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Non-linear recursive models for growth traits in the Pirenaica beef cattle breed

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One of the main goals of selection schemes in beef cattle populations is to increase carcass weight at slaughter. Live weights at different growth stages are frequently used as selection criteria under the hypothesis that they usually have a high and positive genetic correlation with weight at slaughter. However, the presence of compensatory growth may bias the prediction ability of early weights for selection purposes. Recursive models may represent an interesting alternative for understanding the genetic and phenotypic relationship between weight traits during growth. For the purposes of this study, the analysis was performed for three different set of data from the Pirenaica beef cattle breed: weight at 120 days (W120) and at 210 days (W210); W120 and carcass weight at slaughter at 365 days (CW365); W210 and CW365. The number of records for each analysis was 8592, 4648 and 3234, respectively. A pedigree composed of 56323 individuals was also included. The statistical model comprised sex, year-season of birth, herd and slaughterhouse, plus a non-linear recursive dependency between traits. The dependency was modeled as a polynomial up to the 4th degree and models were compared using a Logarithm of Conditional Predictive Ordinates. The results of model comparison suggest that the best models were the 3rd degree polynomial for W120-W210 and W120-CW365 and the 2nd degree polynomial for W210-CW365. The posterior mean estimates for heritabilities ranged between 0.29 and 0.44 and the posterior mean estimates of the genetic correlations were null or very low, indicating that the relationship between traits is fully captured by the recursive dependency. The results imply that the predictive ability of the performance of future growth is low if it is only based on records of early weights. The usefulness of slaughterhouse records in beef cattle breeding evaluation is confirmed.

Keywords: beef cattle, genetic correlation, recursive models, Bayesian analysis, growth

Implications

Live weights at different growth stages are frequently used as selection criteria for carcass weight at slaughter. In this study, non-linear recursive models were applied to study the genetic and phenotypic relationship between weight traits during growth. The results imply that the predictive ability of the performance of future growth is low if it is only based on records of early weights. The usefulness of slaughterhouse records in beef cattle breeding evaluation is confirmed.

Introduction

The economic efficiency of beef cattle production is strongly linked with carcass weight at slaughter (Golden *et al.*, 1998; MacNeil 2003; Bouquet *et al.*, 2010). In many breeding programs, carcass weight is included in selection goals as one of the most relevant traits. However, phenotypic records for this trait are not available for the potential candidates for selection. Weight records at different growth stages are therefore widely used as selection criteria on the basis that there is a strong and positive genetic correlation between early weights and weight at slaughter (Meyer *et al.*, 1993; Altarriba *et al.*, 2009; Bouquet *et al.*, 2010). The breeding scheme established by the Pirenaica breeders association (Confederación Nacional de Asociaciones de Vacuno Pirenaica (CONASPI)) uses weight records between 110 and 310 days of age as predictors for future weight at slaughter (Altarriba *et al.*, 1996; Varona *et al.*, 1997).

Nevertheless, the potential presence of compensatory growth (Smith and Hodnett, 1962; Blanco *et al.*, 2009; Neto *et al.*, 2011) may reduce the efficiency of the use of early weights as a predictor of weight at slaughter. In a previous study with the same population (González-Rodríguez *et al.*, 2011), it was shown that genetic correlations between weight gain and weights recorded earlier in life were very low and that

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residual correlations between them may even be negative. These results imply the presence of compensatory growth in the Pirenaica beef cattle population, something that has also been suggested by Blanco *et al.* (2009).

From an alternative perspective, recursive models (Gianola and Sorensen, 2004) may be a valuable approach for the analysis of sequential traits as successive weights during growth. As argued by Valente *et al.* (2013), recursive models allow the estimation of the genetic effects acting directly on one trait, without the influence of other traits. This approach is able to analyze weights without the phenotypic influence of a trait measured in a previous stage. Further, non-linear versions of recursive models (López de Maturana *et al.*, 2009; Ibáñez-Escriche *et al.*, 2010; Varona and Sorensen, 2014) could help to describe the kind of relationship between weights that may appear as compensatory growth.

The aim of this study is to explore the possibilities of recursive models for the analysis of successive weights in Pirenaica beef cattle. The objective is to describe the genetic determinism of the beef cattle growth process from an alternative point of view.

Material and methods

Data

The data sets used in this study were provided by two organizations: (i) the Pirenaica Breeders Association (CONASPI) contributed 173 719 live weights records and a pedigree of 205 307 cases from 1989 to 2009; (ii) the System of Identification and Traceability provided 28 724 carcass weight records recorded at slaughterhouses from 2003 to 2009. Live weights registered between 80 and 160 days of life were used to adjust the phenotypes of weight at 120 days (W120) and records between 170 and 250 were used to adjust weight at 210 days (W210). Both traits were adjusted using sex-specific average daily gain in the population and the closer available weight, following the recommendations of the Beef Improvement Federation (2010). The same strategy was used with carcass weights between 250 and 480 days of age to predict carcass weight at 365 days (CW365).

