Genetic parameter estimates for birth and weaning weights, pre-weaning daily weight gain and three type traits for Charolais beef cattle in Spain

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Abstract

Genetic parameters were estimated using REML in a multiple-trait animal model including genetic direct and maternal effects for birth and weaning weights, pre-weaning daily weight gain and three linearly scored traits (muscularity, skeletal size and general appearance) in 3,428 Charolais calves. The three complex type traits were scored at weaning on a nine-point scale. Fixed effects considered were herd-year-season of birth, sex of the calf and parity number of the dam. The fixed effect of weaning season and the linear covariate of age at weaning were considered for all variables except for birth weight. All fixed effects contributed significantly (P < 0.001) to variations in all traits except for the effect of weaning season which was not significant for the general appearance score. The percentage of variance explained by the model averaged 50.74% for the considered traits. Average birth and weaning weights and pre-weaning daily weight gain were 42.95, 278.21 and 1.11 kg, respectively, while muscularity, skeletal size and general appearance scores averaged 5.33, 5.19 and 5.36, respectively. Direct heritabilities were 0.36, 0.36, 0.22, 0.50, 0.52 and 0.52 for the six traits, respectively. The corresponding maternal heritabilities were 0.37, 0.32, 0.18, 0.15 and 0.13, respectively. Direct genetic correlations among these traits varied from low and negative (-0.11) between birth and weaning weights to extremely high and positive (0.95) between muscularity and skeletal size scores. Type traits can be effectively used to improve the efficiency of beef production for Charolais calves in Spain.

Additional key words: general appearance, genetic correlation, growth traits, heritability, muscularity, skeletal size.

Resumen

Estimación de parámetros genéticos del peso al nacimiento, peso al destete, ganancia diaria nacimiento-destete y tres caracteres morfológicos en ganado vacuno de raza charolesa en España

Se han estimado los parámetros genéticos de los caracteres, peso el nacimiento, peso al destete, ganancia media diaria predestete, y tres caracteres morfológicos lineales (desarrollo muscular, desarrollo esquelético y aptitud funcional) en 3.428 terneros Charoleses usando REML en un modelo animal multicarácter, incluyendo efectos genéticos directos y maternos. Los tres caracteres de tipo fueron registrados en una escala lineal de uno a nueve puntos. Los efectos fijos considerados en el modelo son rebaño-año-estación de parto, sexo del ternero y el número de parto de la vaca. Se consideró el efecto fijo estación de destete y la covariable edad al destete para todas las variables, excepto para el peso de nacimiento. Todos los efectos fijos fueron significativos (P < 0.001) en todas las variables, excepto el efecto estación de destete, que no fue significativo para el carácter aptitud funcional. El porcentaje de varianza explicada por el modelo fue en promedio el 50,74% para los caracteres estudiados. Las medias de los caracteres peso al nacimiento, peso al destete y ganancia media diaria predestete fueron 42,95, 278,21 y 1,11 kg respectivamente, mientras que la puntuación media para desarrollo muscular, desarrollo esquelético y aptitud funcional fue 5,33, 5,19 y 5,36, respectivamente. Las estimaciones de heredabilidad en el componente genético directo fueron 0,36, 0,36, 0,22, 0,50, 0,52 y 0,52 para los seis caracteres, respectivamente. Las heredabilidades correspondiente al componente genético maternal fueron 0,37, 0,32, 0,18, 0,18, 0,15 y 0,13, respectivamente. La correlación genética directa entre estos caracteres varió desde pequeña y negativa (-0,11) entre el peso al nacimiento y peso al destete a elevada y positiva (0,95) entre desarrollo muscular y desarrollo esquelético. Los caracteres de tipo pueden ser utilizados con eficiencia como objetivo de selección en los programas de mejora genética de la raza charolesa en España.

Palabras clave adicionales: aptitud funcional, correlación genética, desarrollo esquelético, desarrollo muscular, heredabilidad.

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Introduction

Animal genetic improvement programmes involve two main methodologies for increasing the productivity of farm animals; selection of the best animals within a breed or population or to use the best breeds or breed combination through crossbreeding systems (Kinghorn, 1987; Koots *et al.*, 1994). Selection within breed is the method of choice to improve beef production from Charolais in Spain. Birth and weaning weights and linear scores for muscularity, skeletal size and general appearance at weaning have been recorded for Charolais in Spain. Linear assessment of type traits have undoubted economic importance, although applications in beef cattle under non-intensive production systems are scarce.

