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Genetic relationships among calving ease, calving interval, birth weight, and weaning weight in the Asturiana de los Valles beef cattle breed¹

J. P. Gutiérrez,*2 F. Goyache,† I. Fernández,† I. Alvarez,† and L. J. Royo†

*Departamento de Producción Animal, Universidad Complutense de Madrid, Avda, Puerta de Hierro s/n, E-28040-Madrid, Spain; and †SERIDA-Somió, C/ Camino de los Claveles 604, E-33203 Gijón (Asturias), Spain

ABSTRACT: The aim of this paper was to estimate direct and maternal genetic parameters for calving ease (CE), birth weight (BrW), weaning weight (WW), and calving interval (CI) to assess the possibility of including this information in beef cattle improvement programs. Field data, including a total of 59,813 animals (1,390 sires and 1,147 maternal grand sires) from the Asturiana de los Valles beef cattle breed, were analyzed with a multivariate linear model. Estimates of heritability for direct genetic effects (CED, CID, BrWD, and WWD) were 0.191 ± 0.019 , 0.121 ± 0.013 , 0.390 ± 0.030 , and 0.453 ± 0.035 , respectively, whereas those for maternal genetic effects (CEM, BrWM, and WWM) were 0.140 ± 0.015 , 0.208 ± 0.020 , and 0.138 ± 0.022 , respectively. Genetic correlations between direct or maternal genetic effects across traits were, in general, positive and moderate to low. However, genetic correlation for the pair CED-BrWD was positive and high (0.604 \pm 0.064). Genetic correlations between the direct and maternal genetic effects within a trait were negative and moderate (-0.219 ± 0.097 for CE, -0.337 ± 0.080 for BrW, and -0.440 ± 0.102 for WW). Genetic correlations for CED-BrWM and CED-WWM were -0.121 ± 0.090 and -0.097 ± 0.113 , respectively. The genetic correlation for CEM-CID was unfavorable (0.485 \pm 0.078), and those for CEM-BrWD (-0.094 ± 0.079) and CEM-WWD (-0.125 ± 0.082) were low and negative. The genetic correlation between CID and WWM was favorable (-0.148 ± 0.106) . Overall, the data presented here support the hypothesis that maternal effects for CE and BrW are not the same and that the genetic relationships between CI and maternal effects for WW in beef cattle follow a similar pattern to that reported between CI and milk yield in dairy cattle. Moreover, the need to include direct and maternal breeding values in beef cattle selection programs is suggested.

Key words: calving ease, cattle, genetic correlation, genetic parameter, maternal effect

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INTRODUCTION

Difficult calvings are of primary economic importance in beef cattle. Dystocia influences calf survival, culling and fertility rates, and need for veterinary assistance (Meijering, 1984). Although improvement in beef cattle has traditionally focused on production traits, breeding programs should consider all traits of economic importance to optimize total genetic gain (Phocas et al., 1998; Albera et al., 2004a). In this respect, the genetic relationships between calving ease (**CE**) and major produc-

²Corresponding author: gutgar@vet.ucm.es Received March 22, 2006. Accepted August 24, 2006. tive and reproductive traits, such as birth weight (**BrW**), weaning weight (**WW**), and calving interval (**CI**), should be ascertained.

Although a few recent papers have focused on the genetic parameters for CE (Carnier et al., 2000; Phocas and Laloë, 2003; Albera et al., 2004b; Eriksson et al., 2004a), the information available on the genetic relationship between CE and other traits apart from BrW is still scarce (Koots et al., 1994a,b; Albera et al., 2004b; Eriksson et al., 2004b). This is especially the case with respect to the genetic relationship between the maternal genetic effect for CE and the genetic effects for the other traits (Phocas and Laloë, 2004).