Three subsets of data composed by records from individuals with available phenotypic information for each pair of traits were then created. These subsets consisted of 8592, 4648 and 3234 records for W120-W210, W120-CW365 and W210-CW365, respectively. Means and phenotypic standard deviations are presented in Table 1. In addition, an operational pedigree composed of 56 323 individuals generated from the genealogical information provided by CONASPI with the software RenumF90 (Misztal, 2012) was established.

Table 1 *Means and phenotypic standard deviations for the analysed traits*

		1st Trait		2nd Trait	
Data set	*n*	Mean (kg)	s.d.	Mean (kg)	s.d.
W120-W210	8592	160.2	29.29	275.2	48.43
W120-CW365	4648	167.9	32.89	303.0	49.28
W210-CW365	3234	285.5	46.32	301.1	48.14

s.d. = standard deviation; W120 = weight at 120 days of age; W210 = weight at 210 days; CW365 = cold carcass weight.

Model of analysis

Each subset of data was analyzed using a bivariate recursive model for traits taken in pairs (W120-W210, W120-CW365 and W210-CW365). For traits registered early in life or independent (*I*, as W120 or W210), the following model was assumed:

$$\mathbf{y}_I = \mathbf{X}_I\mathbf{b}_I + \mathbf{Z}_I\mathbf{u}_I + \mathbf{e}_I$$

where $\mathbf{y}_I$ is the vector of phenotypic records, $\mathbf{b}_I$ is the vector of systematic effect (year-season of birth, sex and herd), $\mathbf{u}_I$ is the vector of additive genetic effects and $\mathbf{e}_I$ is the vector of residual effects. Further, $\mathbf{X}_I$ and $\mathbf{Z}_I$ are incidence matrices that link phenotypic records with systematic and additive genetic effects.

Traits measured latterly or dependent (*D*, as W210 or CW365) were analyzed with four alternative models:

$$\mathbf{y}_D = \lambda_{DI}\mathbf{s}_I + \mathbf{X}_D\mathbf{b}_D + \mathbf{Z}_D\mathbf{u}_D + \mathbf{e}_D \quad (1)$$

$$\mathbf{y}_D = \lambda_{DI}\mathbf{s}_I + \lambda'_{DI}\mathbf{t}_I + \mathbf{X}_D\mathbf{b}_D + \mathbf{Z}_D\mathbf{u}_D + \mathbf{e}_D \quad (2)$$

$$\mathbf{y}_D = \lambda_{DI}\mathbf{s}_I + \lambda'_{DI}\mathbf{t}_I + \lambda''_{DI}\mathbf{r}_I + \mathbf{X}_D\mathbf{b}_D + \mathbf{Z}_D\mathbf{u}_D + \mathbf{e}_D \quad (3)$$

$$\mathbf{y}_D = \lambda_{DI}\mathbf{s}_I + \lambda'_{DI}\mathbf{t}_I + \lambda''_{DI}\mathbf{r}_I + \lambda'''_{DI}\mathbf{d}_I + \mathbf{X}_D\mathbf{b}_D + \mathbf{Z}_D\mathbf{u}_D + \mathbf{e}_D \quad (4)$$

where $\mathbf{y}_D$ is the vector of phenotypic records for 2nd or dependent traits (W210 and CW365), $\lambda_{DI}, \lambda'_{DI}, \lambda''_{DI}$ and λ'''_{DI} are the recursive parameters that relate the phenotypic records with the vectors $\mathbf{s}_I$, $\mathbf{t}_I$, $\mathbf{r}_I$ and $\mathbf{d}_I$, whose elements are

$$s_{Ij} = \{y_{Ij} - \overline{y}_I\}$$

$$t_{Ij} = \left\{\frac{(y_{Ij} - \overline{y}_I)^2}{100}\right\}$$

$$r_{Ij} = \left\{\frac{(y_{Ij} - \overline{y}_I)^3}{10000}\right\}$$

$$d_{Ij} = \left\{\frac{(y_{Ij} - \overline{y}_I)^4}{1000000}\right\}$$

where y_{Ij} is the phenotypic record for the *j*th individual and $\overline{y}_I$ is the average performance for the independent trait.

Additionally, $\mathbf{b}_D$ is a vector of systematic effects (year-season of birth, sex, herd and also slaughterhouse for CW365), $\mathbf{u}_D$ is the vector of additive genetic effects and $\mathbf{e}_D$ is the vector of residual effects. $\mathbf{X}_D$ and $\mathbf{Z}_D$ are incidence matrices that relate phenotypic records with systematic and additive genetic effects, respectively.