Genetic improvement in the efficiency of beef production has been a long-standing concern of beef cattle breeders (Harris and Newman, 1994). Gutiérrez et al. (2002) stated that cattle breeders have long held the belief that type traits are good indirect indicators of cattle performance. Therefore, morphological assessment is a common activity in most dairy cattle improvement programmes. In Europe, however, little is known about the use of type traits under extensive system conditions where beef production is based on cow-calf relationship for the production of weaned calves. Moreover, birth and weaning weights and pre-weaning daily weight gain are expected to vary under different environments and production systems. These traits are expected to be influenced by direct and maternal genetic effects. Therefore, it is of great interest to evaluate their potential for improving beef production. Understanding of the genetic and environmental factors affecting these variables and their genetic relationships is required to implement optional breeding and selection programmes.

The traits considered in this study have not been used previously in the genetic evaluation of Charolais calves under an extensive beef production system in Spain. Thus, the objective of this research work was to estimate direct and maternal genetic effects on birth and weaning weights, pre-weaning daily weight gain and linear scores for muscularity, skeletal size and general appearance scored at weaning for Charolais calves in Spain. This information is required to investigate future improvement possibilities.

Material and Methods

Study site

their Charolais offspring cows and were permanently grazing under variable nutritional conditions, depending on the season of the year, in the dehesa zone. Dehesa is a complex agro-forestry system located in the south-west and central parts of the Iberian Peninsula and characterized by its very harsh conditions. Climate conditions varied from cold and rainy winters with precipitation in the form of snow to extremely dry and hot summer months. In addition to these harsh climatic conditions, there are some soil restrictions which limit the system's productive potential and make it unsuitable for intensive practice. More details on the characteristics of the zone are available in the work of Hernández (1998). Charolais herds always demonstrated good tolerance against adverse climatic conditions and poor range and excellent mothering ability. Beef production from Charolais in Spain is based on the cow-calf relationship for the production of weaned calves.

Data

Field data were obtained from the National Association of Charolais Breeders in Spain (NACB, Cáceres, Spain) and were collected between 2002 and 2004. Table 1 presents a summary of the data set analyzed in this work. A total of 3,428 records including dates and weights of birth and weaning and scores for muscularity, skeletal size and general appearance of 1,795 male and 1,633 female Charolais calves, belonging to 104 herds enrolled in the nucleus scheme of the breed were used.

Complete pedigree information was available over the study period. Number of calves/sire ranged from 2 to 65 and number of herds connected by each sire ranged between 2 and 20. Therefore, many genetic links existed among the herds due to the use of artificial insemination (AI). Although the majority of sires (87%) are used for natural service, AI sires in Charolais population in Spain have more daughters than natural service sires. Of the total number of calves considered in this study (3,428), 1,524 calves (44%) were progeny of AI sires.

Characteristic	Value
Calves, no.	3,428
Sires, no.	267
Calves/sire, range	2-65
Connected herds by each sire, range	2-20
Dams, no.	2,682
Parities, no.	1-12
Years of birth of calves	2002-2004,
	inclusive
Herds, no.	104

 Table 1.
 Description of the set of data for birth and weaning traits in Charolais calves

Calving was less concentrated in the summer months (Fig. 1). The suckling period varied from 4 to 12 months and averaged 230 d. Morphological evaluations were made according to the official method of the NACB in Spain by three expert technicians. Visits were not made regularly but in function of the weaning time and circumstances of each herd. However, the minimum number of visits/year was never less than two. Birth weights were recorded by the farmers, but technicians of the NACB in Spain measured weaning weights simultaneously with the morphological assessment. Charolais calves were normally slaughtered at 10-12 months of age to satisfy the market demand for red meat.

Variables

The present study included six variables. Three variables (birth and weaning weights and pre-weaning

daily weight gain) were measured in kilograms and the other three (muscularity, skeletal size and general appearance) were scored at weaning on a nine-point scale with one point intervals. Pre-weaning daily weight gain was calculated as the difference between birth and weaning weights divided by the length of the period between them. Muscularity scores were determined in function of calf performance in the following five traits: withers width, back width, buttocks width, rounding of rump and buttocks and loin width. Skeletal size score takes into account five traits (circumference of the canon bone, body length, rump length, rump width and height at withers). Finally, the general appearance of the calf was determined by four traits as follows: muzzle width, fore legs (front and side views), rear legs (rear and side views) and topline.