Genetic parameters have been estimated for productive (Gutiérrez et al., 1997; Gutiérrez et al., 2006), reproductive (Goyache and Gutiérrez, 2001; Goyache et al., 2003, 2005), and type traits (Gutiérrez and Goyache, 2002; Gutiérrez et al., 2002) in the Asturiana de los Valles beef cattle breed. Our interest is to ascertain the genetic basis of traits that have been shown to

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be important, so as to include these in the breeding objective (Phocas et al., 1998).

The aim of this study was to estimate the genetic relationships between CE and major traits used as indicators of productive and reproductive performance in suckling cow production systems to evaluate the possibility of including this information in beef cattle improvement programs.

MATERIALS AND METHODS

Asturiana de los Valles is a beef cattle breed mainly exploited under semiextensive or extensive conditions in the wet Cantabrian range area of Northern Spain. Nutrition is primarily dependent on natural pastures, with grazing in communal pastures of medium-high altitude during 8 to 9 mo of the year and wintering on valley pastures at an average altitude of 300 m with supplemental hay. Natural service is used for breeding in 71% of the farms studied, although in less than half of these, AI is also used in a portion of the cows. In the remaining 29%, AI is used exclusively. Farmers desire sires with ease of birth and good conformation, whereas the main selection criteria for females are ease of birth and fertility.

Animal care and use committee approval was not obtained for this study because the data were obtained from an existing database. Production data and pedigree information of the Asturiana de los Valles breed were obtained from the performance recording database (the CORECA database) implemented by the Regional Government of the Principado de Asturias (Northern Spain), through the Asturiana de los Valles Breeders Association (ASEAVA). Due to the small size of the farms, performance recording was implemented on nucleus farms, grouping farms according to their proximity and their production system, further considering the nucleus as the management unit (Gutiérrez et al., 1997; Goyache et al., 2003).

Animals with identification errors or ambiguous birth dates were excluded from the analysis. Contemporary groups were defined based on nucleus-year of calving. Production data included only single calving records with calf alive at weaning, regardless of whether weight at weaning was recorded. Total records available were as follows: 38,764 CE, 34,406 CI, 35,310 BrW, and 29,381 WW). Calving ease was considered as a trait of the calf. Age of calf at weaning in those records for which it was available ranged from 90 to 270 d.

Calving interval was computed as the interval, in days, between 2 consecutive calving dates. Some cows had incomplete calving date information. Following previous studies, only CI records ranging from 290 to 630 d were admitted and used for further analyses (Goyache and Gutiérrez, 2001; Gutiérrez et al., 2002; Goyache et al., 2005). Performance recording included the parity number regardless of whether the first calving was actually recorded. Thus, following the aforementioned papers, cows were not required to have a first

calving observation to compute CI between later calvings.

Calving ease was recorded using the following scores: 1 (no assistance; 17,888 records), 2 (minor assistance; 17,571 records), 3 (hard assistance; 2,336 records), and 4 (caesarean section; 969 records). Seventy-one, 75, 62, and 76%, respectively, of the records for each calving ease score also had a recorded WW. Due to the small size of the farms, the presence of the farmer during a significant portion of calvings is normal, and his intervention is unavoidable. As a consequence, the percentage of calvings scored as 2 is greater than in other breeds, and only scores greater than 2 are considered difficult births (Goyache et al., 2000). However, significant differences in average birth weight were previously observed between calvings scored as 1 or 2, leading to the separate analysis of these 2 categories of calving difficulty (Goyache et al., 2000; Goyache and Gutiérrez, 2001). Following Goyache et al. (2000) and Goyache and Gutiérrez (2001), abnormal presentations were not considered in the present analysis. Although it has a discrete nature, which theoretically would suggest a threshold model that would better account for the probabilistic structure of the data (Gianola and Foulley, 1983), we modeled CE as a continuous trait and assumed a multivariate normal distribution.

Average values (and SD) of CI, BrW, and WW for each calving ease score class are given in Table 1.