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The statistical analysis was performed using a Bayesian approach. For reasons of simplicity, only the joint posterior distribution for model 4 is described in detail:

$$p\left(\mathbf{b}_I, \mathbf{b}_D, \mathbf{u}_I, \mathbf{u}_D, \mathbf{G}, \lambda_{DI}, \lambda'_{DI}, \lambda''_{DI}, \lambda'''_{DI}, \sigma^2_{EI}, \sigma^2_{ED} | \mathbf{y}_I, \mathbf{y}_D\right) \propto$$
$$p(\mathbf{y}_I|\mathbf{b}_I, \mathbf{u}_I, \sigma^2_{EI}) p\left(\mathbf{y}_D|\mathbf{b}_D, \mathbf{u}_D, \mathbf{y}_I, \lambda_{DI}, \lambda'_{DI}, \lambda''_{DI}, \lambda'''_{DI}, \sigma^2_{ED}\right)$$
$$p(\mathbf{b}_I) p(\mathbf{b}_D) p(\mathbf{u}_I, \mathbf{u}_D|\mathbf{G}) p(\mathbf{G}) p(\lambda_{DI}) p\left(\lambda'_{DI}\right) p\left(\lambda''_{DI}\right)$$
$$p\left(\lambda'''_{DI}\right) p(\sigma^2_{EI}) p(\sigma^2_{ED})$$

where **G** is the additive genetic (co)variance matrix, σ^2_{EI} and σ^2_{ED} are the residual variances for the independent and the dependent traits, respectively, and

$$p(\mathbf{y}_I|\mathbf{b}_I, \mathbf{u}_I, \sigma^2_{EI}) \propto \prod_{j=1}^{n} \frac{1}{\left(2\pi\sigma^2_{EI}\right)^{\frac{1}{2}}} \exp\left[-\frac{\left(y_{Ij} - \mathbf{x}'_{Ij}\mathbf{b}_I - \mathbf{z}'_{Ij}\mathbf{u}_I\right)^2}{2\sigma^2_{EI}}\right]$$

where x'_{Ij} and z'_{Ij} are vectors of the incidence matrices that correspond to the *j*th individual for the independent trait, *n* is the number of records, and

$$p\left(\mathbf{y}_D|\mathbf{b}_D, \mathbf{u}_D, \mathbf{y}_I, \lambda_{DI}, \lambda'_{DI}, \lambda''_{DI}, \lambda'''_{DI}, \sigma^2_{ED}\right) \propto \prod_{j=1}^{n} \frac{1}{\left(2\pi\sigma^2_{ED}\right)^{\frac{1}{2}}}$$
$$\exp\left[-\frac{\left(y_{Dj} - \mathbf{x}'_{Dj}\mathbf{b}_D - \mathbf{z}'_{Dj}\mathbf{u}_D - \lambda_{DI}s_{Ij} - \lambda'_{DI}t_{Ij} - \lambda''_{DI}r_{Ij} - \lambda'''_{DI}d_{Ij}\right)^2}{2\sigma^2_{ED}}\right]$$

where x'_{Di} and z'_{Di} are vectors of incidence matrices corresponding at *j*th individual for the dependent trait.

The prior distribution for the additive breeding values was the following multivariate Gaussian distribution:

$$p(\mathbf{u}_I, \mathbf{u}_G|\mathbf{G}) \propto \frac{1}{(2\pi)^{\frac{n}{2}}|\mathbf{A} \otimes \mathbf{G}|^{\frac{1}{2}}} \exp\left[-\frac{(\mathbf{u}_I, \mathbf{u}_D)'(\mathbf{A} \otimes \mathbf{G})^{-1}(\mathbf{u}_I, \mathbf{u}_D)}{2}\right]$$

where **A** is the additive relationship matrix. The prior distributions for systematic effects, recursive parameters and variance components are assumed to be bounded uniform distributions between −10 000 and 10 000 for systematic effects and recursive parameters and between 0 and 10 000 for variance components.

The analysis was a Bayesian inference through Gibbs sampler algorithm (Gelfand *et al.*, 1990) using a modified version of program TM (Legarra *et al.*, 2008). For the Gibbs sampler implementation, samples from the full conditional distributions are needed. In this case, the full conditional distributions for systematic and additive genetic effects are Gaussian distributions as well as the conditional distributions of the recursive parameters. The conditional distributions for the residual variances are inverted χ^2 distributions and, finally, the conditional distribution for the additive (co)variance matrix is an inverted Wishart distribution. The Gibbs sampler was implemented with a single long chain of 525 000 iterations after a burn-in of 25 000 iterations. Convergence was checked using the Raftery and Lewis (1992) algorithm.

Comparison between models

Alternative models were compared with a leave-one-out cross-validation, an approach (Gelfand *et al.*, 1992) that is based on the prediction ability of the posterior distribution as a measure of the fit of model. We consider the data vector $y' = (y_i, y_{-i})$ where y_i is the *i*th datum, and $\mathbf{y}_{-i}$ is the vector of data with *i*th datum deleted. This procedure needs to build the posterior predictive density for each record y_i conditioned to model M and the vector of data, but leaving out each particular record, $\mathbf{y}_{-i}$ (Sorensen and Gianola, 2002):

$$p(y_i|\mathbf{y}_{-i}, M) = \int p(y_i|\theta, \mathbf{y}_{-i}, M) p(\theta|\mathbf{y}_{-i}, M) d\theta$$

where θ is the vector the parameters of the model. In example, the vector of parameters for model 4 is

$$\theta = \left\{\mathbf{b}_I, \mathbf{b}_D, \mathbf{u}_I, \mathbf{u}_D, \mathbf{G}, \lambda_{DI}, \lambda'_{DI}, \lambda''_{DI}, \lambda'''_{DI}, \sigma^2_{EI}, \sigma^2_{ED}\right\}$$

