

REALIZED GENETIC PARAMETERS OF GROWTH AND REPRODUCTIVE TRAITS AFTER 25 YEARS OF SELECTION IN THE ASTURIANA DE LOS VALLES BEEF CATTLE BREED

25 AÑOS DE SELECCIÓN EN LA RAZA DE CARNE ASTURIANA DE LOS VALLES: ANÁLISIS DE LOS PARÁMETROS GENÉTICOS EN CARACTERES DE CRECIMIENTO Y REPRODUCTIVOS.

Cortes O.¹, Carleos C.², Baro J.A.³, Fernández M.A.⁴, Villa J.⁴, Menéndez-Buxadera A.¹, Cañón J.^{1*}

¹Departamento de Producción Animal. Facultad de Veterinaria. Universidad Complutense de Madrid. Madrid. España. jcanon@vet.ucm.es

²Dpto. Estadística e Investigación Operativa. Universidad de Oviedo. Oviedo. España

³Dpto. CC. Agroforestales. ETSIIAA. Universidad de Valladolid. Palencia. España

⁴ASEAVA. Llanera. Asturias. España

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Abstract

After 25 years of selection, genetic parameters estimates in the Asturiana de los Valles cattle breed are revisited. Two reproduction traits, calving ease and calving interval, and one growth trait, weaning weight, were analysed for this study. A total of 198,277 records for calving ease, 51,161 for weaning weights, and 123,532 for calving interval were available. Uni- and bi-variate model were used in the analysis, and the maternal effect was included for WW. Heritabilities for reproductive traits were lower than for growth traits and the univariate and bivariate models achieved similar heritability estimates. The maternal effect was smaller than the direct genetic effect for WW, and negative correlation was detected among them in accordance with similar studies for cattle beef breeds. The genetic correlation among WW and CE was moderate and negative (-0.262) and the WW-CE genetic correlation was quite low (0.056). The bivariate model exposed an increase in the accuracy of the estimated breeding values for the three traits analyzed. Genetic trends were estimated to evaluate the genetic change over the last 25 years. The highest genetic progress was attained by WW, with a regression coefficient of the breeding values on the year estimated at 0.225. The genetic trend for CE was negligible and CI evidenced a small, negative genetic change (-0.128)

Resumen

Se han analizado los parámetros genéticos de dos caracteres reproductivos, facilidad de parto e intervalo entre partos y un carácter de crecimiento, peso al destete, en la raza de carne Asturiana de los Valles después de 25 años de selección como una representación de los principales caracteres de interés económico en esta raza. En el análisis se utilizaron modelos uni y bivariado incluyendo el efecto materno en el peso al destete en ambos modelos. La heredabilidad estimada para el carácter de crecimiento fue superior a la de los caracteres reproductivos. Los modelos uni y bivariado dieron estimas de heredabilidad similares para todos los caracteres. En el peso al destete el efecto materno estimado fue inferior al efecto genético directo y su correlación resultó negativa, como se ha descrito previamente en otros estudios. Las correlaciones genéticas entre los caracteres fueron -0.262 entre peso al destete e intervalo entre partos y de 0.056 peso al destete y facilidad de parto. La fiabilidad de los valores genéticos estimados fue mayor con el modelo bivariado. En los 25 años de selección el mayor progreso genético corresponde con el peso al destete, con un coeficiente de regresión de 0.225, para el intervalo entre partos el progreso genético también fue favorable, con un coeficiente de regresión negativo (-0.128), y para la facilidad de parto no se observó una tendencia significativamente diferente de cero.

