

Multi-trait and random regression approaches for addressing the wide range of weaning ages in Asturiana de los Valles beef cattle for genetic parameter estimation¹

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ABSTRACT: Weaning weight (WW) records of 24,066 Asturiana de los Valles beef cattle, including the progeny of 557 sires and 10,653 dams, were analyzed using a multitrait animal model (MAM) and a random regression model (RRM) in order to estimate the variance components and the breeding value of the animals. Three definitions of WW were used: early weaning (EW) for animals weaned before the age of 180 d; standard weaning (SW) for animals weaned between 180 and 240 d old; and late weaning (LW) for animals weaned between the ages of 240 and 365 d. The heritabilities (h^2) were high (from 0.49 to 0.63), which fully agrees with previous estimates for this breed. The genetic correlations between EW and SW were 0.86, and lower between EW and LW at 0.543 to 0.622, using

MAM and RRM models, respectively. Ranking of sires displayed changes depending on age at weaning of their offspring, which could explain the modest genetic progress reached using MAM evaluation. The first 2 eigenvalues of the random regression coefficient matrix explained 66 and 30% of the genetic variance, which implies important genetic variation underlying the form of the growth curve of the animals during the weaning period. The evaluation of sires according to the official method, as currently carried out by the breeders' association (WW adjusted previously to the age of 180 d), does not exploit the genetic differences in response to their production system where the calf is weaned at variable ages.

Key words: cattle, weaning weight, random regression, longitudinal data

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INTRODUCTION

The main output of the Asturiana beef cattle breed is calf sale at weaning, approximately at 8 to 9 mo old. Yet at least 3 distinctive production systems are present in this breed, with the age at weaning being quite different (Rodríguez and Goyache, 1996). Accordingly, the weight at weaning (**WW**) is one of the main traits included in the breeding program.

Traditionally, WW is adjusted for calf age under the assumption that growth from birth to weaning is linear, and a preadjusted age-constant weight (BIF, 1996; ICAR, 2007) is then used (i.e., by regressing the

uncorrected WW on weaning age). However, studies have shown a curvilinear pattern for preweaning growth (Robertson, 1974), and the regression of uncorrected WW on linear and quadratic weaning age has been proposed as a better method for eliminating the bias (Woodward et al., 1989). At present the estimation of the breeding value (**BV**) of sires and dams in this breed takes linearly preadjusted WW to the age of 180 d (ASEAVA, 2006) using a univariate animal model (**UAM**).

Factors affecting the WW in this breed have received great attention and various papers have been published (Gutiérrez et al., 1997; Goyache et al., 2003; Gutiérrez et al., 2006). In these articles age at weaning has been incorporated as a covariable, which means that WW is considered as the same trait along the age trajectory, with no genetic differences in the shape of the growth curve. This is contrary to results from Meyer (2001) and Nobre et al. (2003) that show the existence of important genetic variability in the live weight curve during the preweaning period.

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Two of the aforementioned papers applied a multiple-trait animal model (**MAM**) on repeated records of live weight. However, when repeated records of live weight are available for each animal frequently result in MAM (co)variances being erratic and difficult to interpret because some kind of harmonic trends throughout the time period are expected from a biological point of view.

An alternative approach (Kirkpatrick et al., 1990) proposed the use of covariance functions to model the (co)variances of a longitudinal trait or repeated records. Meyer and Hill (1997) showed the equivalence between covariance functions and the random regression model (**RRM**) approach, which was first applied by Schaeffer and Dekkers (1994) to dairy cattle for the analysis of test day milk production records. A recent paper from Schaeffer (2004) reviewed a great number of publications using this RRM statistical procedure in different animal breeding scenarios.

The objective of this paper was to estimate the (co)variance components and BV for WW, accounting for the variability in age at weaning by using MAM and RRM, and comparing these results with the classical UAM currently used in the breeding program of this breed.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database, which is under the custody of the official breeder organization ASEAVA.

The performance recording program of the Asturiana breed is based on county farm groups according to their management systems (Gutiérrez et al., 1997). Birth weight and WW records from 28,644 animals born between January 1994 and December 2001 were provided by ASEAVA, with the age at weaning varying from 95 to 345 d. After editing and validating the data, sires with less than 10 offspring were deleted and a total of 24,066 records from 557 sires and 10,653 dams were available. These cows are daughters of 711 sires from which 307 are also present as sire of the calf; a total of 707 dams with 1,192 calves are presented in the data vector. The pedigree file included a total of 35,981 animals.

The first model was a UAM, where the response variable is official weaning weight (**OW**), previously adjusted at 180 d of age, the official procedure used by ASEAVA for BV estimation (ASEAVA, 2006). The second model was a MAM multitrait animal model. The original weaning weight data are classified as 3 traits: early weaning (**EW**; animals weaned between 90 and 180 d old), standard weaning (**SW**; weaned between 180 and 240 d), and late weaning (**LW**) (weaned between 240 and 345 d). Each animal is expected to have a record for 1 of these 3 traits and missing records for the other 2. The numbers of observations and the general means are presented in Figure

1a and 1b. The distribution of sires and dams with calves by the different weaning types is shown in Table 1.

The third model analyzed (RRM) is based on quadratic (order 2) random regression.