The values of the posterior predictive density $p(y_i|\mathbf{y}_{-i}, M)$, also known as CPOi (Conditional Predictive Ordinate), can be used as a measure of the fit for the *i*th specific record and

$$\text{CPO}_M = \prod_{i=1}^{n} p(y_i|\mathbf{y}_{-i}, M)$$

is a direct measure of the global fit of all records (Ibáñez-Escriche *et al.*, 2009). A lower CPO_M indicates a lack of fitness of the model M. Under a Markov Chain Monte Carlo scheme, such as the Gibbs sampler, these values are approximated through

$$\hat{p}(y_i|\mathbf{y}_{-i}, M) = \frac{1}{\sum_{j=1}^{iter} \frac{1}{p\left(y_i|\theta_j, \mathbf{y}_{-i}, M\right)}}$$

where $p(y_i|\theta_j, y_{-i}, M)$ is the predictive density of *i*th data at the *j*th iteration of the Gibbs sampler given the current sample of the vector of parameters (θ_j), and *iter* is total number of iterations after convergence. As suggested by Geisser (1993), the Logarithm of CPO for model M ($\log \text{CPO}_M$) can be calculated through

$$\log \text{CPO}_M = \sum_{i=1}^{n} \log(\hat{p}(y_i|\mathbf{y}_{-i}, M))$$

In this work, it was used as a diagnostic measure to evaluate the predictive ability of the model: models with highest $\log \text{CPO}_M$ are understood as the models with the best predictive ability of data.

Calculation of unconditional breeding values and additive (co)variance matrix

The implementation of recursive models provides predictions of breeding values for the independent ($\mathbf{u}_I$) and the dependent trait ($\mathbf{u}_D$), but the last are conditional to the recursive relationships with the independent trait. Under the standard linear recursive models (Gianola and Sorensen, 2004; Valente *et al.*, 2013), the breeding value for the dependent trait for the *j*th individual can be deconditioned ($u^*_{D_j}$) using the following expression:

$$u^*_{D_j} = u_{Dj} + \lambda_{DI} u_{Ij}$$

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However, under the proposed non-linear recursive model, the deconditioning procedure becomes more complex when higher order polynomials are assumed. Nevertheless, the dependency between both models at a given phenotype (k) for the independent trait of the jth individual can be approximated by using a 1st order Taylor expansion of the non-linear recursive function $f(y_{Ij})$:

$$y_{Dj} = f\left(y_{Ij}\right) + \mathbf{x}_{Dj}^{'}\mathbf{b}_D + u_{Dj} + e_{D_j} \approx$$
$$f\left(y_{Ij} = k\right) + \frac{f^{'}\left(y_{Ij} = k\right)}{1!}\left(y_{I_j} - k\right) + \mathbf{x}_{Dj}^{'}\mathbf{b}_D + u_{Dj} + e_{Dj}$$

as

$$y_{Ij} = \mathbf{x}_{Ij}^{'}\mathbf{b}_I + u_{Ij} + e_{Ij_j}$$

The unconditional breeding value for the jth individual and for the dependent trait (u_{Dj}^{*}) is approximately

$$u_{Dj}^{*} = \omega_k u_{Ij} + u_{Dj}$$

being

$$\omega_k = f^{'}\left(y_{Ij} = k\right)$$

Further, under this linear approximation, the unconditional matrix of additive genetic (co)variance between traits $\left(\mathrm{G}_k^{*}\right)$ at the phenotypic value k of the independent trait can be calculated as:

$$\mathbf{G}_k^{*} = (\mathbf{I} - \Lambda_k)^{-1}\mathbf{G}_0(\mathbf{I} - \Lambda_k)^{-1'}$$

where

$$\Lambda_k = \begin{bmatrix} 0 & 0 \\ \omega_k & 0 \end{bmatrix}$$

and

$$\mathbf{G}_0 = \begin{bmatrix} \sigma_{AI}^2 & \sigma_{AID} \\ \sigma_{AID} & \sigma_{AD}^2 \end{bmatrix}^{'}$$

being σ_{AI}^2 the additive variance for the independent trait, σ_{AD}^2 the additive variance for the dependent trait, and σ_{AID} the additive covariance between the independent and dependent traits. These are the parameters that provided the McMC estimation under models 1 to 4. Thus, the unconditional genetic (co)variance matrix at this phenotypic value for the independent trait is approximated as:

$$\mathbf{G}_k^{*} = \begin{bmatrix} \sigma_{AI}^2 & \sigma_{AI}^2\omega_k + \sigma_{AID} \\ \sigma_{AI}^2\omega_k + \sigma_{AID} & \omega_k\left(\sigma_{AI}^2\omega_k + 2\sigma_{AID}\right) + \sigma_{AD}^2 \end{bmatrix}^{'}$$

Further, the unconditional genetic correlation at the phenotypic value k of the independent trait is calculated through

$$r_k = \frac{\sigma_{AI}^2\omega_k + \sigma_{AID}}{\sqrt{\sigma_{AI}^2\left(\omega_k\left(\sigma_{AI}^2\omega_k + 2\sigma_{AID}\right) + \sigma_{AD}^2\right)}}$$

