with CI below 7. A high percentage of calves classified as 0 (34.3%) are weaned with CI higher than 6.

Most parents in the AV population are phenotypically normal dams (class 0) and double muscled sires (class 2). Therefore, CI distributions of their offspring are very close between them and with the general CI distribution (Figure 1). However, the mode of phenotypically poor muscled dams' offspring is at 6 (Table 4). CI distributions of no-double muscled sires' offspring are very similar and their mode is 4 (Figure 2). CI frequencies of the offspring of dams scoring 2 or 1 in degree of muscularity are very similar and with mode at 12 (Figure 2).

Table 5.
Phenotypic means, standard deviations (s.d.) and frequencies (in percentage) of CI score by muscularity of calf at birth

Muscularity of calf at birth	Number	Mean	s.d.	Mode	CI score frequencies		
					1 to 6	7 to 10	11 to 19
Class 2[a]	906	11.8	3.2	12	5.7	24.6	69.7
Class 1[b]	436	9.6	3.1	8	12.8	51.0	36.2
Class 0[c]	1,143	5.7	2.5	6	65.7	29.8	4.5

Unequal letters express means significantly differences for P<0.05.

The use of sires scoring 0 or 1 for muscularity gives a high probability to obtain a poorly muscled calf at weaning, unlike the use of good or excellent conformed dams. It could be partially explained by the fact that the probability of mating class 0 sires with class 0 dams is 8% superior than with other dam classes, whereas the mating between class 2 sires and class 2 or 1 dams is 11% more frequent than with poor muscled dams (P<0.001).

Factors Affecting Culard Index

Table 2 shows the significance of the sources of variation involved in model adjusted to know the importance of environmental factors affecting the phenotypic expression of muscular hypertrophy. Coefficient of determination was 26.7 %, showing high-unexplained variability.

Month of calving, calving number of the dam, calf sex, degree of muscularity of the dam, degree of muscularity of the sire and age of calf at weaning influence significantly CI.

CI means are higher in calves born from July to December than in first six months of the year. CI means of calves born in the first half of the year are close to the general CI mean, while calves born in the second half of the year show a CI mean in the 110% of the general CI mean.

CI means are very close from second calving cows' offspring to adult cows' offspring (Table 4). CI means from heifers and old cows' offspring are 92 and 93% respectively on adult cows' offspring CI mean. Male calves CI mean is 7% superior than female calves CI mean.

Degree of muscularity of the sire influences CI in a lesser extent than degree of muscularity of the dam. Muscularity of the dam explains 20% of the sum of squares of the model and the sire's degree of muscularity explains only 1.5%. Muscled sires' offspring have a CI mean 4 and 7% superior than classes 0 and 1 sires' offspring respectively. Muscled (Class 2) dams' offspring present a CI mean 11 and 30% superior than well and poorer conformed dams' offspring.

CI increases 0.007 units/day with a slope of ±0.6 between 3 and 9 months of age.

CI influence on preweaning traits

Birth weight, actual weaning weight, 180-days adjusted weaning weight, preweaning average daily gain and incidence of dystocia depend significantly on CI, as a linear covariate. Only birth weight depends significantly on CI, as a quadratic covariate (Table 6). CI explain much of birth weight variance (21.5% for the linear covariate and 1.7% for the quadratic covariate) but only 1-3% of the preweaning growth characters and dystocia.

Table 6.
CI influence on birth weight, weaning weight, 180 days adjusted weaning weight, preweaning average daily gain and dystocia, treated as linear and quadratic covariate

Dependent variable	Linear covariate	Quadratic covariate
Birth weight	0.42***	0.03***
Actual weaning weight	1.29***	0.07
Adjusted weaning weight	1.34***	0.06
Average daily gain	0.006***	0.0002
Dystocia	0.017***	0.0002

*P<0.05; **P<0.01; ***P<0.001

CI as a covariate detects differences in preweaning performance at different calf ages. Calves with CI=1 were more than 6 Kg lighter at birth than CI=16 calves. Calves with CI=16 are 20 Kg heavier at weaning and its preweaning average daily gain is 90 g/day higher than CI=1 calves.

Dystocia increases with CI; CI=16 calves would cause 124% dystocia than CI=1 calves. The increase of dystocia is higher than for birth weight. The influence of calf birth weight on dystocia has been taken into account in the model as a linear covariate. The higher increase of dystocia than birth weight by CI point could be explained by the action of a threshold for calving ease (MEIJERING 1984).

Genetic Components Affecting Culard Index

Genetic parameters affecting CI are presented in Table 7. CI in AV breed shows a moderate heritability (0.19) and a lower maternal influence (0.14) with a negative covariance between both parameters. Total heritability (DICKERSON 1947) was 0.20.