The 3 mathematical models look the same in matrix notation, although the interpretation of each symbol varies:

$$\mathbf{y} = \mathbf{X}\mathbf{f} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{c} + \mathbf{e}, \quad [1]$$

with

$$\text{var} \begin{pmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{c} \\ \mathbf{e} \end{pmatrix} = \begin{pmatrix} \mathbf{A} \otimes \mathbf{G} & 0 & 0 & 0 \\ 0 & \mathbf{I} \otimes \mathbf{M} & 0 & 0 \\ 0 & 0 & \mathbf{I} \otimes \mathbf{C} & 0 \\ 0 & 0 & 0 & \mathbf{I} \otimes \mathbf{R} \end{pmatrix},$$

where \mathbf{y} is a vector of WW records; \mathbf{f} is the vector of fixed effects representing number of calvings (3 levels: 1, 2, and greater than 2) and sex of the calf; \mathbf{a} is a vector of random animal additive genetic effects; \mathbf{m} is a vector of permanent maternal environment (**PME**) random effects; \mathbf{c} is a vector of contemporary group (**CG**) random effects, defined as the county-management-year-season; \mathbf{e} is a vector of random residual effects (temporary environment); \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 are incidence matrices connecting the effects with the response vector; \mathbf{A} is the numerator relationship matrix; \mathbf{I} is an identity matrix; and \otimes is the direct product operator. The interpretation of \mathbf{G} , \mathbf{M} , \mathbf{C} , and \mathbf{R} depends on the particular model being fitted. Specific details for each model follow.

For UAM:

\mathbf{y} includes the n OW records.

\mathbf{a} has 35,981 identities.

\mathbf{m} has 10,653 levels of permanent maternal environment.

\mathbf{c} has 704 levels of CG.

\mathbf{e} is a vector of homoscedastic effects.

\mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 are zero-one matrices.

\mathbf{G} is a 1×1 matrix with the additive variance for OW.

\mathbf{M} is a 1×1 matrix with the PME variance for OW.

\mathbf{C} is a 1×1 matrix with the CG variance for OW.

\mathbf{R} is a 1×1 matrix with the residual variance of OW.

For MAM:

\mathbf{y} contains the n original (nonadjusted) EW, SW, and LW records.

\mathbf{f} also includes fixed linear and quadratic coefficients for age at weaning within each weaning category.

\mathbf{a} has 35,981 identities for each of EW, SW, and LW.

\mathbf{m} has $3 \times 10,653$ levels of PME.