In an equivalent way, for the residual variances

$$\mathbf{R}_0 = \begin{bmatrix} \sigma_{EI}^2 & 0 \\ 0 & \sigma_{ED}^2 \end{bmatrix}^{'}$$

and

$$\mathbf{R}_k^{*} = \begin{bmatrix} \sigma_{EI}^2 & \sigma_{EI}^2\omega_k \\ \sigma_{EI}^2\omega_k & \sigma_{EI}^2\omega_k^2 + \sigma_{ED}^2 \end{bmatrix}^{'}$$

Thus, the unconditional heritability at the phenotypic value k of the independent trait is calculated by:

$$h_k^2 = \frac{\left(\omega_k\left(\sigma_I^2\omega_k + 2\sigma_{ID}\right) + \sigma_D^2\right)}{\left(\omega_k\left(\sigma_I^2\omega_k + 2\sigma_{ID}\right) + \sigma_D^2\right) + \sigma_{EI}^2\omega_k^2 + \sigma_{ED}^2}$$

Results and discussion

The posterior mean and s.d. for the variance and covariance components, genetic correlations, heritabilities and recursive parameters together with the respective diagnostic measures for model comparison (log CPO) are presented in Tables 2, 3 and 4, for analyses of the W120-W210, W210-CW365 and W210-CW365 data sets, respectively. The results of model comparison by log CPO indicated that the model that presented a better predictive ability included a cubic recursive function for the analyses W120-W210 and W120-CW365, while for W210-CW365 a square dependence was chosen. The selected models indicate non-linear relationships between traits as reflected in Figures 1, 2 and 3 where the recursive functions are plotted.

The posterior mean estimates of the heritabilities for the independent traits or those registered early in life (W120 and W210) ranged between 0.33 and 0.43. They are in line with previous estimates from the literature obtained in the same breed (Varona *et al.*, 1997; Altarriba *et al.*, 2009; Varona *et al.*, 2012), or other beef cattle populations (Ríos-Utrera and Van Vleck, 2004; Bouquet *et al.*, 2010). The estimates of heritabilities in the dependent traits (W210 and CW365) ranged between 0.28 (W210) to 0.38 (CW365), although they cannot be directly compared with previous estimates, because they are conditioned to the independent trait.

For the selected models, the posterior estimates of the genetic correlations between both traits ranged from −0.034 (W120-CW365) to 0.164 (W120-W210), as shown in Tables 2, 3 and 4. These genetic correlations are much smaller than previous estimates (Altarriba *et al.*, 2009). However, it should be emphasized that the genetic correlations reported here have to be understood as between independent and dependent traits marginalized with respect to each other via the recursive function. In fact, the results are coherent with the authors' previous estimates of genetic correlations between early weights and subsequent gains of weight (González-Rodríguez *et al.*, 2011). It should be also noted that the magnitude of the heritabilities for the dependent traits and the genetic covariance between them become

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Table 2 *Posterior mean (and s.d.) estimates of genetic and residual variance, genetic covariance, genetic correlation, heritability, parameters of recursive models and log CPO for the traits W120-W210*

Parameters	Model 1	Model 2	Model 3	Model 4
σ_g^2 W120	225.05 (23.86)	224.41 (23.36)	222.68 (23.35)	224.94 (24.69)
σ_g^2 W210	224.84 (26.74)	221.98 (27.06)	218.22 (26.5)	215.31 (27.34)
Cov_g	40.05 (22.49)	38.47 (23.1)	35.95 (23.09)	31.52 (23.08)
σ_e^2 W120	448.31 (17.91)	448.72 (17.62)	449.85 (17.7)	448.35 (18.39)
σ_e^2 W210	539.36 (20.45)	539.08 (20.65)	540.37 (20.5)	541.97 (20.94)
r_g	0.179 (0.099)	0.173 (0.102)	0.164 (0.104)	0.145 (0.105)
h^2 W120	0.334 (0.032)	0.333 (0.031)	0.331 (0.031)	0.334 (0.033)
h^2 W210	0.294 (0.032)	0.291 (0.032)	0.287 (0.032)	0.284 (0.033)
λ_{DI}	1.002 (0.028)	1.004 (0.029)	1.057 (0.032)	1.06 (0.032)
λ'_{DI}	–	−0.133 (0.025)	−0.122 (0.025)	−0.065 (0.051)
λ''_{DI}	–	–	−0.184 (0.048)	−0.17 (0.049)
λ'''_{DI}	–	–	–	−0.112 (0.087)
Log CPO	−40 461.366	−40 457.728	−40 449.83	−40 460.38

σ_g^2 = genetic variance; Cov_g = genetic covariance; σ_e^2 = residual variance; r_g = genetic correlation; h^2 = heritability; λ_{DI} = recursive parameter; λ'_{DI} = square potency; λ''_{DI} = cube potency; λ'''_{DI} = 4th potency; W120 = weight at 120 days of age; W210 = weight at 210 days.