Introduction

Beef cattle farming is an important component of sustainable agriculture in much of Europe. The large variety of environmental, social and marketing conditions in Europe has favored the maintenance of a wide spectrum of beef cattle breeds, especially in the South of Europe as meat consumption of local cattle breeds is higher than in

North. Periodic reviews of beef improvement programs are both for benchmarking and as an opportunity to evaluate their efficacy, to understanding the phenotypic trends and to estimate the genetic parameters changes of the traits under selection. Asturiana de los Valles is an autochthonous beef cattle breed mainly located in the north of Spain (Asturias). As in any beef cattle breed, traits related to reproduction and growth should be considered as the main variables within the breeding objectives (Phocas *et al.*, 1998; Albera *et al.*, 2004). In beef cattle, weights at different ages (birth, weaning or yearling weights) or weight over certain ages interval have been traditionally adopted as the selection criteria. Weight traits are easy to measure and have high correlations among them. Also a high correlation has been demonstrated among weight measures at early ages and calving ease (CE) (Meijering *et al.*, 1984; Koots *et al.*, 1994). So, an increase in the birth or weaning weight (WW) may be detrimental for calving ease comprising the traditionally semi-extensive rearing of the Asturiana de los Valles breed. Furthermore, this breed is regarded as well adapted to local environmental conditions and maternal behaviour could be affected as growth traits increase. The heritability estimated for growth traits, like weaning weights, is relatively high, (Koots *et al.*, 1994; Phocas & Lalöe 2004; Roughsedge *et al.*, 2005) but is lower for reproductive traits, especially in those traits, like calving ease, where phenotype scores are sensitive to subjectivity and strongly influenced by non-genetic factors (MacNeil *et al.*, 1984; Cundiff *et al.*, 1986; Meyer *et al.*, 1990). So, for reproductive traits larger data sets are required to obtain reliable genetic parameter estimates. Finally, in traits measured at an early age, phenotypes are affected by two separated divergent components, the calf effect and the maternal effect, which contribute to making the definition of breeding objectives difficult (Phoca & Lalöe 2004). In this complex situation where different traits, some with negative genetic correlations, are economically important, the estimation of genetic parameters is crucial to planning breeding programmes and to understanding the phenotypic trends of the traits under selection. There are published studies based on growth and reproductive traits in cattle breeds (Eriksson *et al.*, 2004; Cammack *et al.*, 2009; Casas *et al.*, 2010; MacNeil & Vukasinovic, 2011). However, the information available on the genetic relationship between calving ease and calving interval (CI), as reproduction traits, and weaning weight, as a growth trait, is relatively scarce. In spite of the great number of phenotypes registered in the Asturiana de los Valles breed program, previous analysis for growth and reproductive genetic parameter traits (Gutierrez *et al.*, 1997; Goyache *et al.*, 2005; Gutierrez *et al.*, 2006; Gutierrez *et al.*, 2007; Cervantes *et al.*, 2010; Pun *et al.*, 2011) have been based on relatively limited databases, including only animals registered until 1997. Therefore, those genetic parameter estimates should be jointly revisited, along with their effect on the different trait trends. The aims of the current study were (1) to estimate genetic parameters of growth and reproductive traits, taking into account the direct and maternal genetic effect and the genetic correlations between them and (2) to analyze the trend of the breeding values after 25 years' selection.

Material and methods

The Asturiana de los Valles bovine breed is located in the north of Spain over the Cantabrian range under semi-extensive conditions. Animals graze on communal pastures during 8 to 9 months and winter on valley pastures that need supplemental hay. The initial phenotypic and pedigree database covered 24 years (1987-2011) of information on the Asturiana de los Valles beef cattle breed.

Animals

Pedigree information on the Asturiana de los Valles breed was provided by the official breed association (ASEAVA). Those animals with identification or birth weight errors were excluded for further analysis. Finally, a total of 276,654 pedigree records were included in the statistical analysis.

Traits

Reproductive and growth traits analyzed included weaning weight (WW), calving ease (CE) and calving interval (CI). Phenotypic records of those animals with birth or identification errors were excluded for further analysis. Also, values lower than 300 days or higher than 730 for CI days were discarded.

Traditionally, calving ease was recorded following the criteria: (1) no assistance; (2) minor assistance; (3) hard assistance; and (4) caesarean. In our data scores 1 and 2 were considered as a single group due to slight differences between them.

After editing the database, a total of 198,277 calving ease records registered in 76,895 cows, 51,161 weaning weights records registered in 25,495 cows, and 123,532 calving interval records registered in 44,812 cows were included for the analysis.