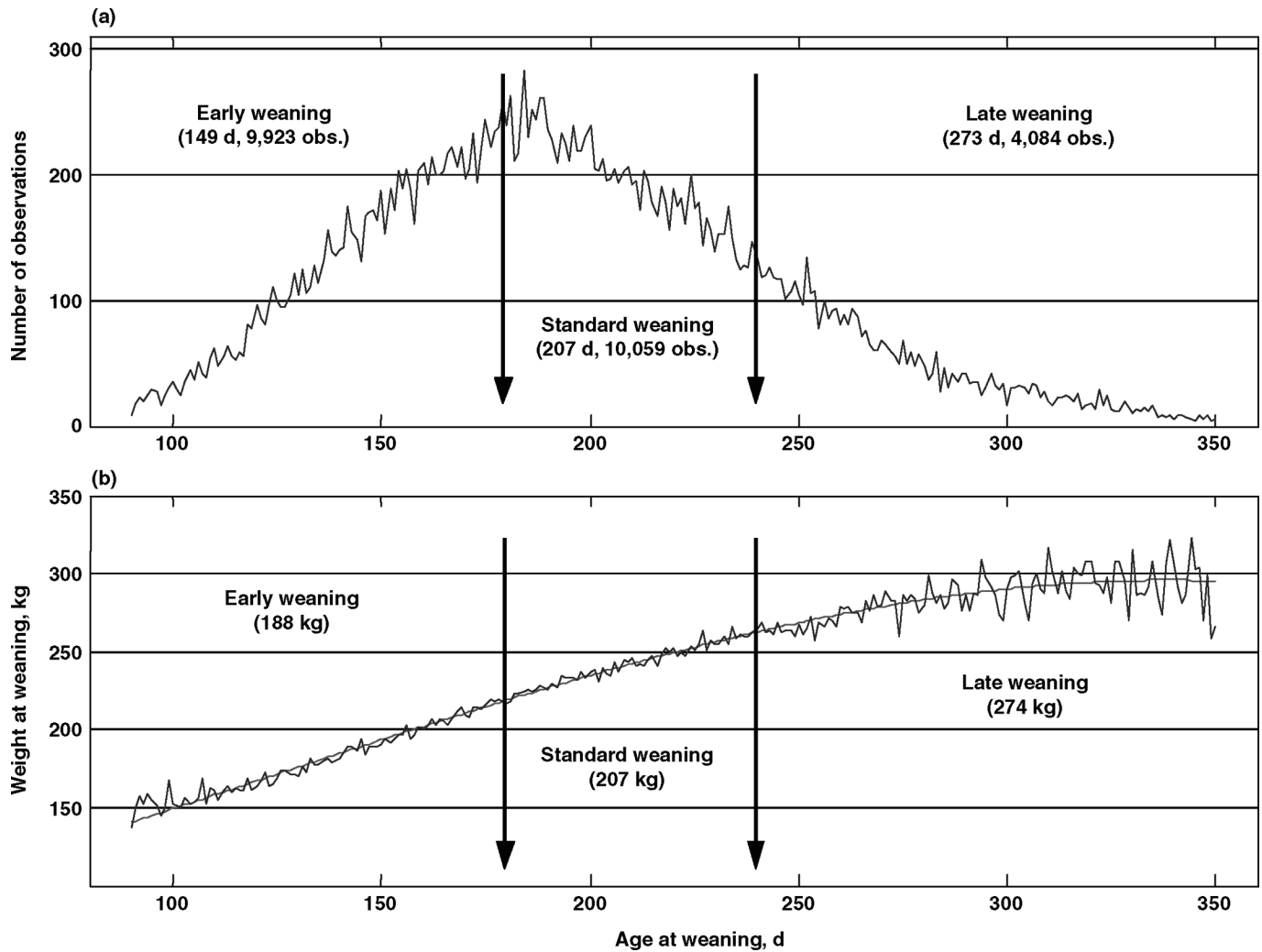


Figure 1. Distribution of (a) records and (b) weight at weaning across ages at weaning. Obs. = observations.

c has 3×704 levels of CG.

e is a vector of homoscedastic effects for each of EW, SW, and LW.

X , Z_1 , Z_2 , and Z_3 are zero-one matrices.

Table 1. Number of the sires and dams with offspring registered in the different types of weaning combinations

| Type of weaning | Early | Standard | Late |
|-----------------|--------------------|----------|-------|
| Early | 535 ^{1,2} | 529 | 435 |
| | 6,168 | 2,963 | 1,076 |
| Standard | | 551 | 456 |
| | | 6,462 | 1,605 |
| Late | | | 457 |
| | | | 3,073 |

¹First line is the number of sires and the second line is the number of dams.

²Diagonal is the number of sires or dams with offspring in 1 type of weaning category. Off diagonal is the number of sires or dams with offspring distributed in a combination of 2 types of weaning categories.

G is the animal variance-covariance 3×3 matrix among EW, SW, and LW.

M is the PME variance-covariance 3×3 matrix among EW, SW, and LW.

C is the CG variance-covariance 3×3 matrix among EW, SW, and LW.

R is a diagonal matrix with 3 diagonal blocks, $[R_{EW}, R_{SW}, R_{LW}]$, where R_i is equal to the residual variance of i times a $n_i \times n_i$ identity matrix, $i \in \{EW, SW, LW\}$; $n_{EW} + n_{SW} + n_{LW} = n$.

For RRM:

y contains the n original (nonadjusted) WW records.

f same as for UAM, plus fixed linear and quadratic coefficients for age at weaning.

a is a vector of random order regression coefficients of order 2 for each additive genetic effect, that is, $3 \times 35,981$ levels.

\mathbf{m} is a vector of random regression coefficients of order 2 for each of PME effect ($3 \times 10,653$ levels).

\mathbf{c} is a vector of random regression coefficients of order 2 for each CG effect (3×704 levels).

\mathbf{e} is a vector of heteroscedastic random residual effects; 5 age groups (90 to 150 d, 150 to 180 d, 180 to 210 d, 210 to 240 d, and 240 to 345 d) of different variances are considered.

\mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 are composed of zeroes and Φ -values; that is, Legendre's orthogonal polynomials evaluated at standardized ages ($[-1:1]$) of corresponding individual measurements.

\mathbf{G} is the variance-covariance 3×3 matrix of the additive genetic random regression coefficients.

\mathbf{M} is the variance-covariance 3×3 matrix of random regression coefficients for PME.

\mathbf{C} is the variance-covariance 3×3 matrix of random regression coefficients for CG.

\mathbf{R} is a diagonal matrix with 5 diagonal blocks, $[\mathbf{R}_1, \mathbf{R}_2, \mathbf{R}_3, \mathbf{R}_4, \mathbf{R}_5]$, where

\mathbf{R}_i is the residual variance of WW within 1 of the i th age group \times an identity matrix.

For UAM and MAM, the genetic parameters, heritability (h^2) and genetic correlations were estimated combining the adequate variance components for the 3 traits estimated through UAM or MAM. For RRM the genetic variance for the trait at age j was estimated by

$$\sigma_{g_j}^2 = \Phi_j \mathbf{G} \Phi_j'$$

following Jamrozik and Schaeffer (1997), where Φ_j is a vector of Legendre's polynomials evaluated at age j . The genetic covariance between ages j and k is obtained by

$$\sigma_{g_{jk}} = \Phi_j \mathbf{G} \Phi_k'$$

The variance for the PME random effects at age j is estimated by

$$\sigma_{m_j}^2 = \Phi_j \mathbf{P} \Phi_j'$$

and for the CG random effects:

$$\sigma_{c_j}^2 = \Phi_j \mathbf{P} \Phi_j'$$

For RRM the solutions for each animal were obtained for the 3 random regression coefficients. Thus, it is possible to calculate an estimate for the breeding value (\mathbf{BV}) for any time point between 3 and 10 mo of age at weaning. For example, the BV for the animal i at age j will be

$$\mathbf{BV}_j^i = \Phi_j \mathbf{a}_i'$$

Table 2. Genetic parameters for weaning weight in Asturiana de los Valles beef breed estimated by a multitrait animal model and a random regression model

| Genetic parameter and type of weaning ¹ | Multitrait | Random regression |
|--|------------|-------------------|
| Genetic variance, kg | | |
| EW | 761 | 775 |
| SW | 1,274 | 1,203 |
| LW | 1,328 | 1,551 |
| Heritability ² | | |
| EW | 0.57 | 0.60 |
| SW | 0.64 | 0.63 |
| LW | 0.49 | 0.53 |
| Genetic correlation ² | | |
| EW-SW | 0.86 | 0.86 |
| EW-LW | 0.62 | 0.54 |
| SW-LW | 0.90 | 0.88 |

¹EW = early weaning, SW = standard weaning, and LW = late weaning.