Table 7.
Genetic parameter values and standard errors (below) affecting Culard Index

	h^2	m^2	r_{am}	σ_{am}/σ^2	h^2_T
Culard index	0.19	0.14	-0.24	-0.04	0.20
	0.07	0.10		0.01	

Discussion

Results showed in this paper reveal a wide variability in MH expression in AV cattle. These variability is affected by AV breed productive system and empirical selection carried out for breeders. AV dams are exploited in mountainous areas and semi-extensive conditions to produce well conformed or double muscled calves at weaning by mating with double muscled AV sires. AV breeders tend to select for reposition dams showing poor muscularity characteristics in adult ages regardless their actual myostatine genotype. These dams are expected to show a better breeding performance than double muscled dams. This is a very important task in a management system in which a half of the calvings are expected to happen without assistance (GOYACHE et al. 2000).

CI can be useful to characterise this variation in MH expression. Factors affecting CI are in the same sense than expected according with the literature. MH is more evident in healthy animals with good feeding (VISSAC and LAUVERGNE, 1968; VISSAC et al. 1973) and is more pronounced in males than in females (MENISSIER 1982). Influence of month of calving and calving number of the dam on CI can be explained taking into account that AV calves born in the second half of year show higher average daily gains at weaning than those born in the first half (data not shown) and the minor ability of heifers and old dams (9 or more calvings, see Table 4) to nurse their offspring.
Results concerning the influence of muscularity of dams and sires on CI should be taken with precaution. Muscularity classifications of sires and dams can not be considered an accurate indicator of their actual myostatin genotype. Phenotypes corresponding to homozygous normal and heterozygous animals for myostatin are very close (KIDWELL et al. 1952) and, in consequence, a reliable classification is difficult, specially in breeds showing a good phenotypical muscular development (VALLS et al. 1972). Other factors can affect the classification of muscularity. Degree of muscularity scores the degree of MH expression at adult age. MH expression tends to disappear in adult animals and specially in females (VISSAC and LAUVERGNE 1969).
The way in which age of calf affects CI is according with expected. MH is not always expressed at birth. ROLLINS et al. (1972) found that a 28% of double muscled calves do not show MH characteristics at birth. Some MH characteristics can not be clearly seen until the age of 3 months. It is generally accepted that MH expression increase from 1 to 18 months; after that time MH expression would tend to disappear as animals approach the adult age (LAUVERGNE et al. 1963).
In addition to use CI to characterise observable variation of MH our index can be used to explain partially the calving and preweaning performance of the calf. Our results are in agreement with literature. Despite the lighter adult weight of double muscled animals it has been stated that double muscled calves have higher average birth weight than normal calves (between 10 and 30%) and a bigger growth ability than normal ones at young ages (MENISSIER 1982). According with literature this higher growth ability would get lower with maturity to find lighter weight in adult age. FITZHUGH and TAYLOR (1971) predicted theoretically this growth trend for animals showing a higher maturity (weight at constant age/adult weight) at younger ages.
CI has moderate heritability. This result suggest that CI is not only depending on a major gene. If CI was only dependent on the action of a major gene the estimated heritability should be higher. In this sense MACKELLAR (1968, cited by MENISSIER 1982) estimated the heritability of the double muscled trait evaluated in 4 classes as $\mathbf{h^2} = 0.58 \pm 0.08$. Expression of muscular hypertrophy characterised by CI could be a relatively different trait with respect to latent MH, which would be monogenically determined. Some authors suggest that additive modifier genes affecting MH expression are probably responsible for muscular development in normal animals (VALLS ORTIZ et al. 1972; MENISSIER 1982). SHI et al. (1993), in Limousin cattle, obtained for muscular development at weaning similar estimations of heritability to those obtained at present analysis.
We can not reject that observable variability of MH expression was partially sustained by the action of additive modifier genes (MENISSIER 1982). In any case the possible additive genetic influence on MH expression would take a lesser role. It is always possible that the segregation of myostatin gene was involved in this genetic

determination, but if we accept that MH genetic expression mechanism under the responsibility of myostatin gene involves dominance, its participation in the genetic determination of CI could increase residual, and not genetic additive variance.
However, to ascertain this topic it would be necessary to genotype involved animals for myostatin mutations to include unambiguous genotypes in the analysis. This is out of the aim of the present paper. The genetic analysis within available CI classes is not reliable because of it would lead to obtain biased results and would increase the error of the estimations by means of the reduction of useful data.

Implications

Despite the well-know monogenic determination of muscular hypertrophy in cattle, the MH expression can be measured as a continuous trait. The index assayed can characterise a wide phenotypical variability in MH expression.
Our results do not allow to reject the classical hypothesis accepting that observable variability of MH expression is partially sustained by the action of additive modifier genes affecting expression of a partially dominant major gene (MENISSIER 1982). In this sense, CI could be an interesting tool to make use of the observable differences in MH expression. Further research is needed to determine the usefulness of CI to improve the phenotypical classification of the calves as well as their performance according to their MH genotype. On the other hand, the possible genetic correlation between CI and growth or calving traits should be clarified.

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Author's addresses
FELIX GOYACHE*, PhD; UIS .J. ROYO, ISABEL ALVAREZ,
SERIDA-CENSYRA-Somió
C/ Camino de los Claveles 604,
E-33208 Gijón (Asturias), Spain

E-Mail:felixgg@princast.es

JUAN P. GUTIÉRREZ, PhD
Dpto. de Produccion Animal
Facultad de Veterinaria
E-28040 Madrid, Spain

*Corresponding author