An inflection point for phenotypic records with errors was detected at 1997 and consequently, previous records were dropped and the final phenotypic database included information from 1997 to 2011. It must be noted that several reports (Gutierrez et al. 1997; Goyache et al. 2005; Gutierrez et al. 2006; Gutierrez et al. 2007; Cervantes et al. 2010; Pun et al. 2011) for growth and reproductive traits in Asturiana de los Valles cattle have been based on records registered until 1997, while such records have been rejected in our final database due to the large number of errors found. Table I shows the number of observations, the mean and standard deviations and the minimum and maximum values for each trait.

Table I. Number of observations, mean and standard error for weaning weight (WW) and calving interval (CI). Frequencies (in percentage) for calving ease (CE). (*Número de observaciones, media, desviación estándar para los caracteres peso al destete e intervalo entre partos. Frecuencias en porcentaje para el carácter dificultad al parto*)

Trait	N	Mean	SD
Weaning weight (WW)	51,161	219.7 ¹	55.2
Calving interval (CI)	123,532	418.1 ²	99.2
	Calving ease (CE)		
	1 ³	2 ³	3 ³
Frequency (%)	97.4	1.6	1

¹In kilograms

²In days

³1 null or minor assistance; 2 hard assistance; 3 caesarean

Statistical analysis

Data were analyzed using ASReML 3 (Gilmour et al. 2000). The non-genetic effects in the models included as fixed effects were: the number of calving (12 levels) and year-month of calving (156 levels); for both WW and CE the model also included the sex (2 levels), and for CE the age at weaning was also included as a cubic covariate. The random effects taken into consideration were direct and maternal genetic effects, the permanent environmental effect, and the combination management-municipality as a temporal effect for WW (324 levels); the maternal effect was excluded from the models for CI and CE.

The components of co-variance were estimated using a univariate and a bivariate model combining WW with CI and with CE. The matrix notation for the univariate model was: $y = Xb + Za + Wm + Pp + Qq + e$

$$\begin{bmatrix} a \\ m \\ p \\ q \\ e \end{bmatrix} \approx N \left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} G & C & 0 & 0 & 0 \\ C & M & 0 & 0 & 0 \\ 0 & 0 & P & 0 & 0 \\ 0 & 0 & 0 & Q & 0 \\ 0 & 0 & 0 & 0 & R \end{bmatrix} \right)$$

where $G = A\sigma_a^2$, $M = A\sigma_m^2$, $C = A\sigma_{am}$, $P = Ip\sigma_p^2$, $Q = Iq\sigma_q^2$, and $R = In\sigma_e^2$. \mathbf{Y} is the vector of observations for WW, CE or CI; \mathbf{b} is a vector of non-genetic effects; \mathbf{a} is a vector of the random direct additive genetic effects; \mathbf{m} is a vector of the random maternal additive genetic effects; \mathbf{p} is a vector of random permanent environmental effects, \mathbf{q} is the vector of random management-municipality effects, and \mathbf{e} is the vector of residuals. \mathbf{X} , \mathbf{Z} , \mathbf{W} , \mathbf{P} , and \mathbf{Q} are incidence matrices relating \mathbf{b} , \mathbf{a} , \mathbf{m} , \mathbf{p} , and \mathbf{q} , to \mathbf{y} . \mathbf{A} is the additive numerator relationship matrix that is created using pedigree information. σ_a^2 is the variance of direct additive genetic effects, σ_m^2 is the variance of maternal additive genetic effects, σ_{am} is the covariance between direct and maternal additive genetic effects, σ_p^2 and σ_q^2 are the variances of permanent environmental and management-nucleus effects respectively, and σ_e^2 is the residual variance. \mathbf{Ip} , \mathbf{Iq} , and \mathbf{In} are identity matrices with order respectively equal to \mathbf{p} , the number of environments; \mathbf{q} , the number of management-municipality levels; and \mathbf{n} , the number of observations. In the univariate models for CE and for CI the random maternal additive genetic effects (\mathbf{m}) and the covariance between direct and maternal genetic effects (C) were excluded.

Additive direct heritability (h^2_{ai}) and additive maternal heritability (h^2_{mi}) were estimated as ratios of additive direct and additive maternal variances to phenotypic variance, respectively. The direct-maternal genetic

correlation ($r_{a,m}$) was computed as the ratio of the direct-maternal genetic covariance ($\sigma_{a,m}$) to the product of the square roots of σ_a^2 and σ_m^2 .