²The SE for the heritability estimates ranged from 0.02 to 0.04, and from 0.03 to 0.05 for estimates of the genetic correlations.

where $\mathbf{a}_i = (a_0^i, a_1^i, a_2^i)$ stands for the solutions for the second order polynomial for animal i . Notice that in this formulation only the coefficients of the polynomial (Φ_j) change. All estimates were obtained with the AS-REML program (Gilmour et al., 2000). The BV from MAM and RRM were employed to compare the possible biases that can affect the evaluation and selection of sires in this breed and to estimate annual genetic progress.

RESULTS

Results showed that the Asturiana breed weaned a calf with an average weight of 223 kg at an average age of 207 d (average of 211 kg when WW is preadjusted at 180 d). Males were heavier (+20 kg) than females. The WW increased with the calving number following a similar pattern for the 3 weaning types analyzed. An adult cow (\geq third calving) of the Asturiana breed weaned a calf 11% heavier than first calving.

The likelihood ratio for MAM (model 1 with 19 parameters) and RRM (model 2 with 21 parameters) was very similar ($-98,049$ and $-98,032$, respectively), whereas it was greater for the UAM ($-98,169$ and 5 parameters). Although there is no formal procedure to contrast these models, using the Akaike and Bayesian criteria recommended by Foulley and Robert-Granie (2002) makes the results from RRM appear more appropriate to the analyzed data.

The genetic parameters, heritability, and genetic correlations estimated by MAM and RRM for the WW are presented in Table 2. The average age within each of the 3 types of weaning was used to obtain the estimates using the RRM. The h^2 by UAM for OW was 0.498 ± 0.02 , a value very close to those estimated by MAM and RRM. The genetic correlations between EW,

Table 3. Level of coincidence (in %) between the univariate animal model (UAM) and the multitrait animal model (MAM), and between the univariate animal model and the random regression model (RRM)¹

| Item | Sires | | Animals | |
|------------------|-------------------|------|--------------|------|
| | Selected/Total | | | |
| | 55/557 | | 3,600/35,981 | |
| | MAM | RRM | MAM | RRM |
| Early weaning | 81.8 ³ | 80.0 | 81.0 | 81.2 |
| Standard weaning | 74.5 | 72.7 | 74.9 | 75.3 |
| Late weaning | 58.2 | 54.6 | 64.3 | 64.2 |

¹The level of coincidence is expressed as the percentage of the 10% best animals or sires in terms of UAM breeding values that remains in the 10% best when genetic merits are estimated with MAM or RRM.

SW, and LW, regardless of the model used, were positive and high, but it seems clear that it is difficult to accept that the 3 expressions of weaning weight across the age trajectory can be considered as the same trait.

According to this pattern of genetic correlations (Table 2), some differences are expected in the ranking of the animals selected as regards predicted BV by the different model and type of weaning. To examine this problem the following strategy was applied: the best 10% of the whole set of animals (35,981 animals in total) and the best 10% of the sires with data (557 sires in total) were selected according to BV estimated by the 3 models. The rationale was to check whether the best sires selected according to the classical procedure used by ASEAVA (UAM with the WW previously adjusted to 180 d) are also the best when BV are estimated using MAM and MRA. The result shows that around 80, 73, and 60% of these were also the best when BV was estimated by MAM or RRM at EW, SW, and LW, respectively (Table 3).

Genetic progress was computed by the regression of the breeding value of the animals on year of birth, as shown in Figure 2. The improvement obtained by UAM was 3.7 kg (0.636 ± 0.07 kg/year) and was higher using the other 2 models but depended upon the age at weaning. When the trait was defined as early weaning, the lowest genetic trend was attained.

It is noticeable that the estimated genetic progress using MAM and RRM were twice as high as by UAM, which assumes a linear growth and is the official method applied. The genetic progress during the 7 yr of data analyzed is, on average, about 3%, a very low value considering that the genetic coefficient of variation ranged from 13.3 to 15.2% for the late and standard weaning traits, respectively.

Following Kirkpatrick et al. (1990), the possible deformations in the form of the growth curve can be estimated by the eigenvalues (λ_i) of the random regression coefficient matrix (Table 4). The result shows that the first and second λ_i accounted for 66.1 and 30.3%