Threshold models have been reported to be superior to linear models in estimation of genetic parameters affecting CE in cattle (Varona et al., 1999a,b; Ramírez-Valverde et al., 2001). However, there is only a slight advantage of the threshold model, and when the amount of information for fixed effects is small, as in the current study, threshold models have problems in estimating variance components (Phocas and Laloë, 2003). Therefore, in this case little incentive exists to use threshold models over linear models (Phocas and Laloë, 2004), especially when taking into account that the use of threshold models significantly increases the computational effort. In addition, Matos et al. (1997), in accordance with several previous studies, found that the goodness of fit of linear and threshold models for discrete data was similar, and with respect to EBV prediction ability (coinciding with our experience), differences between linear and threshold mixed models were negligible.

The analyzed database included a total of 59,813 animals, and the final structure of the data was dependent on the traits involved in each analysis (Table 2). The database included records from the beginning of the performance recording in the second half of the 1980s to the beginning of 2000. Genetic parameters together with their SE were estimated via a multitrait REML procedure applied to mixed linear models. All runs were carried out using the DF-REML program (Meyer, 1998). The fitted models included the following fixed effects: herd-year of calving as contemporary group, calving season (2 levels: from January 1 to June 30 and from

Table 1. Number of records by calving ease score class, percentage of the total number of recorded scores, and means and SD for CI, BrW, and WW by calving ease score class

Calving			CI		2 Bı		WW^4	
ease score ¹	No. of records	%	Mean	SD	Mean	SD	Mean	SD
1	17,888	46.1	336.0ª	147.6	$34.0^{\rm a}$	13.2	164.7 ^a	101.2
2	17,571	45.3	$340.6^{ m ab}$	149.7	$36.3^{ m b}$	13.9	$171.0^{ m ab}$	103.5
3	2,336	6.0	$346.8^{\rm b}$	160.1	$42.0^{\rm c}$	17.0	$172.1^{ m b}$	105.1
4	969	2.5	394.3^{c}	189.1	$41.6^{\rm c}$	17.9	181.1 ^c	112.3

^{a-c}Within a row, different superscript letters indicate means are significantly different according to Duncan's multiple-range test implemented in Proc GLM (SAS Inst. Inc., Cary, NC).

July 1 to December 31), sex of calf (male or female), and age of the dam at calving, in days, as a linear covariant. The model fitted for analysis of WW also included the effect of creep feeding (2 levels: creep and noncreep) and age of calf at weaning, in days, as a linear and quadratic covariate.

Genetic analyses were carried out using a multivariate model involving CE, CI, BrW, and WW. The matrix notation for the model to be solved for a hypothetical trait considering all of the possible random effects, $\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Nm} + \mathbf{Wp} + \mathbf{e}$, had:

$$\begin{pmatrix} \mathbf{u} \\ \mathbf{m} \\ \mathbf{p} \\ \mathbf{e} \end{pmatrix} \sim N \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{G} & \mathbf{C} & \mathbf{0} & \mathbf{0} \\ \mathbf{C} & \mathbf{M} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{P} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix},$$

where $G = A \otimes G_0$, $M = A \otimes M_0$, $C = A \otimes C_0$, $P = I_p$ $\sigma_{\mathbf{p}}^{2}$, and **R** is the covariance matrix of order equal to the number of records, with the diagonal elements equal to the residual variance of the involved trait, and the nondiagonal elements equal to the residual covariance between traits if the element corresponds to records of different traits belonging to the same animal but is zero otherwise, y is the vector of observations, X is the incidence matrix of fixed effects, **Z** is the incidence matrix of animal effects, N is the incidence matrix of maternal genetic effects, W is the incidence matrix of permanent environmental effects, b is the vector of fixed effects, **u** is the vector of direct animal genetic effects, m is the vector of unknown maternal genetic effects, **p** is the vector of permanent environmental effects, e is the vector of residuals, I_p is the identity matrix of order equal to the number of dams, σ_{p}^{2} is the