Traits WW-CE and WW-CI were analysed following the model:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} \\ + \begin{bmatrix} P_1 & 0 \\ 0 & P_2 \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \end{bmatrix} + \begin{bmatrix} Q_1 & 0 \\ 0 & Q_2 \end{bmatrix} \begin{bmatrix} q_1 \\ q_2 \end{bmatrix} + \begin{bmatrix} e_1 & e_{21} \\ e_{12} & e_2 \end{bmatrix}$$

In this model, vectors and incidence matrices correspond to those in the univariate model, and subscripts 1 and 2 denote traits. For example, \mathbf{a} is now a vector resulting from concatenating $\mathbf{a1}$ and $\mathbf{a2}$. The changing elements of the formula are now the following:

$G = G_0 \otimes A$, $M = M_0 \otimes A$, $C = C_0 \otimes A$, $P = Ip\sigma_p^2$, $Q = Iq\sigma_q^2$, and $R = In\sigma_e^2$. G_0 is a 2×2 covariance matrix between direct additive genetic effects for traits 1 and 2. M_0 is a 2×2 covariance matrix between maternal additive genetic effects for traits 1 and 2. C_0 is a 2×2 covariance matrix between direct additive genetic effects for traits 1 and 2. So we have:

$$var \begin{pmatrix} a_1 \\ a_2 \\ m_1 \\ m_2 \end{pmatrix} = \begin{bmatrix} G & C \\ C & M \end{bmatrix} = \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_1 a_2} & \sigma_{a_1 m_1} & \sigma_{a_1 m_2} \\ \sigma_{a_1 a_2} & \sigma_{a_2}^2 & \sigma_{a_2 m_1} & \sigma_{a_2 m_2} \\ \sigma_{a_1 m_1} & \sigma_{a_2 m_1} & \sigma_{m_1}^2 & \sigma_{m_1 m_2} \\ \sigma_{a_1 m_2} & \sigma_{a_2 m_2} & \sigma_{m_1 m_2} & \sigma_{m_2}^2 \end{bmatrix} \otimes A$$

The correlations were estimated for direct genetic effect among the univariate and bivariate models for WW, CE and CI and for maternal genetic effect for WW. Genetic trends were calculated as the regression of the average predicted breeding values of the animals born in the same year on year. The following equation was used:

$$y_i = b_0 + b_1 x_i + e_i$$

in which y_i is the mean breeding value for the traits evaluated in the i th birth year, b_0 is the intercept, b_1 is the slope, x_i is the i th birth year, and e_i is a random error. Regression coefficients and goodness of fit (R^2) values were also derived as part of the procedure.

The accuracy of the breeding values was estimated using:

$$r_{\hat{H}H} = \sqrt{1 - \frac{\sigma_e^2}{\sigma_{ai}^2}} \times 100$$

Where σ_e^2 denotes the prediction error variance for each animal and trait, and σ_{ai}^2 is the additive genetic variance for each trait analyzed.

Results

Phenotypic variances and genetic parameter estimates in the univariate model are given in Table II. The additive variance component relative to the phenotypic one was greater for WW than for CE and CI (0.506, 0.088 and 0.227, respectively). Maternal heritability (0.218) was lower than that in direct genetic effect for WW. The genetic correlation for direct-maternal direct genetic effect was negative for WW (-0.632).

Bivariate genetic parameter estimates and their correlations are shown in Table III. The direct (WW, CE and CI) and maternal heritabilities (WW) were similar to those in the univariate model. Also, the correlation between direct and maternal effect for WW was negative and evidenced similar values in bivariate and univariate models (Table II and 3). The genetic correlation for direct genetic effect in the bivariate model was positive and low in WW-CE (0.056) and negative and higher in the WW-CI bivariate model (-0.262).

The genetic correlations among the total breeding values obtained by the univariate and the bivariate models are shown in Table IV. The high genetic correlation between models for the total breeding values estimated is remarkable. The average of the breeding value accuracies of all the animals analyzed and of the sires with more than 15 offspring was higher in the bivariate than in the univariate model.