Length and width traits and circumference of the canon bone were measured in centimetres using a tape

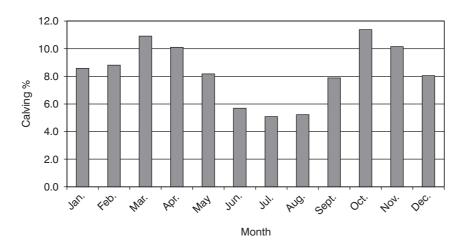


Figure 1. Calving concentration for Charolais in Spain between 2002 and 2004.

measure. Height at withers (vertical distance from withers to the ground, measured behind the fore legs) was taken using a measuring stick while the animal was on the balance. Rounding of rump and buttocks (flat to rounded), legs (X-shaped to O-shaped in front and rear view or from sickled to straight in side view) and topline (from sunken to roached) were evaluated through visual appraisal. Finally, the three conformation complex traits (muscularity, skeletal size and general appearance) were built by weighting the single traits within each group. In all cases, a score of «5» was regarded as the «norm» and scores below or above indicated deviations from normal. High scores indicate calves with a more muscular, skeletally larger and more favourable general appearance. The distribution of the six traits was checked for normality. Distributions were fairly normal and therefore the characteristics of hypothesis testing were met.

Statistical analysis

Genetic parameters were estimated using REML and VCE 4.0 software (Groeneveld and García Cortés, 1998) with a multiple-trait animal model. Random effects considered in the model were animal and maternal genetic effects. The model included herd-year-season (353 levels), sex of the calf (2 levels), parity of the dam (12 levels) and season of weaning as fixed effects. Each year was divided into four seasons: January to March, April to June, July to September and October to December. The linear covariate of calf-age at weaning was also considered. Random effects were

direct and maternal additive genetic effects. The model described was used for weaning weight, pre-weaning daily weight gain and the three linearly scored traits. Birth weight was analyzed following the same model excluding both season of weaning and age of calf at weaning. All known relationships among individuals were considered in the animal model. Phenotypic parameters were estimated by GLM and VARCOMP procedures of SAS (SAS, 1998).

Results

Estimation of phenotypic parameters

Table 2 presents phenotypic means (\pm SD), minimums, maximums and phenotypic coefficients of variation of weight, growth and linear assessment traits along with age at weaning. Table 3 shows the results of the analysis of variance for the six traits analyzed in this work. The results revealed that all fixed effects (herd-year-season of calf birth, parity number of the dam, weaning season and the linear covariate of calf-age at weaning) contributed significantly to variation in all traits except for weaning season that did not affect the general appearance score of the calf. The percentages of variance explained by the model for all traits are in Table 4.

Table 5 presents the least square means of the studied traits for the following effects: sex of the calf, parity number of the dam and season of weaning. As can be seen in the table, males had significantly higher means than females for all traits. Dams between the

Trait ¹	Маан	CD	Ra		
	Mean	SD	Min. Max.	Max.	– CV (%)
BW, kg	42.95	6.79	21.00	70.00	15.80
WW, kg	278.21	60.77	99.00	568.00	21.84
DG, kg d ⁻¹	1.11	0.44	0.21	3.71	39.91
MS	5.33	1.12	2.00	9.00	21.09
SS	5.19	1.11	2.00	9.00	21.44
GAS	5.36	1.00	2.00	9.00	18.66
AW, d	229.68	68.14	121.00	365.00	29.67

Table 2. Phenotypic means, standard deviations (SD), minimums (Min.), maximums (Max.) and coefficients of variation (CV%) for birth and weaning traits and age at weaning in Charolais calves

¹ BW = birth weight; WW = weaning weight; DG = pre-weaning daily weight gain; MS = muscularity score at weaning; SS = skeletal size score at weaning; GAS = general appearance score at weaning; AW = age at weaning.

		F value and significance ²							
	HYS	Sex	Parity	WS	AW				
BW	12.45***	426.22***	6.96***		_				
WW	7.61***	435.12***	14.54***	21.20***	88.45***				
DG	7.46***	207.10***	11.23***	7.52***	2242.55***				
MS	7.09***	113.41***	9.87***	5.88***	220.39***				
SS	7.86***	98.70***	10.40***	3.52*	227.40***				
GAS	7.07***	23.08***	4.23***	2.03 ^{NS}	165.64***				

Table 3. Analysis of variance for birth and weaning traits¹ in Charolais calves

¹ BW = birth weight; WW = weaning weight; DG = pre-weaning daily weight gain; MS = muscularity score at weaning; SS = skeletal size score at weaning; GAS = general appearance score at weaning. ² HYS = herd-year-season of calving; Sex = sex of calf; Parity = parity of the dam; WS = weaning season; AW = the linear covariate of calf age at weaning, d. *** = significant at P < 0.001, * = significant at P < 0.05, ^{NS} = non significant.