Table 2. Structure of data used for estimation of genetic parameters for calving ease (CE), calving interval (CI), birth weight (BrW), and weaning weight (WW)

Item	CE	CI	BrW	ww
Animals, No.	54,400	14,290	54,787	54,790
Animals with records, No.	38,764	12,148	35,310	29,381
Sires with progeny in data, No.	1,379	695	1,380	1,383
Cows with progeny in data, No.	14,424	2,938	14,494	14,506
Sires with record and offspring, No.	236	0	129	138
Cows with record and offspring, No.	1,905	507	266	271
Sire-offspring pairs, No.	9,451	0	19,262	18,309
Dam-offspring pairs, No.	4,176	9,334	8,258	7,396
Nucleus-year, levels	535	502	535	535
Calving season, levels	2	2	2	2
Calf sex, levels	2	2	2	2
Creep feeding, levels	_	_	_	2
Age of cow at calving, covariate	1	1	1	1
Age of calf at weaning, linear covariate	_	_	_	1
Age of calf at weaning, quadratic covariate	_	_	_	1
Mean	1.64^{1}	398.6^{2}	40.5^{3}	225.0^{3}
SD	0.71^{1}	83.0^{2}	7.4^{3}	61.6^{3}

¹Calving ease was scored as: 1 (no assistance), 2 (minor assistance), 3 (hard assistance), and 4 (caesarean section).

¹Calving ease was scored as 1 (no assistance), 2 (minor assistance), 3 (hard assistance), and 4 (caesarean section).

²Calving interval in days.

³Birth weight in kilograms.

⁴Weaning weight in kilograms.

²Calving interval in days.

³Birth weight and weaning weight in kilograms.

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Table 3. Total variance and heritabilities estimated for calving ease (CE), calving interval (CI), birth weight (BrW), and weaning weight (WW)¹

	CE	CI	BrW	WW
$V_{(n)}$	0.301	5,619.0	24.2	842.5
$\begin{matrix} V_{(p)} \\ h^2 \end{matrix}$	0.191 (0.019)	0.121 (0.013)	0.390 (0.030)	0.453(0.035)
m^2	0.140 (0.015)		0.208 (0.020)	0.138 (0.022)
c^2		0.048(0.012)		

 $^{^{1}}V_{(p)}$ = phenotypic variance; h^{2} = heritability for the direct genetic effect; m^{2} = heritability for the maternal genetic effect; and c^{2} = estimate for the permanent environmental effect for CI. The SE are in parentheses.

permanent environmental variance, A is the numerator relationship matrix, G_0 is the covariance matrix for additive genetic effects, M_0 is the covariance matrix for maternal genetic effects, C_0 is the covariance matrix between direct additive and maternal genetic effects, and \otimes is the Kronecker product.

The permanent environmental effect was only fitted for CI, and the maternal genetic effect was only fitted for CE, BrW, and WW. Given that Gutiérrez et al. (1997) have previously shown that the inclusion of a maternal permanent environmental effect in the fitted model had a negligible effect on traits similar to those analyzed here, this effect was not fitted for CE, BrW, or WW to avoid considerable additional computational effort. However, this effect was fitted in the analysis of CI.

RESULTS

Phenotypic variances and genetic parameter estimates are given in Table 3. Estimates of heritability (\pm SE) for the direct genetic effect (**CED**, **CID**, **BrWD**, and **WWD**) were $0.191\pm0.019,\ 0.121\pm0.013,\ 0.390\pm0.030,\$ and $0.453\pm0.035,\$ respectively, whereas the estimates for maternal genetic effects (**CEM**, **BrWM**, and **WWM**) were $0.140\pm0.015,\ 0.208\pm0.020,\$ and $0.138\pm0.022,\$ respectively. A slight maternal permanent environmental effect of 0.048 ± 0.012 was estimated for CI.