Table 3 *Posterior mean (and s.d.) estimates of genetic and residual variance, genetic covariance, genetic correlation, heritability, parameters of recursive models and log CPO for the traits W120-CW365*

Parameters	Model 1	Model 2	Model 3	Model 4
σ_g^2 W120	378.63 (61.4)	383.52 (59.78)	376.86 (60.4)	382.84 (59.65)
σ_g^2 CW365	295.56 (51.09)	289.63 (49.63)	286.61 (55.61)	287.43 (52.54)
Cov_g	38.6 (57.15)	39.59 (55.34)	33.78 (63.41)	32.62 (63.73)
σ_e^2 W120	490.9 (45.12)	487.48 (43.88)	492.04 (44.71)	487.9 (43.91)
σ_e^2 CW365	595.61 (38.61)	598.04 (38.11)	599.65 (41.03)	599.14 (39.45)
r_g	0.114 (0.167)	0.12 (0.162)	0.099 (0.185)	0.099 (0.184)
h^2 W120	0.434 (0.061)	0.439 (0.059)	0.433 (0.061)	0.439 (0.059)
h^2 CW365	0.331 (0.051)	0.326 (0.05)	0.322 (0.056)	0.323 (0.053)
λ_{DI}	0.51 (0.057)	0.509 (0.055)	0.565 (0.065)	0.565 (0.065)
λ'_{DI}	–	−0.099 (0.029)	−0.087 (0.029)	−0.082 (0.066)
λ''_{DI}	–	–	−0.147 (0.053)	−0.147 (0.053)
λ'''_{DI}	–	–	–	−0.008 (0.096)
Log CPO	−22 287.74	−22 285.98	−22 282.21	−22 283.71

σ_g^2 = genetic variance; Cov_g = genetic covariance; σ_e^2 = residual variance; r_g = genetic correlation; h^2 = heritability; λ_{DI} = recursive parameter; λ'_{DI} = square potency; λ''_{DI} = cube potency; λ'''_{DI} = 4th potency; W120 = weight at 120 days of age; CW365 = carcass weight.

smaller as the complexity of the model increases. This phenomenon implies that genetic determinism is better captured by the recursive function as the grade of the polynomial function increases, and, therefore, a lower genetic variation remains in the dependent trait.

Deconditioning breeding values and additive (co)variance matrices under a linear recursive model is an automatic task (Gianola and Sorensen, 2004; Varona *et al*., 2007). However, when the relationship between traits is not linear, this task becomes more complex. Some studies (López de Maturana *et al*., 2009; Ibáñez-Escriche *et al*., 2010) use a linear spline approximation to this non-linear relationship, and they generate spline specific additive (co)variance matrices associated with several parametric subspaces of the independent trait. Under the approach proposed in this study, the non-linear recursive relationship is defined in terms of polynomials up to the 4th order and specific additive (co)variance matrix for each phenotypic value are approximated by a 1st order Taylor expansion of the recursive function.

After deconditioning, the estimates of the genetic correlations can be expressed in accordance with the range of phenotypic values of the independent trait. The plots of the posterior mean estimates of these genetic correlations for the selected models are presented in Figures 4 to 6. These plots confirm the non-linear nature of the relationship between traits. The genetic correlation between W120 and W210 started at 0.7 for very low values of W120 and increased to 0.8 for weights around 140 kg. Later, and for higher values of W120, it decreased to 0.2. The genetic correlation between W120 and CW365 provided a similar plot with a maximum genetic correlation of 0.6 and a reduction of this correlation to zero for large W120 values. Finally, the genetic correlation between W210 and CW365 also decreased with the phenotypic value of W210 and ranged from 0.5 to 0.7. These estimates

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Table 4 *Posterior mean (and s.d.) estimates of genetic and residual variance, genetic covariance, genetic correlation, heritability, parameters of recursive models and log CPO for the traits W210-CW365*

Parameter	Model 1	Model 2	Model 3	Model 4
σ_g^2 W210	642.49 (117.7)	656.32 (120.82)	649.6 (118.43)	649.6 (118.43)
σ_g^2 CW365	312.1 (63.02)	303.74 (65.45)	301.26 (62.17)	301.26 (62.17)
Cov_g	−7.739 (83.65)	−15.31 (83.77)	−27.59 (89.03)	−27.59 (89.03)
σ_e^2 W210	961.75 (90.2)	952.13 (91.98)	956.75 (90.45)	956.75 (90.45)
σ_e^2 CW365	506.18 (47.68)	511.74 (49.85)	511.43 (46.91)	511.43 (46.91)
r_g	−0.015 (0.184)	−0.034 (0.188)	−0.057 (0.196)	−0.057 (0.196)
h^2 W210	0.399 (0.065)	0.407 (0.066)	0.403 (0.065)	0.403 (0.065)
h^2 CW365	0.380 (0.068)	0.371 (0.072)	0.369 (0.067)	0.369 (0.067)
λ_{DI}	0.456 (0.045)	0.458 (0.045)	0.517 (0.0497)	0.514 (0.051)
λ'_{DI}	–	−0.0325 (0.018)	−0.0506 (0.019)	−0.1 (0.044)
λ''_{DI}	–	–	−0.099 (0.028)	−0.081 (0.031)
λ'''_{DI}	–	–	–	0.052 (0.041)
Log CPO	−15 377.69	−15 374.47	−15 375.36	−15 377.23

σ_g^2 = genetic variance; Cov_g = genetic covariance; σ_e^2 = residual variance; r_g = genetic correlation; h^2 = heritability; λ_{DI} = recursive parameter; λ'_{DI} = square potency; λ''_{DI} = cube potency; λ'''_{DI} = 4th potency; W210 = weight at 210 days of age; CW365 = carcass weight.