Table 4. Percentage of variance explained by herd-year-season (HYS), sex of the calf (Sex), parity of dam (Parity) and weaning season (WS) on birth and weaning traits in Charolais calves

Trait ¹	HYS	Sex	Parity	WS	Sum
BW	49.52	11.33	0.74		61.59
WW	33.35	14.65	1.70	3.57	53.27
DG	48.51	2.66	0.64	4.63	56.44
MS	35.04	4.99	1.50	0.22	41.75
SS	38.59	4.12	1.56	0.30	44.57
GAS	37.54	1.14	0.73	1.42	40.83

¹ BW = birth weight; WW = weaning weight; DG = pre-weaning daily weight gain; MS = muscularity score at weaning; SS = skeletal size score at weaning; GAS = general appearance score at weaning.

third and the tenth parity had offspring with significantly heavier birth and weaning weights than the younger or the older dams. The same trend was observed for the type traits as well. Calves weaned from Jul. to Dec. tended to have heavier body weights than those weaned between Jan. and Jun. Pre-weaning daily weight gain was significantly lower for the calves weaned between Jan. and Mar. compared to other seasons. Calves weaned between Jul. and Sep. had the highest score for muscularity followed by those weaned between Apr. and Jun., while no significant differences in muscularity were detected between calves weaned from Jan.-Mar. and Oct.-Dec. and skeletal size score was highest for calves weaned between Jul. and Sep. than the rest of the year. Finally, no significant differences were detected in general appearance score at weaning due to weaning season.

Estimation of genetic parameters

Direct and maternal heritabilities and correlations between direct and maternal genetic effects

Table 6 presents heritability estimates of direct and maternal additive genetic effects and the correlation between them. As can be seen in the table, direct heritability estimates were moderate to high, averaging 0.41. Direct heritabilities for birth and weaning weights and pre-weaning daily weight gain (0.22 to 0.36) can be considered as moderate estimates, while those for the three linear traits (0.50 to 0.52) are considered as high.

Maternal heritabilities were higher for birth and weaning weights (0.32 to 0.37) than for the remaining variables (0.13 to 0.18), indicating the importance of

F. 66 4	Number	BW	, kg	WW,	kg	DG, I	kg d ⁻¹	Μ	[S	S	S	GA	s
Effect of rec	of records	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
Sex:													
Males	1,795	44.92 ^a	0.20	303.93ª	1.98	1.23ª	0.01	5.54ª	0.04	5.39ª	0.04	5.45 ^a	0.03
Females	1,633	41.49 ^b	0.20	270.16 ^b	2.01	1.01 ^b	0.01	5.21 ^b	0.04	5.09 ^b	0.04	5.31 ^b	0.04
Parity:													
1	728	42.09 ^b	0.21	266.80°	2.08	1.07 ^b	0.01	5.06 ^c	0.04	4.96°	0.04	5.22ь	0.04
2	539	42.81 ^b	0.23	284.88 ^b	2.29	1.16 ^a	0.01	5.39 ^b	0.04	5.27 ^b	0.04	5.41ª	0.04
3	527	43.06 ^a	0.23	290.01 ^{a,b}	2.31	1.17ª	0.01	5.44 ^b	0.04	5.33 ^b	0.04	5.43ª	0.04
4	435	43.09 ^a	0.25	295.69ª	2.51	1.21ª	0.01	5.51ª	0.05	5.37 ^b	0.05	5.44 ^a	0.04
5	393	44.08 ^a	0.28	297.26ª	2.79	1.21ª	0.01	5.51ª	0.05	5.46 ^a	0.05	5.52ª	0.05
6	284	43.76 ^a	0.30	290.68ª	2.98	1.19 ^a	0.01	5.44 ^b	0.06	5.39 ^b	0.06	5.48 ^a	0.05
7	220	43.56 ^a	0.34	291.22ª	3.32	1.18 ^a	0.01	5.49ª	0.06	5.33 ^b	0.06	5.44 ^a	0.06
8	143	43.97ª	0.41	284.84 ^a	4.03	1.14 ^a	0.02	5.29°	0.08	5.16°	0.08	5.36 ^b	0.07
9	101	43.98ª	0.48	280.89ª	4.75	1.13 ^b	0.03	5.30°	0.09	5.20 ^b	0.09	5.36 ^b	0.08
10	62	43.31ª	0.61	287.93ª	5.94	1.16 ^a	0.03	5.31°	0.11	5.21 ^b	0.11	5.35 ^b	0.10
11	36	42.47 ^b	0.79	295.79ª	7.72	1.24 ^a	0.04	5.43 ^b	0.15	5.17°	0.14	5.35 ^b	0.14
12	20	40.93 ^b	1.06	278.53°	10.36	1.13 ^b	0.06	5.29°	0.20	5.07°	0.19	5.19 ^b	0.18
WS:													
JanMar.	1,129			267.27°	3.02	1.10 ^b	0.02	5.20°	0.06	5.15 ^b	0.06	5.35ª	0.05
AprJun.	981			286.90 ^b	3.11	1.17 ^a	0.02	5.39 ^b	0.06	5.20 ^b	0.06	5.31 ^{a,b}	0.05
JulSep.	581			296.06ª	3.64	1.21ª	0.02	5.57ª	0.07	5.42ª	0.07	5.39ª	0.06
OctDec.	737			297.95ª	3.34	1.19 ^a	0.02	5.32°	0.06	5.21 ^b	0.06	5.48ª	0.06