Table. 4. Genetic correlations between direct¹ and, when included, maternal¹ genetic effects resulting from the analysis of the genetic relationships among calving ease (CE), calving interval (CI), birth weight (BrW), and weaning weight (WW) carried out using the multivariate model (SE are in parentheses)

	CED	CID	BrWD
CID	0.137 (0.122)		
BrWD	0.604 (0.068)	0.150(0.114)	
WWD	0.358(0.064)	$-0.068\ (0.112)$	0.366(0.057)
	CEM		BrWM
BrWM	0.286 (0.079)		
WWM	$-0.095\;(0.095)$		$0.245\ (0.091)$

¹CED, CID, BrWD, and WWD = direct genetic effects for CE, CI, BrW, and WW, respectively; CEM, BrWM, and WWM = maternal genetic effects for CE, BrW, and WW, respectively.

Genetic correlations between direct or maternal genetic effects across traits were, in general, positive and moderate to low (Table 4). However, that for the pair CED-BrWD (0.604 \pm 0.068) was positive and high, and those for the pairs CID-WWD and CEM-WWM were nonsignificant.

Genetic correlations for CED-CEM, BrWD-BrWM, and WWD-WWM were negative and moderate (Table 5), ranging from -0.219 ± 0.097 for CED-CEM to -0.440 ± 0.102 for WWD-WWM. The genetic correlations for CED and BrWM and for CED and WWM were nonsignificant (Table 5). The genetic correlation between CEM-CID was high and positive (unfavorable; 0.485 ± 0.078) and was nonsignificant for CEM-BrWD and CEM-WWD. The genetic correlations for CID-BrWM, CID-WWM, BrWD-WWM, and WWD-BrWM were nonsignificant. In general, SE of the genetic correlations estimated between direct and maternal genetic effects of different traits were large.

DISCUSSION

In this work, genetic relationships between calving ease and traits usually considered as major indicators of production and reproductive performance in suckling cow production systems have been estimated for the first time in the Asturiana de los Valles beef cattle breed.

Genetic Parameters Within Traits

The current estimates of heritability for the direct genetic effects are in agreement with those reported

Table 5. Genetic correlations between direct¹ and maternal¹ genetic effects (SE are in parentheses)

	CEM	BrWM	WWM
CED	$-0.219^2 (0.097)$	-0.121 (0.090)	-0.097 (0.113)
CID	0.485(0.078)	$0.039\ (0.082)$	$-0.148 \; (0.106)$
BrWD	$-0.094\ (0.079)$	-0.337 (0.080)	$-0.076\ (0.096)$
WWD	$-0.125\ (0.082)$	$-0.117\ (0.077)$	-0.440 (0.102)

¹CED, CID, BrWD, and WWD = direct genetic effects for CE, CI, BrW, and WW, respectively; CEM, BrWM, and WWM = maternal genetic effects for calving ease (CE), birth weight (BrW), and weaning weight (WW), respectively.

²Genetic correlations between direct and the maternal genetic effects for a given trait are in bold.