The evolution of the breeding values from 1997 to 2011 was estimated from the regression coefficient of the breeding values on the birth (Table V). While CE and CI showed null and negative regression values (-0.0004 and -0.128, respectively), the regression coefficient for WW was positive (0.267).

Table II. Estimates of phenotypic variances, direct and maternal heritabilities, total heritability and correlations between direct and maternal genetic effects for all traits analysed in the univariate model. Standard errors are in parentheses (*Estimas del modelo univariado de las varianzas fenotípicas, heredabilidad directa y materna, heredabilidad total y las correlaciones entre el efecto genético directo y materno para los caracteres analizados. Errores estándar entre paréntesis*)

	CE	WW	CI
Animals, No	246,546	89,925	164,532
Animals with records, No	198,277	51,161	123,532
Direct genetics	4934*	888.66	2312.91
Maternal genetics		382.31	
Covariance direct-maternal		-368.66	
Permanent environment	1442.4*	10.039	235.79
System-municipality	1248*	169.85	155.07
Residual	49504*	672.73	7495.07
Total variance	56005.2*	1754.9	10198.84
h_a^2	0.088 \pm 0.004	0.506 \pm 0.021	0.227 \pm 0.004
h_m^2		0.218 \pm 0.017	
$r_{g[a,m]}$		-0.632 \pm 0.025	

*x10⁶

Table III. Estimates of phenotypic variances, direct and maternal heritabilities, total heritability, correlations between direct and maternal genetic effects and correlation between CI/WW and CE/WW following the bivariate model. Standard errors are in parentheses (*Estimas del modelo bivariado de las varianzas fenotípicas, heredabilidad directa y materna, heredabilidad total y las correlaciones entre el efecto genético directo y materno y entre el intervalo entre partos/peso al destete y dificultad al parto /peso al destete. Errores estándar entre paréntesis*)

	Traits bivariate model		Traits bivariate model	
	CE	WW	CI	WW
Animals, No	246,546		164,532	
Animals with records, No	198,277		123,532	
Direct genetics	4918*	941.6	2406.3	970,4
Maternal genetics	-	376.9	-	306,9
Covariance direct-maternal	-	-417.3	-	-375,7
Permanent environment	1441*	254.605	172.981	585.954
System-municipality	124*	166.110	144.560	148.274
Residual	49513*	677.025	7505.84	605.463
Total variance	55390*	1769.7	9610.8	1713.9
h_a^2	0.089 (0.004)	0.532 (0.022)	0.25 (0.008)	0.566 (0.026)
h_m^2	-	0.213 (0.018)	-	0.179 (0.026)
$r_{g[a,m]}$	-	-0.700 (0.023)	-	-0.688 (0.034)
r_a	0.056 (0.040)		-0.262 (0.037)	

*values x10⁶

Table IV. Breeding value correlations between univariate and bivariate models for calving ease (CE), calving interval (CI) and weaning weight (WW). Accuracies of the estimated breeding values in all the animals analyzed and sires with more than 15 offspring in the univariate and the bivariate models (*Correlaciones de los valores genéticos estimados con el modelouni y bivariado en los tres caracteres analizados, peso al destete, dificultad al parto e intervalo entre partos. Fiabilidad de los valores genéticos estimados en todos los animales analizados y en los sementales con más de 15 descendientes*)

Breeding value correlations	CI	CE	WW
EBV animals	0.968	0.996	0.996
EBV sires	0.993	0.996	0.986

Breeding value accuracies	Univariate	Bivariate	Univariate	Bivariate	Univariate	Bivariate
Accuracy animals	29.6	40.8	37.4	45.3	41.1	53.5
Accuracy sires	39.1	64.8	54.5	65.5	51.4	66.3

Table V. Regression coefficients of the breeding values on year and goodness of fit (R^2) for the three traits analysed, Calving ease (CE), calving interval (CI) and weaning weight (WW) (*Coefficiente de regresión de los valores genéticos sobre el año y bondad del ajuste (R^2) en los tres caracteres analizados, dificultad al parto, intervalo entre partos y peso al destete*)