Table 5. Least square means (LSM) and standard errors (SE) of birth and weaning traits of Charolais calves by sex of calf (Sex), parity of dam (Parity) and weaning season (WS)

BW = birth weight; WW = weaning weight; DG = pre-weaning daily weight gain; MS = muscularity score at weaning; SS = skeletal size score at weaning; GAS = general appearance score at weaning. ^{a, b, c:} Means in a column with different superscript differ (P < 0.05).

Trait	h^2	m^2	r (a, m)
BW	0.36 ± 0.04	0.37 ± 0.04	-0.87 ± 0.05
WW	0.36 ± 0.01	0.32 ± 0.01	-0.67 ± 0.03
DG	0.22 ± 0.01	0.18 ± 0.01	0.06 ± 0.03
MS	0.50 ± 0.02	0.18 ± 0.01	-0.68 ± 0.03
SS	0.52 ± 0.02	0.15 ± 0.01	-0.73 ± 0.04
GAS	0.52 ± 0.03	0.13 ± 0.01	-0.81 ± 0.05

Table 6. Parameter estimates \pm SE for birth and weaning traits in Charolais calves

 h^2 = direct heritability; m^2 = maternal heritability; r(a, m) = correlation between direct and maternal additive effects. BW = birth weight; WW = weaning weight; DG = pre-weaning daily weight gain; MS = muscularity score at weaning; SS = skeletal size score at weaning; GAS = general appearance score at weaning.

the maternal effect on birth and weaning weights. Moreover, direct heritability estimate was close to the corresponding maternal heritability for both birth and weaning weights. Direct heritabilities for type traits were clearly higher (0.50 to 0.52) than their

corresponding maternal ones (0.13 to 0.18). On the other hand, direct heritability estimates for birth weight, weaning weight and pre-weaning daily weight gain were close to their corresponding maternal heritability estimates. The correlation between direct and maternal additive genetic effects were always high and negative (-0.87 to -0.67) for all traits except for pre-weaning daily weight gain which was close to zero (0.06).

Genetic and phenotypic correlations

Table 7 presents direct genetic and phenotypic correlations among the traits studied. As can be observed, birth weight had low correlations with the remaining variables ranging from -0.16 to 0.13 for direct genetic correlations and from 0.04 to 0.29 for phenotypic correlations. Direct genetic correlation between birth and weaning weights was clearly low (-0.11). Weaning weight had a fairly high genetic correlation (0.94) with the pre-weaning daily weight gain. Genetic correlations between weaning weight and the three type traits were moderately high and positive (0.47 to 0.69). The corresponding phenotypic correlations were moderate to high (0.45 to 0.60). The three type traits had fairly high positive genetic (0.86 to 0.95) and phenotypic (0.78 to 0.85) correlations.