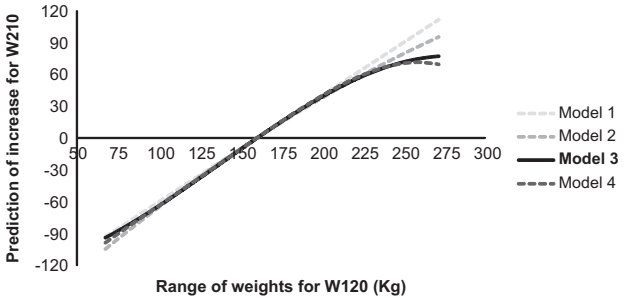


Figure 1 Prediction of the increase for W210 given W120, through the linear and non-linear recursive models. Model 1 = Linear recursive model; Model 2 = Non-linear recursive model with a recursive function of 2nd degree; Model 3 = Non-linear recursive model with a recursive function of 3rd degree; Model 4 = Non-linear recursive model with a recursive function of 4th degree.

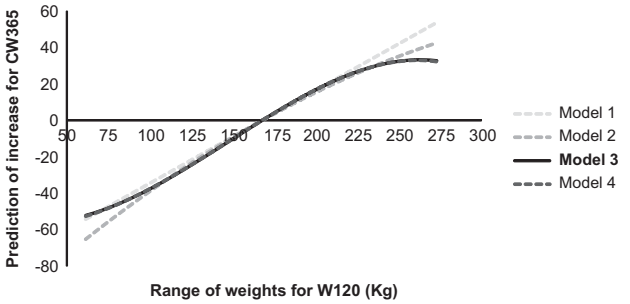


Figure 2 Prediction of the increase for CW365 given W120, through linear and non-linear recursive models. Model 1 = Linear recursive model; Model 2 = Non-linear recursive model with a recursive function of 2nd degree; Model 3 = Non-linear recursive model with a recursive function of 3rd degree; Model 4 = Non-linear recursive model with a recursive function of 4th degree.

were substantially higher than the previous ones and much closer to the previous estimates in the same population for genetic correlation between weights at different ages (Altarriba *et al.*, 2009). It should be noted that a reduction of genetic

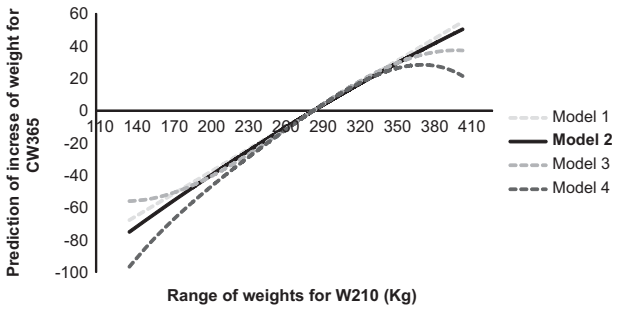


Figure 3 Prediction of Carcass Weight (CW365) given W210, through linear and non-linear recursive models. Model 1 = Linear recursive model; Model 2 = Non-linear recursive model with a recursive function of 2nd degree; Model 3 = Non-linear recursive model with a recursive function of 3rd degree; Model 4 = Non-linear recursive model with a recursive function of 4th degree.

correlation for higher phenotypic values of the independent traits was present in all three data sets analyzed. This fact implies that the weight of the information on the early registered trait in the prediction of breeding values is smaller for higher phenotypic values. Further, the unconditional heritability estimates for the were more stable along the parametric space (Figures 4 to 6) and also within the range of previous estimates from the literature (Ríos-Utrera and Van Vleck, 2004; Altarriba *et al.*, 2009; Bouquet *et al.*, 2010).

In animal breeding, the joint analysis of several traits is usually performed through multi-trait mixed model analyses (Henderson, 1984). These models assume that the relationship between traits is linear and they are not able to differentiate between direct and indirect genetic effects, as those generated by causal relationships between traits (Valente *et al.*, 2013). A linear relationship between traits implies that the increase of one unit for one trait automatically results in a modification of the other trait independent of the range of values that are considered. This assumption makes sense when analyzed traits have their phenotypic expression within a small range

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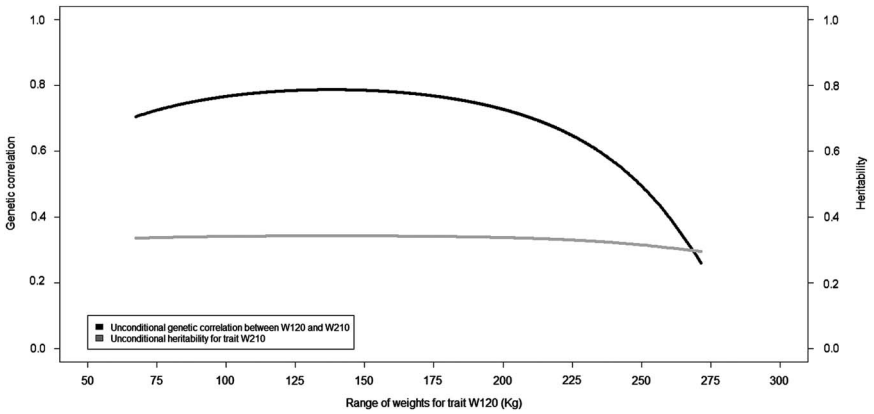


Figure 4 Genetic correlation between W120 and W210, and heritability of W210, for the range of values on the parametric space of W120.

