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Genetic variability underlying maternal traits of Asturiana de la Montaña beef cattle

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Abstract

Genetic variability parameters of traits related to maternal ability (age at first calving–CA1, first calving interval–CI1, and weaning weight–WW) were estimated in an autochthonous beef cattle breed (Asturiana de la Montaña) reared under harsh conditions. The data set comprised 50,749 births on 378 farms from 1994 to 2008. Heritability for CA1 was moderately high (0.22); heritability for CI1 was 0.10. Genetic correlation between these traits was 0.54, and thus favourable to simultaneously selection. Results for WW gave a direct heritability of 0.20 and a maternal heritability of 0.10; the genetic correlation between additive direct effects and additive maternal effects was –0.60 and thus antagonistic, a situation frequently found in similar populations. The change of additive direct values (BVa) for the lapse considered was almost null until 1997, and increased regularly since that year at 0.092 kg yr^{-1}. It should be noted that, at the same time, additive maternal effects (BVm) showed a significant negative tendency of –0.089 kg yr^{-1}. In order to conveniently combine the knowledge on both genetic effects, taking into account the adverse genetic correlation between them, we propose that selection should be based on a global genetic merit index (BVtm) defined as 1⁄2 BVa + BVm. Correlations between BVa and BVtm, and between BVm and BVtm were 0.22 and 0.56, respectively.

Additional key words: additive effects; autochthonous breed; maternal effects; merit index.

Resumen

Variabilidad genética para variables maternas en la raza vacuna Asturiana de la Montaña

Se estimaron parámetros de variabilidad genética para variables relacionadas con el carácter materno (edad al primer parto–CA1, primer intervalo entre partos–CI1, y peso al destete–WW) en una raza autóctona de ganado vacuno de aptitud cárnica (Asturiana de la Montaña) que se explota bajo condiciones climáticas duras. Los datos comprendían 50.749 nacimientos en 378 explotaciones entre 1994 y 2008. La heredabilidad estimada para CA1 resultó moderadamente elevada (0,22); para CI1 la heredabilidad fue de 0,10. La correlación genética entre ambos caracteres fue de 0,54, y por tanto favorable para la selección simultánea. Para la variable WW, la heredabilidad directa fue de 0,20 y la maternal de 0,10; la correlación genética entre efectos aditivos directos y maternos fue de –0,60 y por tanto antagónicos, situación descrita con frecuencia en poblaciones similares. El cambio en los valores aditivos directos (BVa) durante el periodo de estudio fue prácticamente nulo hasta 1997, y desde entonces se incrementó progresivamente en 0,092 kg $año^{-1}$. En el mismo intervalo, los efectos aditivos maternos (BVm) mostraron una tendencia significativamente negativa de –0,089 kg $año^{-1}$. Para combinar adecuadamente la información sobre ambos valores genéticos, tomando en consideración la correlación adversa entre ellos, se propone que la selección debería basarse en un índice de mérito genético global (BVtm) definido como 1⁄2 BVa + BVm. Las correlaciones entre BVa y BVtm, entre BVm y BVtm fueron de 0,22 y 0,56, respectivamente.

Palabras clave adicionales: efectos aditivos; efectos maternos; índice de mérito; raza autóctona.

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Abbreviations used: AIC (Akaike information criterion); BIC (Bayesian information criterion); BV_a (additive direct values); BV_m (additive maternal effects); BV_{tm} (global genetic merit index); CA1 (age at first calving); CI1 (first calving interval); log £ (decimal logarithm of likelihood); WW (weaning weight).

Introduction

Maternal traits configure a beef breed in ways that complement the main set of meat production traits: growth, composition, and quality. Both sets are usually antagonistic from the breeder's perspective, in the sense that genetic improvements in one of them are partially offset by adverse correlated responses in the other set. Modern selection schemes usually address this issue by splitting selection into specialised lineages that interbreed at a final stage, but autochthonous breeds have traditionally opted for an integral approach and balanced features.

Asturiana de la Montaña is an autochthonous beef cattle breed under special protection, reared in Asturias, Spain (Dunner *et al.*, 1993). It is regarded as a maternal breed, with a small potential for meat yield, and resistant to the highland conditions under which it is usually reared. There is no bibliography on its genetic variability, and it was almost not selected at all. Traits such as precocity, measured as age at first calving, and weaning weight, a trait that reflects both growth ability of the calf and rearing ability of the mother, have been regularly collected for the breed. Their estimates may have a central role for the study of the profitability of rearing-related traits in autochthonous breeds with limited censuses, reared in regions of complex orography, and whose offspring are sold immediately after weaning. We present results for the genetic variability underlying age at first calving, first calving interval, and weaning weight for the Asturiana de la Montaña cattle breed.