Discussion

No phenotypic parameter estimates were found in the literature for the same breed under similar production system conditions in Europe. However, the results obtained for weight traits are generally comparable with the results regularly reported for populations with heavy weights of beef cattle. Koots *et al.* (1994), in a review paper of the animal breeding literature covering 51 years (1940 to 1991), showed that several factors included in this study (sex, herd, year of birth) significantly affected beef production traits. MacNeil (2003) found that year of birth, sex of calf and age of dam significantly affected birth, 200 day and 305 day weights of a CGC (Composite Gene Combination) beef population developed by the USDA-ARS (50% Red Angus, 25% Charolais and 25% Tarentaise) (Newman *et al.*, 1993). Additional details concerning the formation of this CGC population can be found in Newman *et al.* (1993). In this study, the percentage of variance explained by the model ranged between 41.75 and 61.59%, indicating good modelling for all traits.

Direct and maternal effects are important in determining the variability of growth traits in beef cattle (Notter and Cundiff, 1991; Rodriguez-Almeida *et al.*, 1997). The moderate to high direct heritability estimates for all traits considered in this study justify the inclusion of these traits in a selection program to improve beef production from the Charolais breed in Spain. In view of these moderate to high heritability estimates (Table 6), together with the moderate phenotypic variation (Table 2), a satisfactory selection response is expected for all traits.

The direct heritability estimate for birth weight in this study (0.36) was somewhat lower than those obtained by Eriksson *et al.* (2004) who reported direct heritability estimates of 0.44 and 0.48, respectively for Charolais and Hereford under intensive beef production system conditions in which less phenotypic variation is expected. Therefore, this would explain their higher estimates. Direct heritability for weaning weight (0.36) is within the range of estimates (0.19 to

 Table 7.
 Direct genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) among birth and weaning traits¹ in Charolais calves

Trait	BW	WW	DG	MS	SS	GAS
BW		-0.11	-0.16	0.13	0.13	0.09
WW	0.29		0.94	0.69	0.65	0.47
DG	0.09	0.57		0.76	0.68	0.50
MS	0.10	0.60	0.19		0.95	0.88
SS	0.11	0.55	0.15	0.85		0.86
GAS	0.04	0.45	0.12	0.78	0.79	

¹ BW = birth weight; WW = weaning weight; DG = pre-weaning daily weight gain; MS = muscularity score at weaning; SS = skeletal size score at weaning; GAS = general appearance score at weaning. Standard errors for genetic correlation estimates ranged between 0.01 and 0.06.

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0.47) reviewed by Groeneveld *et al.* (1998), higher than that (0.20 to 0.22) estimated by Robinson (1996a) and Miller and Wilton (1999) and similar to that (0.38 \pm 0.06) estimated by Montaldo and Kinghorn (2003) for the 200 day weight of different beef breeds.

Gutiérrez and Goyache (2002) reported that traits scoring skeletal size development and animal's size on a linear score showed moderate to high heritabilities (0.23 to 0.33) for the Asturiana de los Valles beef cattle breed. Similar results were reported for the British Holsteins (Brotherstone, 1994; Roughsedge *et al.*, 2000). The present results were clearly higher (Table 6), probably due to breed differences.

As mentioned before, maternal heritabilities estimated in this study were higher for birth and weaning weights (0.32 to 0.37) than for the remaining variables (0.13 to 0.18) indicating the importance of the maternal effect on birth and weaning weights. Moreover, direct heritability estimate was close to the corresponding maternal heritability for both birth and weaning weights (Table 6). These results may indicate the high interference between direct and maternal effects on the genetic progress of these two traits. Therefore, both direct and maternal effects should be considered for birth and weaning weights. Although maternal heritability estimates (0.13 to 0.18) tended to be lower than direct ones (0.50 to 0.52) for type traits, the maternal influence should not be ignored in the genetic evaluation of Charolais calves.

The present results revealed that direct heritability estimates for birth and weaning weights were close to the corresponding maternal ones (Table 6). While, the results reported by MacNeil (2003) revealed that direct heritability estimates for birth and 365 day weights (0.49 ± 0.05) , in both cases) was much higher than the corresponding maternal heritability estimates $(0.11 \pm 0.03 \text{ and } 0.04 \pm 0.02, \text{ respectively})$ for a CGC multibreed population. Similar results were reported by Meyer et al. (1993), Bennett and Gregory (1996) and Eriksson et al. (2004) for several breeds of beef cattle including Charolais. A lower maternal heritability estimate (0.02) was found in the work of Montaldo and Kinghorn (2003) for a multibreed population of beef cattle. Meyer (2001) indicated that maternal effects are considerably more important for purebred breeds than for synthetic ones.