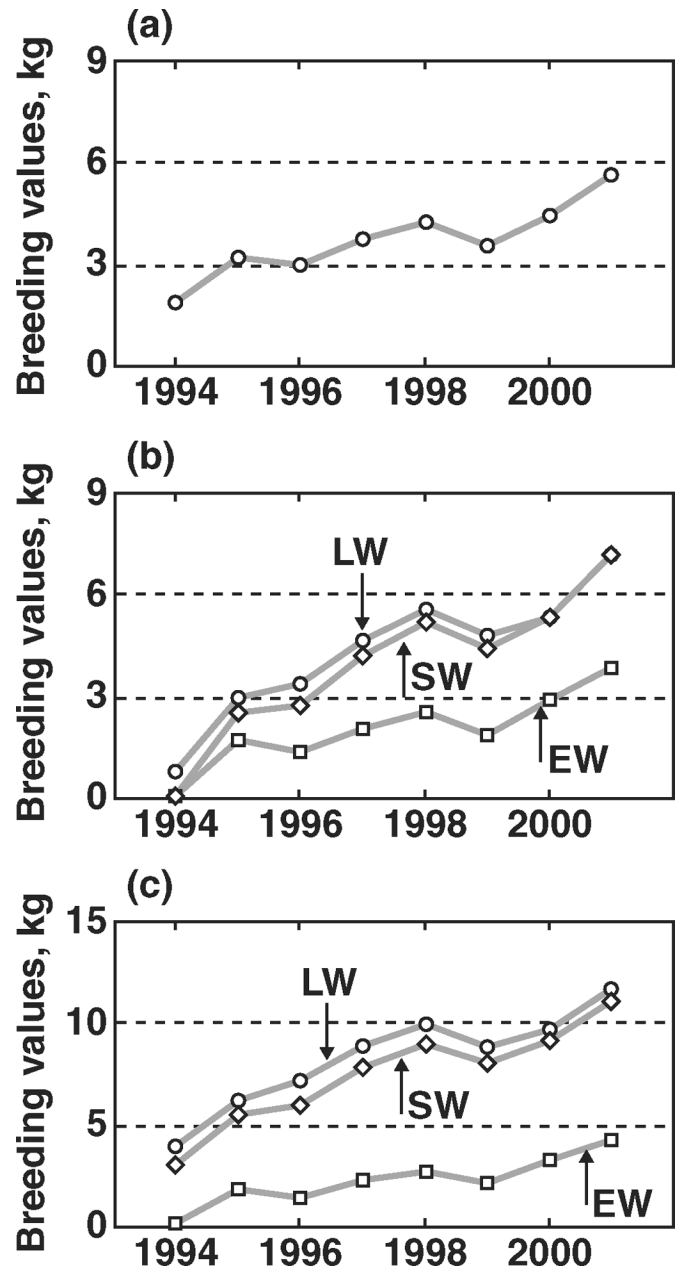


Figure 2. Breeding values across year of birth for weaning weight estimated by (a) the univariate animal model, (b) the multitrait animal model, and (c) the random regression model. EW = early weaning, SW = standard weaning, and LW = late weaning.

of the total genetic variation, respectively, and the associated eigenvectors can be used as vectors of general size and form, respectively, of the growth curve across the age trajectory of this population. This genetic variation can be used if the selection process favored the first or the second λ_i .

This source of genetic variation in the form of the growth curve was evaluated with the BV for WW between 150 and 270 d at weaning according to RRM results, and 2 strategies were examined:

Table 4. Variance-covariance matrix of the additive genetic random regression coefficients (G in the RRM; lower triangular) and the corresponding correlations (marked with *)

| Item | m_0 | m_1 | m_2 | % λ_i ¹ |
|-------|-------|-------|--------|----------------------------|
| m_0 | 805 | 0.41* | -0.77* | 66.1 |
| m_1 | 424 | 1,316 | -0.14* | 30.3 |
| m_2 | -399 | -95 | 330 | 3.6 |

¹Relative eigenvalues of G.

- A) From the BV of the 557 sires with progenies in this data set, the 55 best sires were selected according to their BV at 150 d of age (corresponding to early weaning), and the change of the BV of the same sires in the whole age trajectory between 150 and 270 d was examined in detail.
- B) From the BV of the 557 sires with progenies in this data set, the 55 best sires were selected according to BV at 270 d of age (corresponding to late weaning), and the change of the BV of the same sires in the whole age trajectory between 150 and 270 d was examined in detail.

Individual results from both groups of elite sires were examined in details through the graphic representation of 6 of those sires (Figures 3a and 3b). The 3 sires selected in each strategy were not different when compared at the point of the age at weaning trajectory in which they were selected. This is the only information available when the BV of the sires is estimated by classic methods (UAM in our case); however, RRM provides information with which the breeders can carry out a better and more efficient discrimination among the best sires. Note that the BV was estimated with high levels of accuracy, which can be appreciated by the large number of progenies. Observe that there are no differences among the 3 sires selected by BV at 150 d (Figure 3a); however, sire A shows a significant improvement in genetic potential, so that at 270 d of age at weaning its BV is approximately +65 kg higher than that of sire C. Similar patterns may be described if we consider Figure 3b.

DISCUSSION

The heritability values estimated in this study were higher for all weaning types (early, standard, or late) than the most common beef cattle genetic parameters of this trait (Koots et al., 1994). These trends were similar for MAM and RRM, which is logical because both procedures have the same statistical properties (van der Werf et al., 1998). The segregation of the myostatin in this breed (Dunner et al., 2003), a major gene affecting those traits, could be of one of the main hypotheses to partially justify this higher observed genetic variability.