in the literature, whereas those for maternal genetic effects are substantially lower. Heritability reported here for CED (0.19) is approximately half that reported in the Asturiana de los Valles breed using a threshold sire model and a smaller data set (0.42; Goyache and Gutiérrez, 2001). However, this value is within the accepted range of heritability for the trait reported for multiparous beef cows on the observable scale (Meijering, 1984) and near the mean heritability of 0.16 in adult cows reported by Koots et al. (1994a). In any case, it is greater than the estimates recently reported in the Italian Piemontese breed (Carnier et al., 2000), in 2 beef populations bred in Sweden (from 0.01 to 0.18; Eriksson et al., 2004a,b), and in 4 French beef cattle breeds (from 0.09 to 0.13; Phocas and Laloë, 2004), and within the range reported for 4 British beef breeds (from 0.13 to 0.39; Roughsedge et al., 2005) for the direct genetic effect of calving ease. The estimate of heritability reported here for CID is consistent with those reported previously in the breed (Goyache and Gutiérrez, 2001; Gutiérrez et al., 2002; Goyache et al., 2005) and with the mean value of 0.10 reported by Koots et al. (1994a). Heritabilities reported in the current study for BrWD and WWD are in the range recently reported for the same breed using various models (from 0.336 to 0.401 for BrWD and from 0.211 to 0.438 for WWD; Gutiérrez et al., 2006) and are greater than those usually reported in the literature. Koots et al. (1994a) reported mean heritabilities of 0.31 for BrWD and 0.24 for WWD. In 4 French beef cattle breeds, Phocas and Laloë (2004) reported heritabilities ranging from 0.28 to 0.38 for BrWD and from 0.13 to 0.32 for WWD. Roughsedge et al. (2005) reported estimates of heritability for the direct genetic effect of weaning weight at 200 d ranging from 0.21 to 0.30 using data from 4 British beef breeds.

Heritability estimates for CEM were also slightly greater than other estimates available in the literature, which in most cases ranged from 0.09 to 0.12 (Koots et al., 1994a; Varona et al., 1999a; Carnier et al., 2000; Eriksson et al., 2004a; Phocas and Laloë, 2004). Estimates for BrWM and WWM were also in the range reported by Gutiérrez et al. (2006) in the same breed using various models (from 0.052 to 0.224 for BrWM and from 0.056 to 0.119 for WWM) and tended to be greater than the average of estimates of the heritability of maternal genetic effects (0.14 for BrWM and 0.13 for WWM; Koots et al., 1994a) and greater than those recently reported for 4 French beef cattle breeds (from 0.07 to 0.13 for BrWM and from 0.08 to 0.11 for WWM; Phocas and Laloë, 2004) and for weaning weight at 200 d in 4 British beef breeds (0.07; Roughsedge et al., 2005).

Genetic correlations for CED-CEM, BrWD-BrWM, and WWD-WWM were negative as usually found in the literature. Koots et al. (1994b) reported average values of genetic correlations between direct and maternal genetic effects of -0.30 for CED-CEM, -0.35 for BrWD-BrWM, and -0.25 for WWD-WWM. These values varied from -0.35 to -0.69 for CED-CEM, from -0.39 to -0.49

for BrWD-BrWM and from -0.09 to -0.41 for WWD-WWM in 4 French beef breeds (Phocas and Laloë, 2004) and from -0.12 to -0.76 for CED-CEM and from -0.19 to -0.71 for WW at 200 d in 4 British beef breeds (Roughsedge et al., 2005). Eriksson et al. (2004a) reported genetic correlations for CED-CEM and BrWD-BrWM in 2 Swedish beef breeds ranging from -0.13 to -0.54 and -0.27 to -0.39, respectively. Using linear models and American Gelbvieh data, Varona et al. (1999b) obtained genetic correlations of -0.302 for CED-CEM and -0.359 for BrWD-BrWM.

From a clinical point of view most difficult births occur due to fetal-pelvic incompatibility because size of the calf (basically explained by BrW) exceeds the pelvic opening. In our breed, calves born with difficulty (calvings scored as 3 or 4) were over 6 to 8 kg heavier than those born in easy calvings (Table 1). Because selection for growth can increase BrW to a larger extent than pelvic opening, a negative genetic correlation between these traits can be expected (Meijering, 1984). Phocas and Sapa (2004), analyzing progeny test station data from beef heifers, suggested that maternal effects on CE can be largely explained by size of dam's pelvic opening. These authors reported that if CE was considered as a trait of the dam, genetic correlations between heifer growth traits and CE were not significantly different from zero, whereas genetic correlations between heifer growth and pelvic opening were moderate to high; also, estimates of the genetic correlation between CE and pelvic opening were favorable (varying from 0 to -0.60), thus suggesting that the antagonism observed between CED and CEM may be due to a genetic antagonism between BrW and pelvic opening. However, there is consensus on the poor performance of models involving maternal genetic effects, at least for growth traits. Meyer (1997) reported that large sampling correlations between parameter estimates can artificially bias the estimation of correlations between direct and maternal genetic effects as a function of the values obtained for the other parameters. Moreover, Robinson (1996a,b) pointed out the existence of unaccounted for environmental factors, thus affecting estimations. It has been recently reported that, in the Asturiana de los Valles breed, environmental effects linked to sire affected estimation of genetic correlations for BrWD-BrWM and WWD-WWM (Gutiérrez et al., 2006). This overall situation led Phocas and Sapa (2004) to conclude that the correlation between the direct and maternal effects for WW and CE is negligible.