Trait	Regression coefficient	R^2 (%)
CE	-0.0004	80
CI	-0.128*	82
WW	+0.225*	74

* $p < 0.05$

Discussion

Traditionally the selection criteria of the Asturiana de los Valles farmers have been focused on morphology, well conformed animals, and in the double-muscled character more than in breeding values for growth or reproductive traits. Currently, the frequency of the myostatin (*mh*) allele is 82% and the *mh* homozygote (*mh/mh*), heterozygote (*mh/+*) and normal (*+/+*) genotype frequencies are 69%, 27% and 4%, respectively (data not shown). The *mh* allele has a significant effect on growth traits, a *mh* homozygote calf weight 5 kg more than a normal animal at birth but between 4 and 10 kg less at weaning weight (data not shown). In spite of the higher birth weight and the higher frequency of *mh* homozygote animals in the Asturiana de los Valles breed, only 2.7% of calvings required hard assistance or a caesarean. The main traits included in the beef cattle genetic programs are related to growth traits; however, the relative importance of reproduction traits could be up to 4-fold more important than improvements in production traits when calves are sold at weaning (Melton, 1995). In general, reproductive traits show low heritabilities and are recorded later in the life of the animal than the majority of growth traits, so their improvement has been mainly carried out through crossbreeding and improved management techniques rather than direct selection. However, the important genetic correlations between reproductive traits and others traits with moderate or high heritabilities made indirect selection for reproductive traits feasible (Camamck et al. 2009).

As expected, the results showed that direct genetic heritabilities for reproductive traits (CE and CI) were lower than for production traits (WW). While fertility is a general term and not easily defined, CE has been easily defined and categorized. Notwithstanding, heritabilities for CE were low and of similar magnitude in the univariate and bivariate models (~ 0.09), suggesting that direct selection for CE will result in a low response in an improvement programme of reduced size. Also, the direct genetic heritability for CE (0.09) was lower than that in other bovine beef breeds (Koots et al. 1994; Phocas & Laloe, 2004), even lower than that in previous Asturiana de los Valles breed analyses (Gutierrez et al. 2007; Cervantes et al. 2010). In contrast the heritabilities for WW and CI, and the magnitude of the correlation among direct and maternal genetic for WW were higher than those in previous analyses in the Asturiana de los Valles and Asturiana de la Montaña breeds (Gutierrez et al. 2002; Gutierrez et al. 2006; Gutierrez et al. 2007; Pun et al. 2011; Baro et al. 2012). The differences with previous analyses in the Asturianan de los Valles breed could be due to two reasons. (1) Previous heritability estimates referred to before were based on animals born until 1997 while animals born

before this year were rejected in our database phenotypic records. (2) Also, when the covariance among direct and maternal effect is not negligible, the direct genetic effect is greater (Meyer, 1997), as recorded for CE in Cervantes et al. (2010).

As a consequence of the low CE heritability the regression coefficient for CE showed no genetic change ($b = -0.0004$) from 1997 to 2011. So, taking into account the high frequency of calving ease belonging to level 1 and the low heritability value, the improvement in reproductive traits should focus more on other traits than CE and the improvement in management techniques would be more effective than direct selection in this trait. Furthermore, the current estimate of the genetic correlation between CE and direct WW (0.056) would suggest that an increase in WW is not expected to have an important effect on the correlated response of CE.

CI measure would be an indicator of reproductive health throughout the life of a cow. The direct genetic heritabilities for CI in the univariate and bivariate models (~ 0.24) was higher than that in previous studies in the Asturiana de los Valles breed (Goyache et al. 2002; Gutierrez et al. 2007;) and than the mean value of 0.10 reported by Koots et al. (1994). Also, Gutierrez et al. (2007) reported a negligible correlation between CI and WW (-0.068), suggested by the high estimated SE which includes zero (0.112). In our results the genetic correlation between CI and WW showed a consistent negative value (-0.262). CI needs two calves to be scored, so CI scores have mostly been obtained from well conformed cows that are priority selected by farmers and receive more favourable treatments from farmers and more opportunities to conceive. So a calf born from a best breed conformation cow, which should have a shorter CI, is expected to have a higher weaning weight. However, the negative correlation among CI and WW could be biased because the best conformed cows were managed differently as regards reproduction.