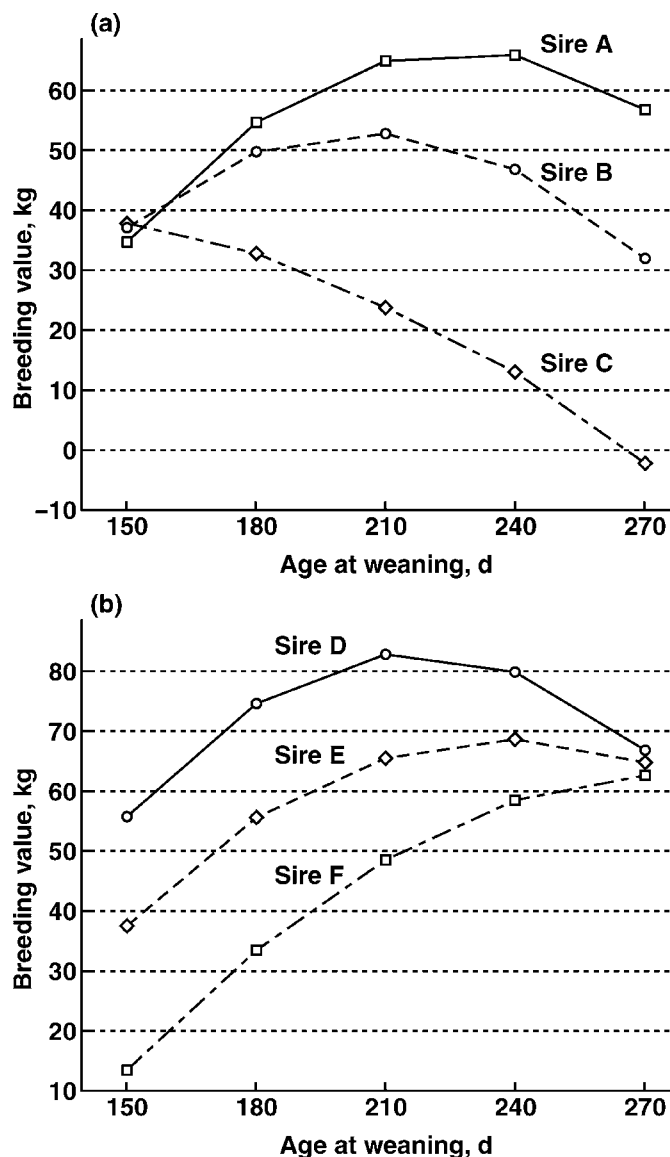


Figure 3. Breeding values across the weaning age trajectory for sires that differ in progeny size (in parentheses): (a) sires A (65), B (127), and C (88) are selected on their breeding value for the weaning weight at the age of 150 d; (b) sires D (33), E (36), and F (98) are selected on their breeding value for the weaning weight at 270 d old.

The small specific differences between RRM and MAM (see Table 2) are due to the fact that the exact age was used in RRM whereas a class is used in MAM for the average age for each category of weaning (early, standard, or late weaning). In general, the literature available on genetic parameters for weaning weight in beef cattle relies on large populations spread worldwide. That is the case of Angus (Dodenhoff et al., 1999), Hereford (de Mattos et al., 2000), Charolais, and Limousin (Phocas and Lal e, 2004) breeds, to mention the most important that have been subject to a long selection period. Thus, their uses and comparison with Asturiana de los Valles results might seem somewhat

dubious. This breed is characterized by a census with relatively low number of animals, is located in the restricted geographical region of Asturias, and has been undergoing a selection program for the last 20 yr. To further illustrate this, it must be considered that references published on this breed (Gutierrez et al., 1997; Goyache et al., 2003; Gutierrez et al., 2006) have shown values similar to those estimated in this study, despite probably using completely different data.

Under the conditions of this study, weaning weight throughout the age trajectory represented in these data sets cannot be considered as the expression of the same trait. The authors have not found any references pinpointing this fact in the genetic analyses of weaning weight in beef cattle. Nonetheless, this conclusion agrees with all trends shown in recent years in the use of random regression models of preweaning growth in beef cattle (Nobre et al., 2003) as well as in sheep (Lewis and Brotherstone, 2002; Fischer et al., 2004). In terms of the information required by the breeding programs of Asturiana de los Valles, it is better to know the BV of each animal not only at a specific age, but also as a function adapted to the overall age at weaning trajectory applied by breeders. This new alternative can contribute to increasing the modest genetic progress results (see Figure 2) attained by the use of the traditional UAM procedure, which offers only 1 BV for each animal.

According to the results of the correlations between the BV obtained through the currently used method (UAM) and the alternative methods (MAM and RRM; Table 3), the present selection procedure based on the previous adjustment of weaning weight at the age of 180 d has limited predictive value under the exploitation conditions of the Asturiana population represented in this study, which could explain the low genetic progress obtained. In order to represent the economical importance of this problem clearly, take into account that at present 41, 41, and 18% of the calves are weaned at early, standard, or late ages, respectively.

Application of random regression and multitrait procedures to this breed has shown a net superiority over the method used by ASEAVA because it allows a greater degree of differentiation to be applied in the sire selection process. Besides that, RRM results offer greater possibilities because new sources of variations of genetic origin linked to the shape of the growth curves have been identified, as shown in Figures 3a and 3b, and were quantified from the eigenvalues of the RRM matrix presented in Table 4.