Correlations between direct and maternal additive genetic effects estimated in this study were generally high and negative. Negative genetic correlations between direct and maternal effects are commonly found in the literature in beef cattle (Koots et al., 1994; Meyer, 1997; Groeneveld et al., 1998; Eriksson et al., 2004). Montaldo and Kinghorn (2003) reported an estimate of $-0.65 (\pm 0.16)$ between direct and maternal effects for birth weight. Groeneveld et al. (1998) stated that the high negative correlation between direct and maternal effects is not clear at all. However, Baker (1980) and Johanson and Morant (1984) suggested that this could be due to a negative dam-offspring correlation (the adverse effect of a high plane of nutrition during rearing of beef heifers on the weaning weight of their calves). Baker (1980) and Robinson (1996b) suggested that direct-maternal correlations may be biased downwards due to negative environmental covariances between maternal effects in adjacent generations. More details on the estimation and interpretation of direct and maternal genetic parameters are given in the works of Meyer (1992), Robinson (1996a,b) and Meyer (1997). In this study, direct and maternal heritabilities had close and high estimates for birth and weaning weights (Table 6). The high negative correlations between direct and maternal effects [r(a,m)] for these two traits indicate unfavourable interference between them. Therefore, selection for direct effect would only, in the long run, be detrimental to maternal ability. The situation seems much better for the three type traits due to their higher estimates for direct than for maternal heritability. This antagonistic relationship should be compensated for by improving managerial practices and using supplemental feeding when necessary.

Groeneveld *et al.* (1998) and Eriksson *et al.* (2004) reported that correlations among maternal and direct effects are usually negative. However, those among direct effects for weight traits at different ages are usually positive. In the present study, birth weight had low correlations with the remaining variables ranging from -0.16 to 0.13 for direct genetic correlations and from 0.04 to 0.29 for phenotypic correlations. These low correlations are favourable because selection for traits like pre-weaning daily weight gain, weaning weight or type traits is not expected to have an effective correlated response in birth weight. This would be useful in avoiding problems related to calving difficulties.

Direct genetic correlation between birth and weaning weights was clearly low (-0.11). Therefore, and as mentioned by Koch *et al.* (1994), direct selection

for weaning weight would lead to unfavourable correlated response in birth weight. These consequences may be alleviated by applying a negative pressure to birth weight while positive pressure is applied to weaning weight (Dickerson *et al.*, 1974).

The high genetic correlation of weaning weight with the pre-weaning daily weight gain (0.94), the moderately high and positive (0.47 to 0.69) genetic correlations between weaning weight and the three type traits and the fairly high and positive genetic correlations among the three type traits, may indicate that selection to improve weaning weight, pre-weaning daily weight gain or any of the three linear traits (muscularity, skeletal size and general appearance) measured at weaning would be expected to have a positive effective correlated response in the rest of these variables. Selection for growth and type traits is generally compatible. Therefore, it would probably be more effective to consider both of them in an appropriate selection index than selecting for either of them alone.

Clement *et al.* (2001) mentioned that random direct and maternal estimates are valid in purebred populations when genetic connections among herds are sufficient. The moderate to high heritability estimates for traits considered in this study, their low estimates for standard error, and the moderate to high genetic correlations among them, the complete pedigree information and the sufficient genetic connections among herds may indicate that random direct and maternal variances obtained in this study are convincing.

The genetic variability found for weight and type traits in this study was high enough to permit genetic progress. This result would justify the inclusion of these traits in a selection program for Charolais breed in Spain. However, the moderate to high negative correlation between direct and maternal genetic effects and the significant influence of environmental factors would indicate that genetic progress through selection is not an easy task.

Direct genetic correlations between birth weight and all other traits were generally low (-0.16 to 0.13)indicating that selection to improve any of these variables is not expected to have an effective correlated response in birth weight. This would be useful to avoid problems related to calving difficulties.

Considering the moderate to high estimates of direct genetic correlation among weaning weight, pre-weaning daily weight gain and the three linear traits, positive correlated responses for these traits is expected when genetic selection is practiced for any of them. Type traits are more recommended for genetic selection due to their higher direct heritability estimates. However, selection for growth and type traits through a selection index with appropriate weights would be more effective than selection for either alone.

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