Material and methods

The breed database comprised 50,749 records, as of December, 2008. The traits "age at first calving" (CA1) and "first calving interval" (CI1) were calculated from 1st and 2nd calving dates (9,374 and 7,163 records, respectively), ranging from 1994 to 2008. These included data for 2,426 consecutive first and second pregnancies of cows born from 548 sires and 1,784 dams; 367 of these dams of dams had their own data. The pedigree consisted of 4,793 animals.

Weaning weights (WW) were obtained from 15,301 records from 1994 to 2008. These came from 378 farms in 59 districts. Those years in which the district failed to record 20 calvings were dropped from the database to avoid undue influence of outliers, so 14,851 records remained. It was considered that acceptable values for weaning ages range from 90 to 290 days and, for weaning weights, from 60 to 260 kg. The final data set included data from 13,971 animals born to 6,878 dams and 968 sires. Out of these, 2,678 cows and 368 sires had data of their own and 264 were present as both sires of dams and sires of calves. A total of 20,337 animals were included in the pedigree file.

Traits CA1 and CI1 were analysed under the following model:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where: y_i is a $n \times 1$ vector, with n records for the i^{th} trait (1 = CA1 and 2 = CI1); b_i is a vector of fixed effects: calving year and district; a_i is a vector of random additive genetic effects; e_i is a vector of random residual effect; X_i and Z_i are incidence matrices for effects.

The following assumptions were made for the model:

$$Var \begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 \\ g_{21}A & g_{22}A & 0 & 0 \\ 0 & 0 & r_{11}I_n & r_{12}I_n \\ 0 & 0 & r_{12}I_n & r_{22}I_n \end{bmatrix}$$

where: g_{ij} is the additive covariance between the traits i and j, and A is the additive relationship matrix; r_{ij} is the residual covariance between the traits i and j, and I_n is the identity matrix of order n (number of recorded animals).

The trait WW was analysed under four models, which differ in the terms accounting for the genetic covariance between direct and maternal effects, and for the maternal environment. The most complex model was:

$$y = Xb + Z_1a + Z_2m + Z_3c + e$$

where: y is a vector of observations; b is a vector of fixed effects: sex (2 levels), parity number (9 levels), and farm-year-season of calving (2,995 levels). In addition linear, quadratic, and cubic regression terms were included with Age at Weaning as regressor; a and m are random effects vectors for direct and maternal genetic effects, respectively; c is a vector of maternal environment random effects (with 6,878 levels); e is the vector of residuals; and X, Z_1, Z_2, and Z_3 are incidence matrices for effects.

The (co)variances of these models were:

$$Var \begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{ma} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_c\sigma_c^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

Table 1. Model comparisons for weaning weight in Asturiana de la Montaña cattle

Model	Genetic effect[1]			Effect c[1]	P[2]	Criteria[3]		
	Additive	Maternal	Covariance			log £	AIC	BIC
A	Yes	No	No	Yes	3	–9603	86	122
B	Yes	Yes	No	No	3	–9594	68	104
C	Yes	Yes	No	Yes	4	–9579	38	74
D	Yes	Yes	Yes	Yes	5	–9565	10	46

[1] Same fixed effects for all models. c: environmental maternal effect, Yes or No indicates whether the effect was included or not. [2] P is number of parameters. [3] Criteria used to assess goodness of fit for the models. The higher the value of log £ (likelihood), or the lower the AIC (Akaike information criterion) or BIC (Bayesian information criterion), the better the fit.

where is the additive variance, is the maternal additive variance, is the covariance between additive and maternal effects, is the maternal environmental variance and is the residual variance; A is the additive relationship matrix, and I_c and I_n are identity matrices of order c (number of dams) and n (number of recorded animals), respectively.

Models were compared with the following criteria: likelihood (log £), Akaike information criterion (AIC) and Bayesian information criterion (BIC). Parameter estimates were obtained with the ASREML program from Gilmour *et al.* (2000).