Genetic Parameters Between Traits

Genetic correlations estimated in the present analysis between direct genetic effects can be compared with other estimates in the literature. Average genetic correlation for CED-BrWD has been reported to be 0.58 (Koots et al., 1994b). Recent estimates ranged from 0.40 to 0.78 in 4 French beef cattle breeds (Phocas and Laloë, 2004) and reached 0.794 in American Gelbvieh (Varona

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et al., 1999b) and 0.62 in Swedish beef breeds (Eriksson et al., 2004a). The genetic correlation for the pair CED-WWD has been reported to be, on average, negative and moderate to high (-0.47; Koots et al., 1994b). However, most recent estimates of this correlation are positive and moderate to low (from 0.12 to 0.28) in French cattle (Phocas and Laloë, 2004) and in British cattle (from 0.04 to 0.44; Roughsedge et al., 2005), thus roughly coinciding with the current estimate (0.358). Correlations of 0.137 (Phocas and Laloë, 2004) and 0.150 (Roughsedge et al., 2005) were also found between CID and BrWD. However, the large SE for these estimates always included zero, thus suggesting that the correlation between CID and WWD may be negligible. The current correlation for BrWD-WWD is within the range reported for the same breed (from 0.352 to 0.422; Gutiérrez et al., 2006) and also reported for French beef breeds (from 0.26 to 0.44; Phocas and Laloë, 2004).

Correlations between the maternal genetic effects of different traits were not always consistent with those recently reported for beef cattle. Varona et al. (1999b) reported a genetic correlation for CEM-BrWM of 0.494 in American Gelbvieh and Eriksson et al. (2004a) reported a genetic correlation of 0.46 in Swedish beef cattle. The current estimate of the correlation for the pair CEM-BrWM (0.286 \pm 0.079) is lower than those recently reported in French beef cattle (ranging from 0.35 to 0.58; Phocas and Laloë, 2004). Estimates of the genetic correlation for BrWM-WWM in the Asturiana de los Valles are within the range recently reported in French beef cattle (from 0.23 to 0.35; Phocas and Laloë, 2004).

Estimates of genetic correlations between direct and maternal effects across traits are scarce in the literature (Phocas and Laloë, 2004; Roughsedge et al., 2005). Varona et al. (1999b) and Eriksson et al. (2004a) reported genetic correlations for CED-BrWM of -0.310 and -0.17, respectively. Correlations between BrWD and CEM were -0.398 (Varona et al., 1999b) and 0.03 (Eriksson et al., 2004a). In general, the correlations reported here are of the same sign but lower in magnitude. Phocas and Laloë (2004) reported genetic correlations of CED with BrWM and WWM ranging, respectively, from -0.31 to -0.60 and from -0.09 to -0.20. These authors also reported correlations between BrWD and WWM that ranged from -0.22 to -0.29. Most estimates between CED and WWM reported by Roughsedge et al. (2005) in British beef cattle breeds were also negative (varying from -0.07 to -0.24), though that for the Aberdeen Angus breed was 0.47. On the other hand, genetic correlations of CEM with BrWD and WWD reported by Phocas and Laloë (2004) ranged from -0.22 to -0.36 for BrWD and from 0 to -0.36 for WWD; the correlations between BrWM and WWD ranged from -0.09 to -0.34. Estimates of the genetic correlation between CEM and WWD in British beef cattle breeds (Roughsedge et al., 2005) varied from -0.05 to -0.52. Estimates of the genetic correlation between CID and CEM have been reported to vary from