The above-mentioned procedures are related to the use of principal components. This statistical technique is used for reducing the number of variables to a few orthogonal combinations of the original variables, which retain most of the variation. In animal breeding studies these tools have not been frequently used, al-

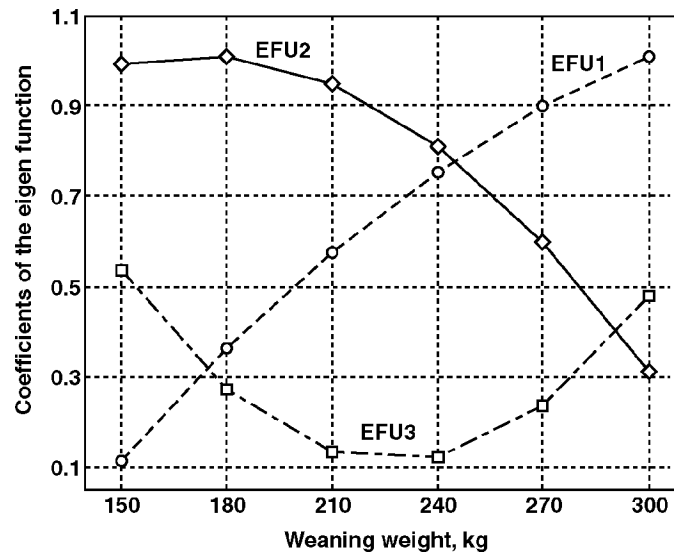


Figure 4. Eigenfunctions (EFU) of the random regression model genetic covariance matrix of weaning weight.

though their first application was published 4 decades ago (Rouvier, 1966). Recently, the publications of Kirkpatrick and Meyer (2004) and Meyer and Kirkpatrick (2005a,b) have made a contribution with many viewpoints showing an advantage in the case of traits whose variation and importance should be quantified on the basis of a function that varies according to a time scale (age in this case) or environment. This is what is defined as function-valued traits (Meyer and Kirkpatrick, 2005a).

According to the latter, eigenfunctions are the equivalent of eigenvectors for function-valued traits. The eigenvalues corresponding to the eigenfunctions ψ_i of matrix G are shown in Table 4; it states that $\psi_i(j) = \sum_{k=0}^2 V_{ik} \Phi_{jk}$, where V_{ik} stands for the k th order coefficient of the i th eigenvector of G , and Φ_{jk} is the k th Legendre's coefficient evaluated at age j . The results are plotted in Figure 4.

The trajectories of the first and second ψ_i show opposite directions and account for 96.4% of the genetic variation (see Table 4). The coefficients of ψ_i represented in the figures can be incorporated (by substituting age) in a model similar to those used in the RRM (model 2). Breeding values of all animals can thus be estimated as a more realistic guide for the selection process. Notice that the first ψ_i shows a clear trend toward greater growth at all ages, whereas the second ψ_i will favor an accelerated increase in WW before 210 d of age and then decline in the rest of the age trajectory. The third ψ_i contrasts animals with heavier WW only at the initial and final age at weaning, although this only accounts for 3.6% of the variation. Further study on the use of ψ_i in beef cattle is necessary

following the encouraging demonstration presented by Druet et al. (2005) in dairy cattle.

Conclusions

The type of trait analyzed (weaning weight) is considered as transversal-longitudinal data under the classification in Fitzhugh (1976), and the total set of weights can represent the shape of the growth curve of the Asturiana breed across the range of ages analyzed, although only 1 record was available for each animal.

The existence of a wide variability in genetic origin has been demonstrated for the shape of the growth curve of this breed. The results of this study demonstrate that the weight at weaning across the whole range of ages in this population may not be considered as the expression of a single character, but of a series of traits that change with age at weaning. Consequently, a reduction of the range of weaning ages would be convenient to prevent the dispersion of selection pressure. Alternatively, the use of random regression models is recommended for use in the official breeding program of this breed. Random regression models excel at incorporating a wide range of ages at weaning, with a far better performance than that provided by preadjustments or by covariate terms under classical regression. Unlike these, it incurs in no further assumptions on linearity of growth, improving accuracy for extreme values.

Further research is necessary in order to check the possibilities that can be derived from random regression analysis in this breed, particularly in relation to the analysis of direct and maternal genetic effects, and their correlation. These must be offset against the limitations imposed by the low precision in weighting and assignment of model factors on the estimation parameters of a complex model such as RRM. On the other hand, rankings obtained by UAM are reliable enough for most purposes, but RRM enables breeders to fine-tune their breeding objectives to their particular management practices regarding age and season of sacrifice.