Results

Table 1 shows results for the model comparisons under different criteria for the WW trait. Incorporation of a maternal genetic effect (model B) improved the fit when compared to a simpler model (A) that incorporates only additive genetic and maternal environment effects, assuming a null covariance between direct additive and maternal genetic effects. Model C showed an even better fit; this model includes direct additive genetic, maternal genetic and maternal environment effects, assuming again a null covariance between direct additive and maternal genetic effects. The most complex model (D) further incorporated the assumption of a non-null covariance between direct additive and maternal genetic effects.

Our results show an antagonist correlation of 0.601 (± 0.11) between direct (a) and maternal (m) genetics for WW. Our genetic variance component estimates correspond to 0.202 (± 0.03) for direct heritability (h^2), and 0.095 (± 0.04) for maternal (m^2). The accumulated variance of maternal environment (σ^2_c), 44.97 and maternal genetic effects (σ^2_m), 37.44, accounted for as much phenotypic variance as additive genetic effects (σ^2_a) at 74.92.

Table 2. Parameter estimates for genetic components of variance for traits 'age at first calving' (CA1) and 'first calving interval' (CI1) in Asturiana de la Montaña cattle

	CA1	CI1
Average (month)	35.6	13.2
Additive genetic variance (month²)	7.5	0.4
Heritability	0.220±0.03	0.097±0.05

On the other hand, Table 2 shows a summary of parameter estimates for genetic components of variance for traits CA1 and CI1.

The estimate for genetic correlation between CA1 and CI1 was 0.542, suggesting that selection pressure on CA1 may cause a correlated response that decreases calving intervals. Breeding values for CA1 ranged from –4.5 to 5.5 months and, for CI1, from –1.02 to 0.8 months. Breeding values of sires with more than 10 progeny were regressed on the calving year to show a significant ($p < 0.01$) and favourable (decreasing) trend for CA1, and a null trend for CI1 (Fig. 1).

Figure 2 shows the evolution of genetic merits on birth year. There is a significant ($p < 0.05$), slightly descending trend that lasts until 1997 both for BV_d (–0.019 ± 0.009 kg yr^{-1}) and for BV_m (–0.016 ± 0.007 kg yr^{-1}). From 1998 on, there is a change in trend for BV_d, with a significant ($p < 0.05$), small increase (0.092 ± 0.01 kg yr^{-1}), and a stronger downward trend for BV_m (-0.089 ± 0.009 kg yr^{-1}).

Discussion

Individuals of the Asturiana de la Montaña cattle breed are farmed with a strong dependence on pas-

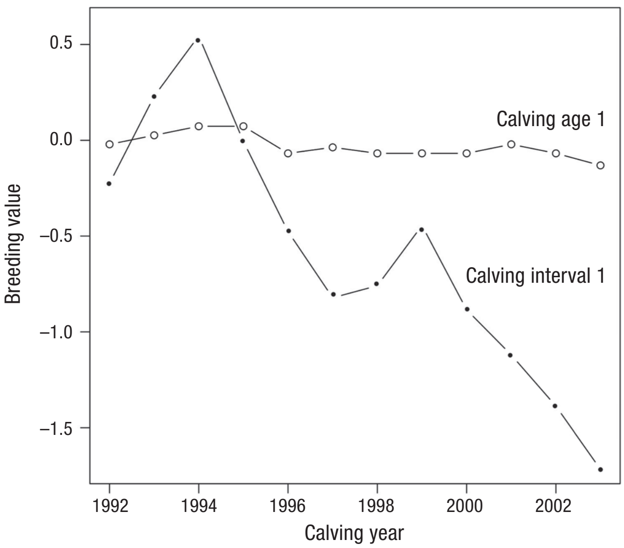

Figure 1. Average breeding values for first calving age (months) by calving year for Asturiana de la Montaña sires with progenies larger than 10.

ture production, and that places a great deal of pressure on their ability to process this feed stuff. Rusticity, as a feature enabling them to withstand these circumstances and resources, is not enough to generate profits in order to attain sustainability in the medium to long term. Other features, such as female reproductive potential and growth of weaned calves, are required.

Precocity is one of the most relevant traits for beef cattle breeding due to its role in farming income through weight and number of marketable units (Núñez-Domínguez *et al.*, 1991). CA1 has been reported to have a negative favourable link with growth traits (Bourdon & Brinks, 1982), and this may lead to reduced CA1 and CI1 when selection is enforced in order to increase WW.