The genetic trend from 1997 to 2011 for CI was negative in the desired direction, but weak ($b = -0.128$ days). It is remarkable that breeding values for CI were not available for breeders, so phenotypic values are the only source of information and, taking into account its low heritability, a weak increase in the genetic merit for this trait is to be expected if selection is based on phenotypic data. Also, short CI could be associated with cows whose first calves are born late and, in these situations, selection of cows with short CI would indirectly increase the age at first calving (Cammarck, 2009).

WW showed the higher direct genetic heritability when both univariate and bivariate models (~ 0.5) were adjusted. This heritability is higher than that in other bovine breeds (Robinson et al. 1996; Miller & Wilton, 1999; Montaldo & Kinghorn, 2003) and in the upper range of estimates by Groenenveld et al. (1998). The high negative correlation between direct and maternal heritability for WW indicated unfavourable interference among them. So, selection for direct effect decreased maternal ability and therefore direct and maternal effect should be considered for WW selection. This negative genetic correlation is commonly found among direct and maternal genetic effects (Groenenveld et al. 1998; Montaldo & Kinghorn, 2003; Eriksson et al. 2004). Nevertheless, Groenenveld et al. (1998) mentioned that negative correlation between direct and maternal effect is not clear. Several reasons have been suggested to explain this antagonism: a negative dam-offspring correlation due to the decrease in cow milk production when calf weaning weights increase or the adverse effect of the heifers' nutrition on the WW of their calves could explain it (El-Saied et al. 2006). Furthermore, Wilson & Reale (2006) mentioned that the negative correlation is the consequence of a pleiotropic effect in order to preserve the genetic variation that limits the selection response.

The genetic trend for WW ($b = 0.268$ kg.) showed a slight genetic gain from 1997 to 2011. Furthermore, the phenotypic increase for WW over the last 25 years was low (7%) (data not shown) in spite of the high heritability estimated (0.53). This result suggests that the genetic progress for WW was lower than expected, probably due to the high frequency increases in mh homozygote animals (67% mh/mh) in the Asturianan de los Valles breed and their weaning weights being lower than that of normal animals. The negative correlation between the direct and the maternal genetic effect could slow down the WW phenotypic increase, as reflected the expression in Willham (1972) for selection response, $(\sigma_a^2 + 1.5\sigma_{am} + 0.5\sigma_m^2)/\sigma_p$, where negative $\sigma_{a,m}$ values result in decreased responses. In order to combine both contrary genetic effects, the maternal and direct WW effects could be included in the selection criteria for the Asturiana de los Valles breed. Also, the lower offspring from artificial insemination rather than natural services sires and other criteria than breeding values used to select sires by the breeders could explain this result.

The uni- and bivariate models produced similar genetic parameter estimates and, as expected (Kadarmideen et al. 2003), high correlations between univariate and bivariate estimated breeding values for the three traits analyzed. The higher number of phenotypic observations for CI than for WW allows us to evaluate 3-fold more

animals for WW in the bivariate model (CI-WW) than in the univariate model (WW). As expected, the values of accuracies of the estimated breeding values were higher in the bivariate model than in the univariate one and higher in sires than in all the animals. Also, the higher genetic correlation between CI-WW than between CE-WW is likely to explain the higher increase in accuracy for CI than for CE in the bivariate model. So the bivariate model could be considered as an alternative method to estimate breeding values for the three traits analysed.

Conclusions

As expected, heritability for WW was clearly higher than for CI and CE. In spite of the high heritability estimated for WW its genetic trend over the 25 years of selection was low. This is also the situation for traits CE and CI. Customary selection, as carried out by Asturiana de los Valles breeders, prioritizes morphology and double-muscled phenotypes, jointly with the pleiotropic effect of the mh allele on weaning weight, and could slow down the WW genetic trend. Our results indicated low genetic correlation between WW and CE, and moderate negative ones between WW and CI. The high negative genetic correlation estimated between direct and maternal genetic effect for WW suggests that both effects are suitable for inclusion as selection criteria for the Asturiana de los Valles beef cattle breed.

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