-0.05 to 0.38 (Roughsedge et al., 2005). Estimates between CID and WWM reported by Roughsedge et al. (2005) were also positive and moderate to low (varying from 0.00 to 0.38), though that for the South Devon breed was -0.72.

The overall scenario discussed above with respect to CE-BrW genetic correlations, supports the hypothesis that maternal effects for CE are mainly due to size of pelvic opening (Meijering, 1984; Phocas and Sapa, 2004). Genetic correlations between direct effects of CE and BrW are usually high, thus pointing out basically the same genes affect these traits (Koots et al., 1994b). However, most genetic correlations estimated between the maternal effects of these traits and also between direct and maternal genetic effects have been moderate to low, thus highlighting the possibility that the genes involved in regulation of the maternal effects for CE and for BrW are not the same (Phocas and Sapa, 2004). Moreover, genetic correlations for the pairs CEM-WWM and BrWM-WWM tend to be low, as has been previously highlighted for BrWM-WWM in the Asturiana de los Valles breed (Gutiérrez et al., 2006). Furthermore, the genetic relationships for the pairs CED-WWM and BrWD-WWM are not significant, indicating that selection for increased maternal merit for WW would not affect to a large extent CE or calf size at birth.

Though SE obtained here are large, current results can also be useful to ascertain the genetic relationships between the maternal genetic effects for preweaning growth traits and reproductive performance (here identified as WW and CI). Meyer et al. (1994) reported a genetic correlation between milk yield and WWM in beef cattle of 0.80, suggesting that milking ability is the main determinant of maternal effects on the preweaning growth of beef calves. In beef cattle, no information is available on genetic correlations between milk yield and fertility traits. However, if the close genetic relationship between cow's milking ability and maternal effects for preweaning growth traits is accepted (Meyer et al., 1994), our estimate of -0.148 would point to a similar relationship between CID and milk yield, namely unfavorable and from moderate to low, which has been reported repeatedly in dairy cattle (see Phocas and Sapa, 2004, for a review). However, Phocas and Sapa (2004), in beef heifers under progeny test at a test station, found a slightly favorable genetic correlation between fertility measured as calving success and milk yield. These authors argued that genetic relationships between milk yield and fertility traits in dairy cattle can not be directly extrapolated to beef cows because energy requirements for milk production are much lower for beef than for dairy cows, and body tissue mobilization during lactation is not as important as it is in dairy cows. As a consequence, selection for greater milk yield (or maternal merit for WW) would not have detrimental effects on beef cow reproduction, at least when cows were given adequate food (Phocas and Sapa, 2004). Our results agree with this conclusion. The Asturiana de los Valles breed is managed under difficult conditions in semiextensive or extensive mountainous systems highly dependent on natural pastures with large mobilization of body reserves.

IMPLICATIONS

In this study, direct and maternal genetic correlation matrices and variance components were estimated for calving ease, calving interval, birth weight, and weaning weight in the Asturiana de los Valles breed as a contribution to ascertainment of the performance of suckling cows. The complex pattern of genetic relationships observed between direct and maternal effects on the analyzed traits suggests the need to include direct and maternal breeding values of these traits in selection programs focused on increasing the profits of beef cattle herds. The reported correlation matrices can be useful to implement multitrait breeding value evaluations to aid in sire selection to produce replacement heifers for the herd. Moreover, the present results provide additional information on the nature of genetic effects on the traits analyzed, especially for the maternal genetic effect on weaning weight and its relationship with calving interval.

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