Average weights were lower than those found for the Asturiana de los Valles cattle breed by the authors (Menéndez Buxadera *et al.*, 2008), particularly for WW, which was 80 kg lower. This may be partly due to differences in farming regimes and in effective population sizes (*Ne* < 50, Baro *et al.*, 2007) that constrain selection rates.

There are two thorough reviews on genetic components of variance for WW in beef cattle, by Meyer (1997) and by Quintanilla (1998), as well as reports for Angus cattle by Dodenhoff *et al.* (1999), for Hereford from Mattos *et al.* (2000), and for Charolais and Limousin by Phocas & Laloe (2004). Gutiérrez *et al.* (1997) estimated parameters for WW in Asturiana de los Valles which were much higher for but similar for maternal effects (= 0.115). Regarding the correlation between additive and maternal effects, their results show the same degree of antagonism that was found for Asturiana de la Montaña in this paper. At present, most studies in the literature (see Cundiff, 1972; Gutiérrez *et al.*, 1997) show such antagonistic correlations, which effectively limit selection for increased WW, as per the expression in Willham (1972) for selection response, $(\sigma_a^2 + 1.5\sigma_{am} + 0{,}5\sigma_m^2)/\sigma_p^2$, where negative values for σ_{am} result in decreased responses.

Several interpretations have been suggested for the antagonism, such as alleged artefacts in the statistical model (Robinson, 1996), and sampling covariances between measured animals (Clement *et al.*, 2003; Bijma, 2006; Heydarpour *et al.*, 2008). These are not likely to be the reasons for the results presented here, because there are records for 38% of the cows and sires as well as their progeny, and 27% of the sires had data from female and male progeny. The antagonism is considered a settled issue in a meta-analysis performed by Wilson & Reale (2006), which provided support for the hypothesis that it effectively limits selection response as a pleiotropic effect preserving genetic diversity.

Our results suggest that present genetic progress (Fig. 2) is much lower than theoretically estimated. However, they agree with data published previously for the breed structure (Cañón *et al.*, 1994). The small size of herds and their traditional management my have

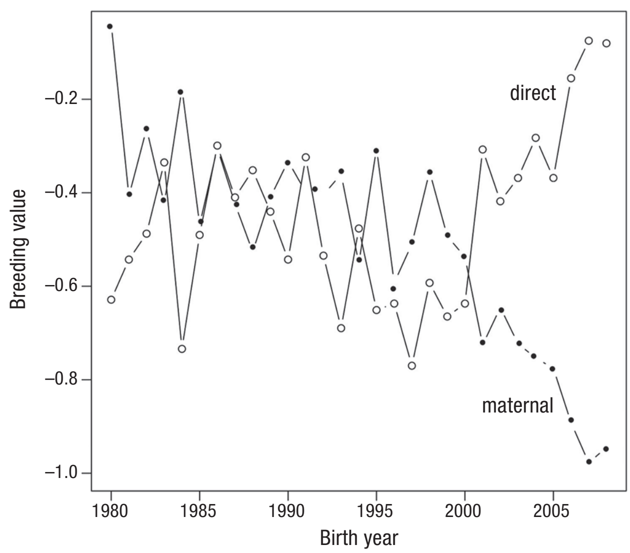

Figure 2. Breeding values for direct and maternal effects on weaning weight (kg) by weaning year in Asturiana de la Montaña cattle.

an adverse effect on maternal effects for weaning weights. An advantageous alternative would be to take measures of total genetic merit (BV_{tm}) as selection criteria, based on expressions derived from the formulae in Wilson (1984), such as:

$$BV_{tm} = ½ BV_a + BV_m$$

The estimated correlations were 0.218 between BV_a and BV_{tm}, and 0.562 between BV_m and BV_{tm}. These values suggest that the use of BV_{tm} as selection criteria may lead to favourable correlated responses for both traits. Total genetic merit may be regarded by breeders as a valuable tool for increasing their main source of value: the weaning weight of calves.

This study shows evidence of wide genetic variability both for WW and CA1 in Asturiana de la Montaña. Genetic progress was found to be negligible for these traits, nevertheless. Genetic antagonism between direct genetic and maternal effects is largely to blame, coinciding with similar reports in the literature, and it establishes a limit to selection. We conclude that a combined predictor of genetic merit in the cows, such as Wilson's total genetic merit, would be most useful for the breed's selection programme.

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