LITERATURE CITED

- ASEAVA. 2006. Catálogo de Sementales 2007. Raza Asturiana de los Valles y Raza Asturiana de la Montaña. <http://www.viaganadera.com/aseava> Accessed Oct., 2007.
- BIF. 1996. Guidelines for uniform beef improvement programs. 7th ed. Kansas State Univ., Colby.
- de Mattos, D., I. Misztal, and J. K. Bertrand. 2000. Variance and covariance components for weaning weight for Hereford in three countries. *J. Anim. Sci.* 78:33–37.
- Dodenhoff, J., L. D. Van Vleck, and D. E. Wilson. 1999. Comparison of models to estimate genetics effects for weaning weight of Angus cattle. *J. Anim. Sci.* 77:3176–3184.
- Druet, T., F. Jaffrézic, and V. Ducrocq. 2005. Estimation of genetic parameters for test day records of dairy traits in the first three lactations. *Genet. Sel. Evol.* 37:257–271.
- Dunner, S., M. E. Miranda, Y. Amigues, J. Cañon, M. Georges, R. Hanset, J. Williams, and F. Méniissier. 2003. Haplotype diversity of the myostatin gene among beef cattle breeds *Genet. Sel. Evol.* 35:103–118.
- Fischer, T. M., J. H. J. van der Werf, R. G. Banks, and A. J. Ball. 2004. Description of lamb growth using random regression. *Livest. Prod. Sci.* 89:175–185.
- Fitzhugh, H. A. 1976. Analysis of growth curves and strategies for altering their shape. *J. Anim. Sci.* 42:1058–1072.
- Foulley, J. L., and C. Robert-Granie. 2002. Basic tools for the statistical analysis of longitudinal data via mixed model. Course notes from satellite workshop during the 7th World Congr. Genet. Appl. Livest., Montpellier, France.
- Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 2000. ASREML Reference Manual. NSW Agric. Biom. Bull. NSW Agriculture, Locked Bag, Orange, NSW 2800, Australia.
- Goyache, F., I. Fernández, L. J. Royo, I. Alvarez, and J. P. Gutierrez. 2003. Factors affecting actual weaning weight, preweaning average daily gain and relative growth rate in Asturiana de los Valles beef cattle breed. *Arch. Tierz. Dummerstorf.* 46:235–243.
- Gutiérrez, J. P., J. Cañon, and F. Goyache. 1997. Estimation of direct and maternal genetic parameters for preweaning traits in the Asturiana de los Valles beef cattle breed through animal and sire model. *J. Anim. Breed. Genet.* 114:261–266.
- Gutiérrez, J. P., I. Fernández, I. Alvarez, L. J. Royo, and F. Goyache. 2006. Sire \times contemporary group interactions for birth weight and preweaning growth traits in the Asturiana de los Valles beef cattle. *Livest. Prod. Sci.* 99:61–68.
- ICAR (International Committee for Animal Recording). 2007. International Agreement of Recording Practices. <http://www.icar.org/> Accessed Dec. 5, 2007.
- Jamrozik, J., and L. R. Schaeffer. 1997. Estimates of genetic parameters for a test day model with random regression for production of first lactation. *J. Dairy Sci.* 80:762–770.
- Kirkpatrick, M., D. Lofsvold, and M. Bulmer. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. *Genetics* 124:979–993.
- Kirkpatrick, M., and K. Meyer. 2004. Direct estimation of genetic principal components: Simplified analysis of complex phenotypes. *Genetics* 168:2295–2306.
- Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994. Analysis of published genetic parameters estimates for beef production traits. 1. Heritability. *Anim. Breed. Abstr.* 62:309–338.
- Lewis, R. W., and S. Brotherstone. 2002. A genetic evaluation of growth in sheep using random regression techniques. *Anim. Sci.* 74:63–70.
- Meyer, K. 2001. Estimates of direct and maternal covariance functions for growth of Australian beef calves from birth to weaning. *Genet. Sel. Evol.* 33:487–514.
- Meyer, K., and W. G. Hill. 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. *Livest. Prod. Sci.* 47:185–200.
- Meyer, K., and M. Kirkpatrick. 2005a. Restricted maximum likelihood estimation of genetic principal components and smoothed covariance matrices. *Genet. Sel. Evol.* 37:1–30.
- Meyer, K., and M. Kirkpatrick. 2005b. Up hill down dale: Quantitative genetics of curvaceous traits. *Philos. Trans. R. Soc. B* 360:1443–1455.
- Nobre, P. R. C., I. Misztal, S. Tsuruta, J. K. Bertrand, L. O. C. da Silva, and P. S. Lopes. 2003. Analysis of growth curves of Nellore cattle by multiple-trait and random regression models. *J. Anim. Sci.* 81:918–926.
- Phocas, F., and D. Lalöe. 2004. Genetic parameters for birth and weaning weight in French specialized cattle breeds. *Livest. Prod. Sci.* 89:121–128.
- Robertson, C. W. 1974. Comparison of various methods for adjusting weaning weights of calves to an age-constant basis. PhD Diss. Univ. of Tennessee, Knoxville.
- Rodríguez, A. A., and F. Goyache. 1996. Sistemas de producción llevados a cabo con la raza Asturiana de los Valles. El Programa

- de Mejora Genética de la Raza Asturiana de los Valles. Co-ordinator: J. Cañon. *Bovis* 69:13–24.
- Rouvier, R. 1966. L'Analyse en composantes principales: Son utilisation en génétique et ses rapports avec l'analyse discriminatoire. *Biometrics* 22:343–357.
- Schaeffer, L. R. 2004. Application of random regression models in animal breeding. *Livest. Prod. Sci.* 86:35–45.
- Schaeffer, L. R., and J. C. M. Dekkers. 1994. Random regressions in animal models for test-day production in dairy cattle. Pages 443–446 in *Proc. Fifth World Congr. Genetics Applied to Livest. Prod.*, vol. XVIII. Guelph, Ontario, Canada.
- van der Werf, J. H. J., M. E. Goddard, and K. Meyer. 1998. The use of covariance functions and random regressions for genetic evaluation of milk production based on test day records. *J. Dairy Sci.* 81:3300–3308.
- Woodward, B. W., E. J. Pollak, and R. L. Quaas. 1989. Adjusting weaning weights of Simmental beef calves to an age-constant basis. *J. Anim. Sci.* 67:20–27.