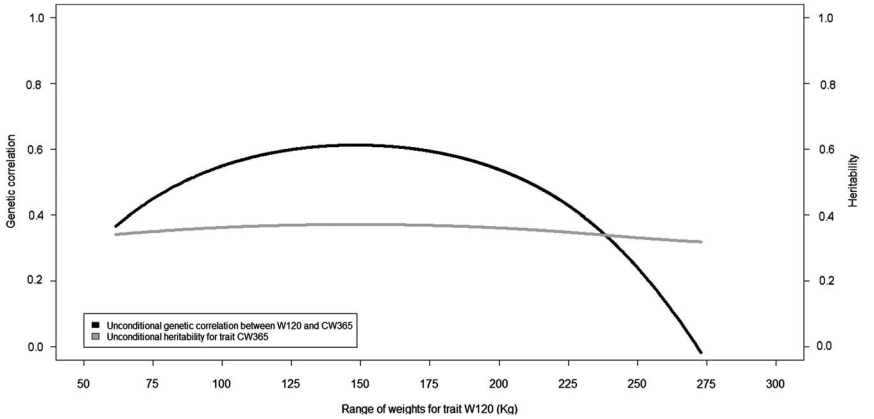


Figure 5 Genetic correlation between W120 and CW365, and heritability of CW365, for the range of values on the parametric space of W120.

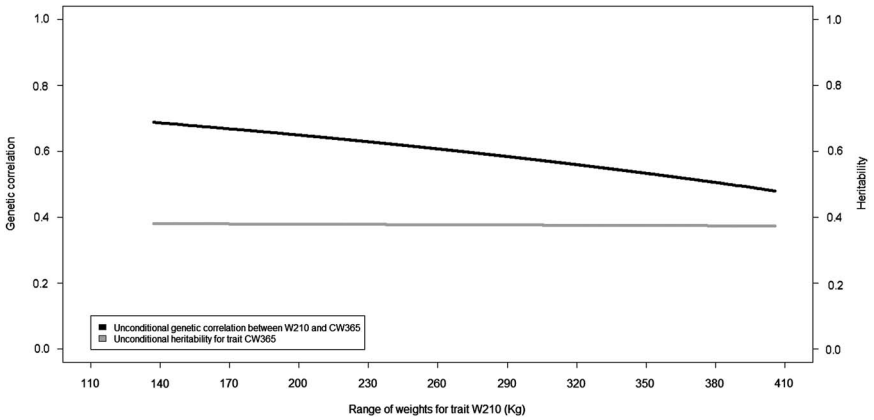


Figure 6 Genetic correlation between W210 and CW365, and heritability of CW365, for the range of values on the parametric space of W210.

of phenotypic values. However, when the traits have a very wide phenotypic range of values, it seems plausible that the relationship between them is not linear. For example, Ibáñez-Escriche *et al.* (2010) analyzed the percentage of stillborns in pigs with respect to litter size and showed that there was a small relationship between lower values of litter size which increased as the litter size increased. Non-linear recursive models offer greater flexibility than recursive linear or standard multivariate mixed models as they allow the description of the non-linear relationship between traits, as previously noted by Maturana *et al.* (2009) and Ibáñez-Escriche *et al.* (2010). The current study puts forward an alternative version to the proposal of these authors that uses a polynomial function. It avoids the assumption or calculation of the points of change among sequential segments. Another significant advantage of this approach is that its implementation can be easily achieved with a slight modification of any standard software for mixed model Bayesian analysis.

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The results of the analysis presented here suggest that the estimated breeding values performed by using the standard mixed model may not be realistic in extensive beef cattle populations since it assumes a general pattern of dependence between phenotypes along the growth curve and it does not allow the relationship between observations to vary with the magnitude of the phenotype in previous stages of growth, which occurs when compensatory growth is present.

The results of this study also confirm that the efficiency of selection schemes for growth based exclusively on records of weights previous to slaughter are questionable due to the low correlation between successive growths (González-Rodríguez *et al.*, 2011). Therefore, the use of records of weight at slaughter in related individuals becomes especially relevant (Altarriba *et al.*, 2009); alternative models that allow for non-linear dependence may also improve the predictive ability of genetic evaluation. However, the results of this study are restricted by the fact that the available phenotypic records are adjusted to specific ages. Thus, some relevant information about the non-linear nature of growth may be lost. Further research must be done to define a more general framework that allows to model the dependency between phenotypic records in a wider spectrum.

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